DIVERSITY OF MARINE SPONGES IN THE NORTHWEST ATLANTIC

by

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Submitted in partial fulfilment of the requirements for the degree of Doctor of Philosophy

at

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DALHOUSIE UNIVERSITY

DEPARTMENT OF BIOLOGY

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This thesis is dedicated to Ransom A. Myers, and my mother, Judith Rivinus Fuller, who would both be glad to know it is finally finished. It is also dedicated to Daniel Kehler, who inspired me to do graduate work in the first place.

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Abstract

This study documents the marine sponge fauna (Phylum Porifera) in the Northwest Atlantic, through the used of fishermen's local ecological knowledge, fisheries observer data, trawl survey data and in situ exploration. A review of the role of structural benthic species, including ascidians, bryozoans, corals, hydroids and sponges as ecosystem engineers provides the context within which to discuss the contribution of sponges to seafloor habitat heterogeneity. Fishermen's knowledge is useful in identifying areas of high concentration of benthic structural species, but is not particularly useful in determining the distribution of specific sponge species, with the exception of glass sponges, with the common name "Russian Hat". Fisheries observer data from the Scotia Fundy Region and trawl survey data from the Newfoundland Region were obtained from the years 1977-2001 and 1973-2007 respectively. Despite the lack of systematic collection of information on sponge catches, prior to 2002, the information recorded show broad scale patterns of sponge distribution from the Scotian Shelf to the Eastern Arctic, and this thesis brings this information together for the first time. The move to deeper and more northern waters following the groundfish collapse in 1992 resulted in large catches of sponges, up to 5000kg per set, on the Labrador Shelf and Eastern Arctic. The combination of fishermen's information, observer data and in situ research on the Scotian Shelf resulted in the identification of a previously undescribed and globally unique population of Vazella pourtalesi, a Hexactinellid sponge, in the Family Rossellidae. The impacts of fishing on the sponge community of the Gulf of Maine were examined by quantifying the sponge community inside and outside of the Western Gulf of Maine Closed Area. After two years, the sponge community within the closed area was dominated by the demosponge, *Iophon* sp. while the area that remained open to fishing had a higher diversity of sponges. The information presented in this thesis can inform marine ecosystem management, particularly in light of international obligations to protect vulnerable marine ecosystems.

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Chapter 1

Introduction

On the study of sponges..."the subject is actually repulsive from its difficulties" (Carter, 1875b)

Marine sponges are ubiquitous throughout all benthic marine environments, from rocky intertidal areas to the soft sediments of the deep sea, and consequently contribute to the diversity and habitat of many benthic ecosystems (i.e. (Bergquist, 1978) and references therein). In her seminal text, Bergquist defines the sponge (Phyla Porifera) as a "sedentary, filter feeding metazoan which utilizes a single layer of flagellated cells to pump a unidirectional water current through its body" (Bergquist, 1978). Bacescu (1971) stated that next to tropical coral reefs, sponges constitute "one of the richest and most interesting biotypes" in the marine environment. Roughly 8000 species have been identified to species level (Van Soest et al., 2010), although almost every investigation from coral reefs to the deep sea yields new species (Schonberg, 2000; Diaz et al., 2007; Vacelet et al., 2007; Vacelet & Kelly, 2008; Ise & Vacelet, 2010). Areas of high concentration of an individual species or species complex have received particular attention for their ecological importance; such examples include the Hexactinellid sponge reefs off the coast of British Columbia, Canada (Conway et al., 1991; Cook et al., 2008); dense sponge fields dominated by the Demosponges of the family Geodidae in particular known as "ostur" in the Northeast Atlantic (Klitgaard & Tendal, 2004); patches of the Rosselid (Class Hexactinellida) sponge Pheronema carpenteri, also in the Northeast Atlantic (Rice et al., 1990); and Hexactinellid dominated sponge communities in Antarctica (Dayton, 1979; Barthel, 1992).

Most chemical and ecological research on sponges has been conducted in tropical environments, primarily due to the ease of collection and the accessibility of sponges on coral reef ecosystems (Wulff, 2001). A significant amount of the research on sponges has focused on biochemistry and biotechnology, as a result of anti-bacterial and anti-tumor chemical components (Becerro, 2008). There is an increasing interest in the microbial communities existing within sponges, for the potential development of pharmaceuticals (Kennedy et al., 2007; Vogel, 2008), climate change related ecosystem monitoring (Lemoine et al., 2007) and furthering basic understanding of biological symbioses (Taylor et al., 2007; Webster & Blackall, 2009).

Ecological research on sponges has typically focused at the species level and as such has not made its way into broader theoretical ecology fields (Becerro, 2008).

Nevertheless, the functional role of sponges has been investigated in tropical, temperate and polar regions and can include alteration of substrate, bentho-pelagic coupling, provision of habitat for other species, and contribution to benthic habitat heterogeneity (Bell, 2008).

Sponges can occupy a significant portion of the sea floor, at a broad range of depths and many species have three-dimensional morphology, thus making them important structural features of benthic communities (Conway et al., 1991; Barthel, 1992; Butler et al., 1995; Freese et al., 1999).

Because of the difficulties in assessing basic biological variables such as growth rates, fecundity, and age at maturity, as examples, as well as the inherent difficulty in identifying sponges to the species level, there has been a relative lack of inclusion of sponges in monitoring and conservation programs, even in tropical coral reef ecosystems where the knowledge of sponge ecology is most advanced (Wulff, 2001). The loss of

structural species in the marine environment has gained the attention of researchers both in coastal ecosystems as well as the deep sea, and has the potential for cascading effects (Stachowitsch, 1984; Butler et al., 1995; Pinnegar et al., 2000; Coleman & Williams, 2002). In areas immediately adjacent to the coast, sponges are vulnerable to eutrophication (Butler et al., 1995), temperature increase (Cerrano et al., 2000) and oxygen deficiency (Stachowitsch, 1984). Marine sponges may be particularly vulnerable to fishing activities as they are easily detached from the sea floor (Tilmant, 1979; Van Dolah et al., 1987; Freese et al., 1999), sublittoral populations can be very slow growing (Conway et al., 1991; Beaulieu, 2001; Leys et al., 2007) and many species have brooded larvae with very limited planktonic stages (Fell, 1979). In undisturbed subtidal environments, sponge communities are thought to be quite stable and long-lived (Bergquist, 1978; Ayling, 1980). In the deepsea environment, sponge communities may remain stable over decades (Leys & Lauzon, 1998) and even centuries (Conway et al., 1991; Beaulieu, 2001). It is generally accepted that fishing with bottom tending gear has a negative impact on structural species, globally, and the move toward ecosystem-based fisheries management and protection of vulnerable marine ecosystems has resulted in the need for research on distribution and species composition of corals and sponges in particular (Rodgers, 2008; FAO, 2009).

With the exception of early taxonomic descriptions, sponges in the Northwest Atlantic have been largely overlooked. For example, there is no current, inclusive key to the sponges of the Gulf of Maine / Scotian Shelf area. Commonly used field guides (De Laubenfels, 1949; Hartman, 1958; Gosner, 1971; Pollock, 1998) include the Phylum Porifera, but do not include all species and contain taxonomic misinterpretations at the Order level. Literature describing sponges from the Northwest Atlantic is at least half a

century old (Lambe, 1896, 1900; Whiteaves, 1901; Lundbeck, 1902; Arndt, 1935; Old, 1941), although there have been more recent inclusions of sponges in marine research in the Gulf of Maine (Witman & Sebens, 1990; Knight et al., 2006), Bay of Fundy (Ginn et al., 2000; Kenchington et al., 2007) and Scotian Shelf.

The goal of my research was to expand upon the existing knowledge of sponges in the Northwest Atlantic, using time series information available in Canadian fisheries observer databases and Canadian fisheries research trawl survey records, information held by resource users in this case, fishermen, and to examine the ecological role of sponges in the marine environment. I also had an interest in the impact of fishing on marine sponges, based on my research on bycatch in scallop dredges in the Bay of Fundy (Fuller et al., 1998; Kenchington et al., 2007), where clear changes were observed in the composition of the catch as compared to an assessment completed in 1967 (Caddy et al., 1970). This thesis is structured as five papers (Chapters two, three, four, five and six) and a final concluding section (Chapter seven).

• In Chapter two, I review published information on the functional roles of colonial marine invertebrates as "ecosystem engineers". I also collected published information on associated fauna of structural marine species, specifically sponges, hydroids, bryozoan, ascidians and corals. I compare species richness (SR), species diversity (H' and Fisher's Alpha) and species evenness (J) of associated fauna across taxonomic groups. I also examine the patterns of species richness and diversity across biogeographic scales of latitude and depth, and with the volume of the host animal.

- In Chapter three, I describe the information collected from fishermen on sponge and coral distribution in the Northwest Atlantic, and their perceptions of the importance of these animals as habitat. Many of the interviews were conducted jointly with Susan Gass (School of Research and Environmental Sciences, Dalhousie University) and the information on coral distribution in particular is included in (Gass & Willison, 2005). The information presented on the importance of corals for habitat for other marine species, as perceived by fishermen is presented for the first time. I discuss the importance of collecting and using fishermen's knowledge in ecosystem based management processes and in using fishermen's knowledge as a basis for natural science exploration.
- In Chapter four, I present the information on sponges contained in the Scotia Fundy Fisheries Observer database (1977-2001) and the Newfoundland multi-species fisheries research trawl survey (1977-2007). The data presented are those originally requested in 2001 (with the exception of trawl survey data provided until 2007) and therefore does not represent all currently available information on sponge distribution in Atlantic Canada. The distribution of large catches of sponges is discussed in relation to commercial fishing activity. I also present species identification and distribution of sponges on the Newfoundland shelf, collected in trawl surveys. The distribution of sponge catch and description of the sponge community in these areas has been previously published in reports related to

- fisheries management objectives for the protection of vulnerable marine ecosystems (Fuller et al., 1998; Kenchington et al., 2010).
- In Chapter five, I describe a unique population of the glass sponge, *Vazella pourtalesi* (Hexactinellida: Rossellidae), on the Scotian Shelf in the Northwest Atlantic. This is the first description of this monospecific population, and represents a unique vulnerable marine ecosystem on the continental shelf.
- In Chapter six, I present the effects of an area closed to fishing in the Gulf of
 Maine on the sponge fauna and associated species. The Western Gulf of
 Maine Closed area was closed to bottom fishing in 1998 and the differences
 in sponge species diversity and biomass in areas open and closed to fishing
 activity are presented.
- In Chapter seven, I discuss the implications of my research as a basis for future study on the sponges of the Northwest Atlantic as well as for fisheries management, in the context marine ecosystem-based management within the national and international framework.

Chapter 2

Habitat Engineering by Sessile Marine Invertebrates: Associated Faunal Diversity and Broad Scale Patterns

2.0 Introduction

"Beneath the surface beauty, there is a marvellous complexity of structure and function." (Carson, 1956)

The processes through which living species physically or chemically alter the surrounding environment have been collectively defined as "ecosystem engineering" (Jones et al., 1994, 1997). Ecosystem engineering provides a context within which to discuss, both qualitatively and quantitatively, biological mediation of physical ecosystem processes, specifically how species affect ecosystem function (Hooper et al., 2005). Similar constructs, such as those associated with "keystone species" and "apex predator", have allowed ecologists to examine relationships among species and to predict ecosystem effects of changes in abundance or distribution of particularly influential organisms. Community ecologists have long studied the direct effects of trophic relationships and competitive interactions on community structure. Indirect effects of living organisms on the biotic and abiotic environment are more difficult to test and have received less attention than direct interactions (Wilson, 1980, 1997).

In the interests of stimulating empirical research in this field, Jones et al. (1994) developed a conceptual model to categorize ecosystem engineers and quantify indirect

interactions that modify the physical environment. They describe living organisms as either allogenic or autogenic engineers defined, respectively, as either "changing the environment by transforming living or non-living materials from one physical state to another, via mechanical means" or "changing the environment via their own physical structures, i.e. their living or dead tissues." Animals are frequently categorized as allogenic engineers because of their ability to mechanically alter or create structure from non-living resources, while plants are often considered autogenic engineers because of their stationary physical structure. While useful, this classification by no means excludes plants or animals from either category of engineering (Jones et al. 1994, Jones et al. 1997).

Partially as a result of ongoing human impact on natural ecosystems, and the need to justify the value of biodiversity as it declines, there has been an increase in research describing and quantifying the effects of ecosystem engineers, and in developing new models of ecological theory that can be used in applied settings (Hastings et al., 2007). The expansion of the ideas put forward by Jones et al. (1994) is testimony to the interest in understanding indirect interactions and in examining the effects of habitat on species diversity. Some of the more obvious terrestrial allogenic ecosystem engineers include termites (*Macrotermis michaelseni*) (Dangerfield et al., 1998), prairie dogs (*Cynomys ludovicianus*) (Ceballos et al., 1999), kangaroo rats (*Dipodomys spectabalis*) (Schooley, 2000), and beavers (*Castor canadensis*) (Wright et al., 2002; Wright, 2009), whose burrowing and building activities alter soil structure and water courses, affecting the distribution and abundance of co-occurring species. Although less empirical research has been undertaken on the engineering properties of plants, examples exist in the literature that describe processes that can be considered engineering. For example, trees can shed

branches and leaves into stream areas and the forest floor, altering water flow and the soil environment and creating habitats and physical structure for other animals (Jones et al. 1994 and references therein).

In the marine environment, engineering activities include macrofaunal burrowing, (Riisgard & Banta, 1998; Berkenbusch & Rowden, 2003; Curran, 2003) mediation of the chemical environment by tubeworms (Cordes et al., 2003) and creation of habitat complexity by structural species, such as sea grasses, kelp beds and mangroves (Ewel et al., 1998; Field et al., 1998; Smith & Witman, 1999; Angel & Ojeda, 2001; Somerfield, 2002; De Troch et al., 2003), which provide nursery grounds (De la Moriniere et al., 2002; Nagelkerken et al., 2002) and alter sedimentation processes (Furukawa et al., 1997; Terrados & Duarte, 2000; Agawin & Duarte, 2002). The structure provided by marine invertebrates offers secondary substrate for settlement of species on the animal surface, within the body cavity and canals, and in the interstices between individuals of a colony. Mussels (Lohse, 1993; Gunther, 1996; Seed, 1996), oysters (Coen et al., 1996; Lenihan & Peterson, 1998; Cranfield et al., 1999; Lenihan, 1999), corals (Abele, 1976; Scott, 1987), and sponges (Klitgaard, 1995; Ribiero et al., 2003) create complex habitat for a variety of associated fauna. Structural species can facilitate a compounding engineering effect by providing substrate for colonization by other ecosystem engineers (Rice et al., 1990; Rogers, 1999; Beaulieu, 2001). All these activities modify, maintain and create habitat for other species.

Habitat created by the body structure of a living species can be considered a direct provision of resources and was, therefore, excluded from the original definition of autogenic engineering (Jones et al., 1994) which specifies the importance of indirect

interactions in altering the physical environment. Given that the "architecture" of biologically produced habitat does in fact result in physical modification of the ecosystem, and that habitat provision is more closely aligned with engineering than trophic relationships, it has since been included in the suite of interactions resulting in modification of the physical environment (Jones et al., 1997). Many marine invertebrates exhibit plant-like qualities, in that they are attached to the substrate with limited mobility, yet they feed, egest and reproduce as animals. Because of their sessile nature and consequent limited ability to physically change the ecosystem, habitat provision is perhaps the most important engineering activity carried out by such organisms.

Ascidians, bryozoans, corals, hydroids and sponges, while taxonomically distinct, function similarly as colony-forming, suspension-feeding marine benthic animals. Others have examined this particular grouping of taxa with regards to larval dispersal (Jackson, 1986), larval palatability (Lindquist & Hay, 1996), regeneration capacity (Henry & Hart, 2005) and percent cover of fouling organisms (Davis & White, 1994). Often the subjects of individual studies on associated species, taxonomy or biogeography, these animals have not been considered more generally in terms of their role as ecosystem engineers, either within a taxonomic group or as a guild.

The purpose of this review is to summarize the relevant literature on engineering activities of these invertebrates, focussing specifically on the direct provision of habitat.

Broad scale patterns of the communities inhabiting these animals are examined, in particular, relationships with environmental gradients of latitude, depth and host volume.

The ability of these animals to host myriad associates gives them particular importance in terms of maintaining biodiversity, as impacts on the host species will also have impacts on

the associated fauna. This review does not fully examine the relationship between reproductive modes of host and associate or the evolutionary consequences (although this would be an interesting and useful endeavour), but rather establishes the importance of habitat engineering by sessile invertebrates in maintaining marine benthic diversity.

2.1 Ecosystem Engineering Activities

Ascidians, bryozoans, corals, hydroids and sponges differ in their physiology and phylogenies, but behave similarly in the marine ecosystem. Table 2.1 outlines both allogenic and autogenic engineering activities of these animals, all of which serve to alter the physical or chemical environment in some respect. Feeding activity, egestion of prey and bioerosion can result in mechanically engineered habitat for other animals. A key example is coral feeding via mucous net suspensions, which once released into the water column, rise to the surface or settle to the benthos, collecting bacteria and detritus en route (Wild et al., 2004). The mucous and mucous aggregations modify sediment composition and create surface biofilms thereby enhancing the physical environment for other plants and animals (Wotton, 2004). Sediment modification can also occur through egestion of food and waste as undigested particles and faecal pellets collect in nearby sediment depressions. Passive filtration of particles by the deep-water sponge, *Thenea muricata* (Witte et al., 1997) and egestion of zooplankton prey particles by hydroids (Barange & Gili, 1988) results in deposition around the animal base and with sediment modification in favour of deposit feeders. In addition to deposit feeders, organic matter deposition surrounding biological structures positively influences bacterial biomass (Soltwedel & Vopel, 2001).

In order to maintain feeding activity, some sponges have the ability to slough off their external spicule layer to clear sediment and fouling organisms from the sponge surface (Barthel & Wolfrath, 1989). This sloughing action results in deposition of particulate matter and siliceous spicules around the base of the sponges, changing sediment structure and faunal composition.

Clionid sponges and some members of the Orders Poecilosclerida and Haplosclerida are unique among sessile invertebrates in their ability to bore into and excavate calcareous substrates (Rutzler, 2004), such as coral reefs, limestone and bivalve shells. This activity creates rubble and sediments, adding to the substrate, changing grain size and providing habitat for other creatures (Wulff, 2001), although the activity of boring sponges and particularly increased sponge growth concomitant with deteriorating coral reef health can also be seen as reducing available habitat, particularly for organisms dependent on healthy coral for habitat (Hutchings, 1986).

Engineering that results from the structure of the animal itself, as opposed to a behaviour or physical activity, are categorized as autogenic processes. These processes occur at multiple scales, from the individual organism to the patch and seascape scale (Table 2.1). The physical structure of ascidians, bryozoans, corals, hydroids and sponges modifies the physical environment, influencing species diversity through creating habitat for other species, providing topographical complexity and affecting sedimentation processes. These activities are discussed in detail in the following sections.

2.2 Habitat Provision

The published literature on the associated fauna of ascidians, bryozoans, corals, hydroids and sponges yields relatively few studies that adequately quantify the entire macrofauna (>1 mm) of a host species. Many studies focus on dominant associated fauna (i.e. infauna; (Scott, 1987)) or the relationship between a particular taxon and its host, such as fish (Tyler & Bolke, 1972; Rocha et al., 2000) or polychaetes in sponges (Dauer, 1974; Martin et al., 1992; Cinar & Ergen, 1998), shrimp in sponges (Hultgren & Duffy, 2010), crustacea on corals (Abele, 1976; Abele & Patton, 1976; Edwards & Emberton, 1980) or peracarids on ascidians (Sepulveda et al., 2003). In total, data for 87 hosts (35 studies) and their associated communities were collected from the primary literature, including 6 species of ascidians (5 studies), 2 bryozoans (2 studies), 8 corals (5 studies), 3 hydroids (3 studies) and 68 sponges (20 studies).

Despite their importance as hot spots of marine diversity (Reaka-Kudla, 1997; Roberts et al., 2002), few studies of coral reefs document the associated fauna of an individual coral species. Rohde (1992) appropriately notes that the lack of quantitative studies on the associated diversity of tropical habitats is not indicative of the lack of diversity, but rather the impossibility of attaining reliable species counts, due to the great extent of the diversity. The low number of studies on the associated fauna of bryozoans and hydroids may be due to the decreased surface area available for colonization compared to corals and sponges. These organisms also tend to be less conspicuous members of the benthic community, and are more frequently found as epifauna on other organisms, rather than as hosts themselves. Nevertheless, both hydroids and bryozoans are capable of

forming large, dense patches, contributing significantly to the ecological processes of particular location (Bradstock & Gordon, 1983; Genzano et al., 2002). Sponges are the most well-investigated hosts, perhaps because they are easily collected and highly noticeable in places were they are abundant. Collection methods of host organisms vary, especially between shallow-water species, which are typically collected by divers, and deep-water species, most often collected through the sorting of bottom trawl contents, with the occasional study that has used a remotely operated vehicle (ROV). Precise sampling in the deep-water using ROVs, rather than sorting through the contents of trawls, indicates that there is an underestimation of the importance of corals and sponges as habitat for associated fauna (Jensen & Fredericksen, 1992; Beaulieu, 2001; Buhl-Mortensen & Mortensen, 2003; Buhl-Mortensen & Mortensent, 2005).

The associated communities associated vary among individual hosts and within and between taxonomic groups. Community composition and species diversity patterns are discussed next at the scale of the individual host and differences between ascidians, bryozoans, corals, hydroids and sponges are explored.

2.2.1 Individual Host Effects on Associated Fauna

Host body shape and tissue consistency affect the type, abundance and spatial distribution of associated species living on the surface or within the host structure. There have been no studies that have examined the effects of morphology on associated fauna on a broad scale, but a few general comments can be made from observations in the literature. Sponges, corals and ascidians with internal cavities and canals are more likely to contain resident, sedentary species than erect hydroids and bryozoans, which have little internal

space for colonization. Branching bryozoans and those with skeletal spines have been observed as settlement substrate for bivalve plantigrade larvae (Eggleston, 1962; Stebbing, 1971; Moore, 1973), Moore 1973), kamptozoans (Yakovis, 2002) and as habitat for pycnogonids (Wyer & King, 1973), while there are few reports of smooth, encrusting bryzoans hosting other animals. Hydroids provide settlement substrate for juvenile bivalves and their chitinous branches are ideal habitat for amphipods and caprellids (Round et al., 1961; Genzano et al., 2002).

When environmental and geographic variables are constant, host species can differ widely in their ability to accommodate diverse communities of inhabitants. For example, in the South Atlantic, the community associated with the sponges, Ircina campana and Haliclona oculata was dominated (>90% of total biomass) by the polychaete, Syllis spongicola (Wendt et al., 1985). Yet, the sponge Cliona celata, contained no Syllis and was dominated instead by the amphipod Colomastix sp. which comprised 47% of the associated faunal biomass. While no clear explanation is given for these remarkable differences between hosts, the authors' hypothesis was that surface texture and tissue composition are important causal factors. Cliona celata is typically an encrusting boring sponge, although may become massive in shape in some circumstances, and hence is not likely suitable habitat for interstitial worm, but can provide shelter for crustaceans in its excurrent oscules. In their study of the associated fauna of three sponge species in the Aegean Sea, Koukouras et al. (1996) found canal volume to be the best predictor for composition and abundance of inhabitants. Differences between two tubular sponges from Venezuelan coral reefs, Aplysina archeri and Aplysina lacunosa, was attributed to the higher level of complexity of the canal system in A. lacunosa. Associated faunal variations

among 11 sponge species in the Northwest Atlantic, collected at similar depths and with similar local species pools, has been attributed to sponge surface texture; as those species with extended spicule "fur" hosted a greater number of species those with a smooth exterior surface (Scott, 1987; Klitgaard, 1995). In quantifying associated fauna of 44 different corals, the families Siderastreidae and Agariciidae were found to be most commonly inhabited by other species (Scott, 1987).

One of the more noticeable influences of host morphology on associate community composition is the existence of faunal zones on the host body. The ascidian *Microcosmus* spp., is described as having a delineated "topography" of six areas, each hosting a unique faunal assemblage (Monniot, 1962). More commonly, host species can be easily divided into two zones, the holdfast area and the remainder of the body, the establishment of which is attributed to a current velocity gradient increasing from holdfast to the part of the host body furthest from the sea floor. Holdfast areas tend to accumulate sediments and organic matter, creating habitat for deposit feeders and bacteria, while areas experiencing high current velocities are preferred habitat for suspension feeders (Hughes, 1975). Several bivalve species have been observed to settle preferentially on the distal branches of the bryozoan Flustra foliacea (Stebbing 1971), primarily because that these sections experience greater current velocity and enhanced feeding opportunity. However, zonation of associated fauna on a host species can also occur in areas where current velocity has limited influence on faunal composition, as illustrated by the colonization of the upper stalk of the abyssal sponge Hyalonema bianchoratum by Foraminiferans and other suspension feeders (Beaulieu 2001). In this case, infaunal predation is offered as the mechanism responsible for zonation on *Hyalonema* stalks (Beaulieu 2001) where biological interactions rather than

the physical environment, tend to be the primary structuring force (Dayton & Hessler, 1972).

2.2.2 Patterns Between Host Groups

Comparing the associated communities of ascidians, bryozoans, corals, hydroids and sponges is most easily done using biological diversity measures and indices. Despite criticisms of the validity and mathematical appropriateness of various measures of species diversity (Hurlbert, 1971; Rosenzweig, 1995; Lande, 2003), such indices nevertheless provide a quantitative method for comparisons of ecological communities. I used species number (SR), species diversity (Shannon-Weiner H' and Fisher's α), species evenness (J'), rarefaction curves and the density of associated faunal communities (species per litre and individuals per litre) to compare groups of hosts. SR is the number of species recorded as living within or on a host. H' is the most frequently used index in the literature surveyed and was calculated as log base 2 for studies where the index was not provided, but where raw data were available (see Appendix 1). H' is the sum of the proportion of a species within a community and is disproportionately affected by species dominance and inadequately represents rare species. I used Fisher's α as a second measure of species diversity, which is independent of sample size and area sampled and a more appropriate descriptor of rarity (Rosenzweig, 1995; Hayek, 1997). Fisher's α was calculated only for those communities with > 50 recorded individuals, as it is not considered an accurate measure in communities with few individuals (Hayek and Buzas 1997). Species evenness (J' =H'/H_{max}) is a measure of community dominance, where 1 indicates equal abundance of all species present; as J' approaches 0, the community is dominated by one or more

abundant species. Rarefaction curves illustrate species richness (as a function of curve height) and species evenness as a (function of curve slope). Rarefaction curves were generated using BioDiversity Pro (McAleece, 1997), and when not reported in the literature, diversity measures were calculated using PRIMER Version 5 software (Clarke & Warwick, 2001). The range in the number of species found living in or on the host groups (from 2 for bryozoan hosts to 67 for sponges) is partially a reflection of the sample sizes available for each host (Table 2.2).

Most studies did not report the number of individuals collected for each species, thus it is not possible to calculate rarefaction curves for all 87 hosts, consequently, I compared rarefaction curves of selected deep-water and shallow-water hosts, and temperate and tropical hosts where data were available (Figure 2.1). Deep-water coral (*Lophelia pertusa*) and the abyssal sponge (*Hyalonema bianchoratum*) had the highest associated species diversity as compared to shallow-water species. The shallow-water coral, *Pocillopora damicornis*, exhibited the highest species diversity overall. The initial slope of the curve for the community living associated with the ascidian, *Pyura chilensis*, was higher than that for *H. bianchoratum*. The barrel sponge *Spheciospongia vesparia*, and the hydroid *Sertularia operculata*, have much lower expected numbers of species due to associated community dominance by shrimp and caprellids, respectively.

Species richness, Shannon-Wiener diversity (H') and Fishers α were highest in coral and ascidians, with maximum mean species richness found in corals (Table 2.2). The highest mean Shannon-Wiener diversity found for the associated fauna of ascidians. Corals had the highest mean Fishers α diversity followed by ascidians, suggesting the associated

fauna of corals are less likely to be dominated by one species. The data for ascidian communities are predominantly from the *Pyura* genus which is found in dense patches in Chile (Zamorano & Moreno, 1975; Cerda & Castilla, 2001; Castilla et al., 2004), South Africa (Fielding et al. 1994) and Australia (Monteiro et al., 2002). The associated fauna of sponges has been the most frequently and thoroughly investigated of the five types of host organisms, with diversity ranging from a low of H'= 0.13 in the Antarctic sponge, *Tedania trirhaphis*, and a high of H'=5.20 in the north Atlantic sponge, *Stryphnus ponderosus*.

The remarkably few studies on the associated fauna of bryozoans and hydroids (n=2 and n=3, respectively) show a wide range of species richness, with diversity measures being consistently lower than those of other hosts. Bryozoans and hydroids have similar morphologies, with encrusting and branching forms often developing into dense mats and neither have internal body cavities or canals. Both taxa are more frequently cited as epizoites than as hosts themselves. Associated communities of ascidians and bryozoans tend to have the most evenly distributed species composition (Table 2.2). One potential explanation for the existence of less even communities within corals, sponges and hydroids is the production of antifouling chemicals or contain stinging nematocysts, which offer may protection from colonisation by other species (Bakus et al., 1986).

The density of species and individuals within a particular host is also a measure of its habitat suitability and quality. Despite high species diversity, ascidian hosts had the lowest species density, while bryozoans and corals had the highest associated species density. Sponges had the highest mean number of individuals/L, followed by corals, bryozoa and ascidians. There were no data for hydroids as volume was impossible to calculate given the information in the literature.

There are few studies comparing habitat quality or differences among the various taxa of sessile invertebrates, probably because it is difficult to find study areas where members from all taxa exist. In one attempt, Davis and White (1994) compared the percent cover of epibionts on ascidians, bryozoans, coelenterates and sponges. They found solitary ascidians to be most susceptible and the encrusting soft coral and anemone the least susceptible to surface colonizers. Wendt et al. (1985) examined the associated communities of four coral species and three sponge species and concluded that morphological variation both within and among species affected associated fauna, as did the presence of other epifaunal organisms on the host species.

The number of species associated with ascidians, bryozoans, corals, hydroids and sponges is comparable to, and in many cases higher than, that associated with other biological structures, such as mussel beds and kelp holdfasts. Mussel beds host a range of species, with a mean of 58 (sd±79) over five different studies with diversity ranging from H'=1.56 to 3.01 (Suchanek, 1979; Tsuchiya & Nishihira, 1985; Ong-Che & Morton, 1992; Seed, 1996; Van Dover & Trask, 2000). Kelp holdfast habitats host a mean of 30.5 (sd±9.94) other species (Edwards 1980, Sheppard et al. 1981, Dahl and Dahl, unpublished data, Ojeda and Santelices 1984).

One of the key questions regarding the relative importance of biological structures as habitat, is whether or not they are relatively more important from a biodiversity perspective than non-biological habitats. For example, the species richness sediments from beaches, to coastal soft sediments to the deep sea ranges from an average of beaches 21.6 (sd±10.63), to 439.4 (sd±276.72) and 731.4 (sd±468.97), respectively (as calculated from

Table 1 in Gray, (2002)) and richness of the biological habitats reviewed here lie between beaches and coastal sediments.

A more interesting comparison is between species densities of communities living within biological habitat and those associated with nearby non-biological habitat. If we were to assume that 1L of biological habitat is equivalent to 0.01m^2 of non-biological habitat, then mean species density for beaches is 0.16 (sd±0.12), for coastal areas $0.21(\text{sd}\pm0.2)$ and for the deep sea, $1.08(\text{sd}\pm0.77)$ (calculated from Table 1 in Gray (2002)). These estimates are much lower than the estimates of species densities for biological habitat, which range from 2.25 species/L in ascidian hosts to 21.17 species/L in bryozoan hosts (Table 2.2). Intertidal beaches contain an average of $9.36(\text{sd}\pm6)$ individuals per 0.01m^2 ; coastal areas $38(\text{sd}\pm43)$ and deep-water soft sediments $32.6(\text{sd}\pm15.8)$. Biological habitat provided by ascidians, bryozoans, corals, hydroids and sponges contains an average of $214.5(\text{sd}\pm208)$ individuals per litre, with sponges hosting a high of $489.9(\text{sd}\pm1079.23)$ individuals per litre.

The spatial constraints of habitat created by living organisms generate concentrated communities, which can have significant conservation implications. Biological habitats can be considered "hotspots" or "oases", especially in areas of the marine environment that are predominantly comprised of soft sediment. While high species richness can exist in some soft sediment communities, biological habitats offer a distinctly different type of habitat that can accommodate different species and functional groups than species within the sediments. Most importantly, the removal or destruction of host animals, through disease, fishing effects or direct harvesting will also affect species that live within the three dimensional structure of the host.

2.2.3 Skeletal Material as Habitat

Both corals and sponges have hard skeletal components that remain a part of the physical environment following the death of live tissue. The lack of persistent skeletal material in ascidians and hydroids prevents these species from contributing significantly to the physical environment following the death of live tissue. Corals leave behind a solid skeleton, available for colonization by burrowing and sessile fauna, to the extent that coral rubble is often the most abundant hard substrate within a reef system (Scott, 1987). Skeletal material offers no anti-fouling defences via stinging nematocysts or chemical metabolites, thereby creating substrate for a different suite of animals than those living within the live tissue and having little resistance to colonization. Dead coral skeletons have been found to host high numbers of species and different species complexes than live corals in shallow water (Scott, 1987; Capa & Lopez, 2004) and deep-water environments (Jensen & Fredericksen, 1992; Fossa & Mortensen, 1998). Associates of coral cavities and coral rubble are implicated in nutrient regeneration and subsequent maintenance of highly productive reefs in areas that are typically nutrient poor (Richter et al., 2001).

Spicules deposited mainly by sponges of the Rossellid family play a structuring role in the Antarctic benthos by providing hard substrata in an otherwise soft sediment environment, creating refugia from predation and trapping particulate matter within the interstices affecting both sponge species composition and associated faunal communities (Barthel, 1992). At depths of 1250 m in the Northeast Atlantic, spicules from the glass sponge, *Pheronema carpenter*, greatly influence macrobenthic fauna, where ascidians, bryozoa and hydroids colonize the spicule mat, forming a complex of structural species

(Rice et al., 1990). Associated macrobenthic biomass in areas characterized by spicule mats can be 2-3 times higher than the biomass in areas without these mats (Bett & Rice, 1992). The stalks of *Hyalonema* sponges in the abyssal Pacific continue to host a wide variety of organisms following the senescence of the adult sponge (Beaulieu, 2001). Spicules contribute less to the sediment in tropical areas where, siliceous spicules tend to dissolve into the water due to the Si- undersaturated and high pH environments of reef sediments (Rutzler & MacIntyre, 1978). Animals that continue to provide habitat following the death of live tissue increase their longevity as ecosystem engineers.

2.2.4 Topographical Complexity

The emergent structure of ascidians, bryozoans, corals, hydroids and sponges and the tendency to form patches or reefs increases the topographical complexity of the marine environment. Bell et al. (1991) describe complexity as consisting of two components: habitat heterogeneity and habitat structure, where patchiness contributes to heterogeneity across a landscape and habitat structure provides the architectural component. Habitat heterogeneity has a positive effect on species diversity for a wide range of ecosystems (Tews et al., 2004). Biological structures are often the main contributors to habitat heterogeneity in the intertidal area (Thompson et al., 1996). Higher species diversity has been found associated with biologically generated habitat than abiotic structures in shallow water in tropical (Rutzler, 1976) and temperate areas (Thompson et al., 1996). Intertidal beach sediments contain a mean of 21.6 species (Gray, 2002); whereas species richness associated with biogenic habitat found at < 2 m depth is 36.6 (see Appendix 1 for data sources). Deep-water benthic habitats are predominantly sedimented, with high species

richness but limited topographical features. Biological structures in the deep sea can provide significant "oases" for organisms that would not be accommodated within soft sediments (Gage, 1996; Beaulieu, 2001; Baco & Smith, 2003).

Habitat engineering at the patch or reef scale alters species diversity and abundance, both within the patch and the area surrounding the patch (Thrush et al., 2001; Castilla et al., 2004). Observations of the deep-water glass sponge, *Pheronema carpenteri*, show clusters of 6-8 individuals with large empty spaces in between, and the only other sessile megafauna in the vicinity, the hexactinellid *Hyalonema* sp., is closely associated with these patches (Barthel, 1996), indicative of within-patch recruitment. The few observations of Hexactinellid recruitment (Leys & Lauzon, 1998) show large larvae that settle near the parental animal. Settlement of invertebrate recruits on fjord walls in Norway is significantly greater within, than outside patches of high epifaunal diversity as biogenic structure is found to enhance within-patch recruitment, essentially guaranteeing patch maintenance (Smith & Witman, 1999). Species richness increases and community composition changes at the seascape scale in coastal Chile following the invasion of the ascidian *Pyura* praeputialis; over 50% of the species present in the area associate exclusively with the Pyura patches (Castilla et al., 2004). Thrush et al. (2001) show diversity increases in softsediment systems with the presence of sparsely distributed, immobile biological structures, such as ascidians, hydroids and bryozoans.

In addition to enhancing the diversity of invertebrate species, biologically produced habitat structure is important for vertebrate species for shelter and feeding. In the laboratory, a decrease in predation mortality of juvenile Atlantic cod, *Gadus morhua* was observed in the presence of artificial sponges (Lindholm et al., 1999). *In situ* observations

show that selection for structurally complex habitat, including sponges, occurs in age 0 Pacific halibut (*Hippoglossus stenolepis*) and rock sole (*Lepidopsetta polyxystra*) (Stoner & Titgen, 2003). Bradstock and Gordon (1983) describe the fauna associated with coral-like bryozoans as important dietary component of resident fish species, and suggest these areas are preferred feeding groups for snapper (*Chrysophrys auratus*) and tarakihi (*Cheilodactylus macropterus*) in New Zealand. In the Northeast Atlantic, Bruntse and Tendal (2001) note that juvenile redfish (*Sebastes* spp.) are concentrated in areas of high sponge biomass, and Klitgaard and Tendal (2004) report that juvenile Greenland halibut (*Reinhardtius hippoglossoides*) and redfish (*Sebastes* spp) are often caught together with large catches of sponges off the Faroe Islands.

Engineering species can form large dense patches, accrete into dense reef structures, and can also be sparsely distributed, offering limited complexity in areas that are otherwise uniform in topographical structure. The patches of the ascidian *Pyura* on the southern coasts of Chile (Castilla et al., 2004), South Africa(Fielding et al., 1994)and Australia (Monteiro et al., 2002) can cover over 50% of the bottom (Monteiro et al., 2002) and reach densities of 1800 individuals/m² (Castilla et al., 2000). Non-accreting bands of the vase shaped sponge, *Pheronema carpenteri*, extend for 7 km between 700 and 800 meters in the Northeast Atlantic at densities of 15,000 individuals per hectare (Barthel et al., 1996, Rice et al., 1990). The bryozoan *Cellaria* sp. forms dense beds in the Adriatic, covering ~10 000 m² (McKinney & Jaklin, 2001).

Corals, sponges and bryozoans can form dense reefs, with new recruits settling on the non-living structure of dead organisms, taking hundreds to thousands of years to form mounds and reefs. While coral reefs are well known, bryozoans can also form dense reef-

like structures (up to 3m in height), providing important habitat where they are abundant (Moore, 1973; Bradstock & Gordon, 1983; Jackson, 1986; Cranfield et al., 1999). Shallowwater coral reefs are readily recognized among the most important ecosystem engineers in the marine environment and cover approximately 284 000 km² of the world's oceans (Spalding et al., 2001). There is no current comparable estimate to the area of the sea floor covered with cold-water coral although studies to date indicate that global coverage likely equals and potentially exceeds that of shallow-water species (Freiwald et al., 2004). Known cold-water coral reefs extend up to 100 km in length, with those in Norway alone covering ~ 2000 km². The 9000-year old Hexactinellid sponge reefs off the coast of British Columbia (Conway et al., 1991; Cook et al., 2008) consist of mounds up to 30 m high and are the only known extant glass sponge reefs in the world. In contrast to these dense patches and reefs, the glass sponge Hyalonema bianchoratum occurs at 4000 m depth in the Pacific at comparatively sparse densities of 124 individuals per hectare, acting as oases in the abyss and providing habitat to at least 135 associated species (Beaulieu, 2001). Thrush et al. (2001) found that even sparsely distributed sponges, hydroids and bryozoans in softsediment areas increased species diversity in surrounding sediments relative to that in areas with no biogenic topography.

2.2.5 Sedimentation Facilitation

Emergent structures on the sea floor, whether biological or non-biological in origin, can affect near-sea bed hydrodynamic processes by modification of bottom currents. This can result in the preferential deposition of organic matter occurring in depressions at the base of epifaunal structures, thus altering the surrounding sediment characteristics and

increasing local food availability for other benthic organisms (Yager et al., 1993; Soltwedel & Vopel, 2001). Sediments within and surrounding a 10 km² "meadow" of the bryozoan *Cellaria* sp. in the Adriatic Sea contained >90% clay and silt within the patch and <50% clay and silt outside the patch (McKinney & Jaklin, 2001). Accumulation of fine sediments eventually buries parts of the meadow, creating fossilized mounds of bryozoan material. The associated community within the patch consists of sponges, polychaetes, ascidians and other bryozoans (McKinney & Jaklin, 2001).

Geophysical surveys, including seismic testing and side-scan sonar, have revealed biologically mediated sediment mounds. A particularly unique example of these structures is the hexactinellid sponge bioherm assemblage discovered in 1987 in the Hecate Strait, Northeast Pacific (Conway et al., 1991). Initial sponge colonization of coarse sediments in iceberg furrows, followed by sediment baffling, sponge mortality and recruitment over thousands of years, has resulted in mounds ranging from 10 to 600 m in diameter and are up to 30 m high. The emergent structure of the bioherms increases sedimentation rates, which range from 0.3-0.9 mm/y (Conway et al., 1991). Biologically mediated sedimentation processes has created complex habitat for fish and invertebrate animals. The discovery of carbonate mounds in the Porcupine Bight and Rockall Trough regions of the Northeast Atlantic (Hovland et al., 1994; Kenyon et al., 2003) illustrates the potential for sedimentation mediation by cold-water coral structures. Sediment baffling by the scleractinian corals Lophelia pertusa and Madrepora oculata create mounds up to 350 m high and 2 km in diameter. These mounds are created through processes similar to those generated by the sponge bioherms; initial colonization by corals, followed by sediment baffling and accretion of coral skeletal material and sediment over the years. The discovery of carbonate mounds distributed from the Iberian Peninsula to the coast of Norway, including the Darwin Mounds located at 1000 m depth off the United Kingdom may also be linked to areas of hydrocarbon seepage (Hovland et al., 1994). The density and diversity of the biological community tends to increase both on and in the sediments surrounding these mounds with the communities being particularly rich in suspension and deposit feeders (Kenyon et al., 2003).

2.3 Broad Scale Patterns of Associated Faunal Diversity

The existence of communities living within sessile invertebrates allows for comparison with broad scale patterns of species diversity known to exist in abiotic habitats. Despite the complicating interactions between species and their hosts, broad scale patterns of species diversity of associated fauna with environmental gradients can be compared to patterns for species that are not associated with biological habitat. Here, I examine patterns between the diversity indices described above, including species richness (SR), Shannon-Weiner (H'), Fishers α , species evenness (J') and species density and several explanatory variables; the number of individuals collected, latitude, depth and host volume. Many studies either did not report sample volume or reported sampled area sampled rather than volume. Where sufficient information was provided, volume of the host species or sampled area was calculated. For ascidians, the area of the patch was multiplied by the average height of the host species and then by the number of samples taken to obtain total volume sampled. For corals, samples were generally reported in kilograms. To convert to volume, the weight was multiplied by the specific gravity of CaCO₃ (2.65g/cm³) and converted to

litres. For sponge hosts, the mean height of the species was used to calculate the volume, assuming that the sponge was spherical in shape.

Statistical analysis was carried out using SPLUS 6.1.2. Relationships between dependent and independent variables were fit using generalized linear models (GLMs). The variance of the response variables was generally much larger than the mean, and errors were not normally distributed. The relationships between the response and explanatory variables were fitted using the negative binomial distribution for discrete count data and Gamma distribution for continuous variables, as diversity indices were positive measures. The log link function was used for all models, except when testing species evenness (J') where the logit link was used, as J' is constrained between 0 and 1. The appropriateness of distribution family and link function was checked through diagnostic plots of model residuals. To account for the effect of host volume, an offset of log total host volume was used to standardize species richness and the number of individuals. In order to plot fitted curves, the median value of the offset variable was used. Diversity indices, H', Fishers a and J' are already considered standardized and no offset was used. Chi square and F tests for analysis of deviance were used to test significance. F tests were used for over dispersed models, where the residual deviance was more than 1.5 times the degrees of freedom (Crawley, 2002). Model summaries are included in Table 2.3.

Species diversity of a biological community will vary with the number of individuals sampled and the number of individuals is a reasonable proxy for sampling effort. This relationship is most often portrayed using rarefaction curves (Figure 2.1). Pooling the communities of all hosts included in this review shows the number of species per litre of host increasing with the number of individuals per litre (Figure 2.2a, Table 2.3).

This relationship indicates that the habitat is not saturated and further sampling will yield additional species. Interestingly, species evenness (J'), the measure of community dominance, decreases with the log number of individuals showing that communities become less diverse the greater the number of individuals (Figure 2.2b, Table 2.3). This is a distinct effect of biological habitats, where particular associates form a relationship with a host, breed within the host and make it difficult for other species to colonize.

2.3.1 Latitudinal Gradients

Latitudinal gradients in species diversity typically show decreasing diversity with distance from the equator (Hillebrand, 2004) and are perhaps the most prevalent broad scale biological pattern of species distribution. While first established in terrestrial environments, this gradient also exists for many marine taxa (Rex, 1983; Gray, 1997; Roy et al., 1998; Rex et al., 2000; Fuhrman et al., 2008; Fischer, 1960). Many hypotheses have been presented as explanations for this pattern, and a meta-analysis of over 600 gradients from terrestrial, marine and freshwater habitats concludes that the mechanism driving increase richness in tropical areas is a combination of temperature (solar energy) and area effects (Hillebrand, 2004). More recent analyses of marine diversity have found the greatest richness for oceanic species at mid-latitudinal ranges, and coastal species, including corals and seagrasses with highest species richness in the Western Pacific (Tittensor et al., 2010). The authors tested several explanatory variables and found that sea surface temperature accounted for the greatest variability in species richness across both oceanic and coastal species.

By contrast, there have been few studies of broad scale species richness and diversity patterns of entire communities associated with biological hosts or specific "engineered" habitats. Some examples exist, for seagrass beds and terrestrial pitcher plants. Virnstein et al. (1984) investigated latitudinal patterns in the complex communities of seagrass epifauna and found that broad scale patterns were largely dependent on the species group. They found significant decreases in species diversity with latitude for decapods and amphipods, but not for isopods and fishes (Virnstein, 1984), despite the fact that coastal fish diversity has been found to decrease with latitude (Rhode, 1992). A reverse relationship with species diversity and latitude in the aquatic community was found inside pitcher plant (Nepenthes spp.) leaves, where species richness increased in northern communities (Buckley et al., 2003). The explanation given for this anomaly is a top-down effect, whereby increased predator diversity (in this case mosquitoes) in southern latitudes effectively decreased prey diversity within the pitcher plant leaves. Using fisheries observer data, Worm et al. (2003) reported that large pelagic species peaked in diversity between 20° and 30°, in close proximity to complex habitat features and this result was corroborated by Tittensor et al. (2010), who also found that large pelagic diversity correlated with frontal events – equivalent to oceanic habitats. In this review, associated communities of ascidians, bryozoans, corals, hydroids and sponges exhibit a unimodal relationship between species richness (SR), species diversity (H') and species evenness (J') and latitude, with maxima at mid latitudes (Figure 2.3a,b,d, Table 2.3). This is a departure from the typically decreasing relationship of species diversity with distance from the equator, but has been found for other marine species including pelagic fishes (Worm et al., 2003), zooplankton (Angel, 1997) and foraminiferans (Rutherford et al., 1999). The number of individuals was

inversely related to latitude, with communities with high numbers of individuals most abundant in tropical environments (Figure 2.3c). A partial explanation for this is the tendency for associated communities in tropical areas to be dominated by dense colonies of a single species (e.g. (Pearse, 1950; Wendt et al., 1985). This is consistent with the effective evolutionary time hypothesis of latitudinal gradients (Sanders, 1968) as tropical associates have had greater time to evolve symbiotic relationships with their host and the ability to defend their host against other colonizing species. This finding is corroborated by the observations of Lopez et al. (2001) who reported that the frequent and widely distributed sponge associate, polychaete *Haplosyllis spongicola*, exhibits markedly different behaviour in tropical and temperate environments, tending to be strictly endosymbiotic in warm waters, forming dense host specific colonies. By contrast, in northern waters, this species is free living and occurs on a variety of hosts, indicating that competition for suitable habitat is greater in the tropics.

Invertebrate hosts in temperate and Mediterranean climates are harbour associated community diversity. In these areas, habitat structure is perhaps more important in maintaining biodiversity than previously thought. The unimodal pattern may also be the result of limited sampling of associated communities in some regions as compared to others. Conspicuously absent are studies on associated fauna of sessile invertebrates from the Indo-Pacific, one of the more diverse tropical areas in the world. The relationships in Figure 2.2 are also heavily influenced by a single study in Antarctica (Kunzmann, 1996). However, to account for this, I analysed the data without using volume as the offset, which allowed for inclusion of a North Atlantic study on the associated fauna of 11 species of sponge (Klitgaard, 1995) and the unimodal relationship remained. A study of the infaunal

spongicolous amphipods in Antarctica reported high abundance within demosponge hosts, but low diversity as compared to temperate sponge dwelling amphipods (Lorz, 2001).

2.3.2 Depth Gradients

The relationship between species richness and depth has been well investigated in soft sediment areas, where it increases from 200-2500 m and decreases in the abyss (Rex, 1983; Gray, 1997; Rex et al., 2000). Hard substrates have been less rigorously sampled, particularly in the deep sea. Associate community species richness (SR), number of individuals and Shannon-Wiener diversity (H') decrease with depth and there is no significant relationship between species evenness (J') or Fisher's α and depth (Figure 2.4a,b and c, Table 2.3). There is a distinct lack of data on associated communities of host animals between 100 m and 300 m and below 800 m. The one abyssal point at 4100 m, where 134 species (Beaulieu 2001) are associated with the deep sea sponge *Hyalonema bianchoratum* is excluded from the analysis, but indicates that species richness on deep-water hard substrates may in fact be greater than previously thought.

The rarefaction curves plotted in Figure 2.1 show that deep-water corals and sponges have the highest species richness and evenness, though the data for that figure were limited to the few studies for which the number of individuals per species had been reported. Shannon-Wiener diversity was not different between shallow-water and deep-water associated communities, being H'=2.83 and H'=2.4,3 respectively. In contrast, Fishers α is 8.22 for shallow-water communities and 15.00 for deep-water communities, results similar to those presented for hard substrates (Baco & Smith, 2003). Deep-water sponges and corals have been investigated in very few studies, only some of which have

quantified the associated fauna (Klitgaard 1995, Ilan et al. 1994, Rogers 1999, Buhl-Mortensen and Mortensen 2003, Jensen and Frederiksen 1992, Beaulieu 2001). I found no studies that had quantified the associated fauna of deep-water hydroids, bryozoans or ascidians, although available data show decreasing species richness and diversity with depth, this finding must be considered within the context of the relative lack of research of associated fauna of deep-water biological substrates.

Faunal composition of associated communities also varies with depth. Ascidians at the low tide mark, along the South African shoreline, are dominated by polychaetes while those located a few meters deeper in the subtidal, are dominated by crustaceans (Fielding et al. 1994). The studies reviewed here show 57% of deep-water sponge-associated communities dominated by polychaetes whereas only 20% of shallow-water communities were dominated by polychaetes. Crustaceans dominate shallow-water sponge communities (Pearse, 1932, 1950; Rutzler, 1976; Westinga & Hoetjes, 1981; Ilan et al., 1994) and are less common in deep-water, although this could be a sampling effect due to escape of motile fauna during trawl sampling. The single study of abyssal sponges showed Hyalonema stalks dominated by the colonial suspension feeder Epizoanthus (Beaulieu 2001). Polychaetes dominate deep-water *Lophelia* reefs (Jensen and Fredericksen 1992), while crustaceans dominate most shallow-water coral communities (Austin et al., 1980; Tsuchiya & Nishihira, 1985; Wendt et al., 1985). Associated fauna of non-reef forming deep-water corals shows high species richness of crustacea, which are more mobile than many polychaetes and, therefore, colonize individual corals more easily (Buhl-Mortensen & Mortensen, 2003). Deep-water biological substrates warrant further study to determine their relative importance providing habitat relative to shallow-water species.

2.3.3 Host Volume

Species richness increases with habitat area for a broad variety of species (see review in Rosenzweig 1995). Host volume can be considered a proxy for both habitat size and age. An increase in associated species richness with host volume has been documented in sponges (Bakus, 1966; Labate & Gallo, 1974; Frith, 1976; Ubelaker, 1977; Westinga & Hoetjes, 1981; Villamizar & Laughlin, 1991; Duarte & Nalesso, 1996; Cinar & Ergen, 1998; Cinar et al., 2002), corals (Abele and Patton 1976, Gotelli and Abele 1983, Tsuchiya et al. 1986, Jensen and Frederiksen 1992), and with area sampled for ascidians (Fielding et al. 1994, Zamorano and Moreno 1975). While common, the relationship is not ubiquitous, as others have found no correlation of associated species richness with host volume (Pansini, 1970; Sube, 1970; Voultsiadou-Koukoura et al., 1987).

Species richness, number of individuals and species diversity (Fisher's α) were positively related to host volume, although with low levels of significance (Figure 2.5, a-c, Table 2.3). A significant relationship between number of individuals and host volume likely indicates a sampling effect; the greater the volume sampled the greater the number of individual animals found. While a significant factor, host volume does not explain the majority of variability in associated community composition. This is a departure from what is expected in island biogegraphic theory and species area relationships (Rosenzweig, 1995). However, habitat islands consisting of living species are complicated by biological processes, such as production of chemical defences, host patchiness and dispersal patterns as well as the ephemeral nature of biological hosts (Kuris et al., 1980). Despite the constraints of biologically produced habitat, it is the deviations from the expected

relationship between species and area that are of ecological interest (Abele & Walters., 1979). Species dominance and the frequency of entire life cycles being carried out within a host effectively create patterns in species richness that are unrelated to host volume and have more to do with the relationship between host and associate. Nevertheless, as expected, host size can affect species richness and diversity of the associated community, in turn influencing local and regional species richness.

2.4 Nursery Areas, Community Selection and Evolutionary Consequences

Many authors have described the communities of organisms living within sessile invertebrates as an ecological community (Pearse 1932, Bacescu 1971, Westinga and Hoetjes 1981, Villamizar and Laughlin 1991). The treatment of living organisms as generic habitat, in this review thus far, precludes examination of relationships between the host and associated organisms, be they symbiotic, obligate, commensal or mutualistic. The concept of ecosystem engineering focuses on non-trophic, indirect interactions and it is these indirect relationships that link ecosystem engineering with evolutionary processes and community level selection (Wilson 1980).

The animals residing on and within a biological host can be considered a unique community with the various species directly or indirectly dependent on one another, each playing a particular role. Some species act as cleaners, removing debris from the host surface and enhancing filtration of particulate matter; others live within canals and crevices, excreting nutrients that can be used by another member of the community. Associated species can take particular advantage of a host, by reproducing within the host, adapting

morphologically or behaviourally to maximize fitness within their biological habitat. The degree of adaptation is highly dependent on the relationship between associate and host, which can range from the independent extreme of commensalism to the dependent extreme of symbiosis and parasitism. The majority of species associated with biological habitats are commensal and are found elsewhere in the marine environment (Buhl Mortensen et al., 2010). Despite this, many animals show a preference for shelter within biological communities and the high densities of individuals found in biological habitat (Table 2.2) are a clear indication of this preference. There are also numerous examples of species that rarely live outside their biological host or are dependent on the host for one or more life history stages.

The provision of nursery areas within and on sessile invertebrates ties them to the early life history stages of many associates. Emergent epifauna are often preferred settlement substrate for planktonic larvae, providing shelter for many species while in vulnerable juvenile stages. Sponges have been described as a veritable "kindergarten" for marine species living elsewhere in their adult lives (Kunzmann 1992) including pentacrinoids (Barthel 1997) and syllid polychaetes (Dauer, 1974; Betancourt-Lozano et al., 1998). Large patches of the hydroids *Amphisbetia operculata* and *Plumularia setacea* near commercial mussel beds in Argentina, provide the primary substrate for juvenile mussel recruitment with *A. operculata* supporting a juvenile mussel community up to five times its own weight (Genzano et al. 2002). Round et al. (1975) found nine species of bivalve spat on the temperate hydroid *Sertularia operculata* and red king crab larvae (*Paralithodes camtschaticus glaucothoes*) preferentially settle on hydroids in laboratory studies (Stevens 2003). Mussel (*Mytilus galloprovincinalis*) and scallop (*Pecten maximus*)

spat settle on the leafy fronds of the bryozoan, *Flustra foliacea* (Stebbing 1971). The hollow space in vase-like and tubular shaped sponges offers partially enclosed space for refuge and egg release for vertebrate species as well. Some fish in tropical areas have been found to spend their entire lives (Tyler & Bohlke, 1972, Smith & Tyler, 1972, Rocha et al., 2000), while others only lay their eggs (Antarctica:(Konecki, 1989; Barthel, 1997), Red Sea: (Fishelson, 1966), Northeast Pacific: (Long, 1968)) or take refuge (Dayton et al., 1974; Moreno, 1980), within the sponge cavity. Up to 8000 eggs have been found in the cavity of a Rossellid sponge, with 20% of sponges surveyed containing fish eggs, which were found nowhere else on the benthos (Barthel, 1997).

The life history of species living within a host can be tightly linked to the host species, with one or more life stages directly associated with biological habitat. A review of the fauna associated with the coral *Oculina varicosa* revealed that 48 out of 55 dominant species bred within the community with 9 species spending their entire life cycle within the coral head (McCloskey, 1970). Twenty-nine percent of the associated fauna of the demosponge *Mycale microsigmatosa* was found incubating either eggs or embryos (Ribeiro et al. 2003). Fauna that reproduce within a host species often exhibit direct larval development as the host offers protection for juveniles. Male and female shrimp, *Spongicola japonica*, mate and live as pairs inside the sponge cavity, with direct development of juveniles following spawning activity (Saito & Konishi, 1999), whereas free-living spongicolids have planktonic larvae (Saito & Takeda, 2003). The diversity and abundance of the endobiotic community is influenced by the reproductive schedule of the dominant associates. Direct development within the biological host may limit the dispersal

of juvenile inhabitants, creating an "island" community within the host, where migration and emigration is limited and individuals are highly related.

In addition to direct development, animals inhabiting the body of another animal, in a non-parasitic relationship, can develop behavioural traits specifically adapted to living within the host species. For example, alpheid shrimp frequently live in high density, multigenerational populations in tropical sponges (Pearse 1932, 1950, Rutzler 1976) and exhibit eusociality (Duffy, 1996; Duffy, 2000), where overlapping generations co-exist and distinct altruistic behaviour resulting in cooperative care of young (Wilson 1971). Similar societies exist in the terrestrial colonies of ants, termites and bees. Duffy et al. (2000) hypothesize that the evolution of social structure and cooperation of shrimp within the sponge is an adaptive response to competition for limited habitat. In this case, habitat provision by biological structure promotes both defence of and competition for space. Comparison of amphipod interactions showed those living within a fast growing, branching sponge occurred at high densities with quick dispersal following emergence from the female brood pouch and amphipods living within the longer-lived ascidian exhibited intrasexual competition, territoriality and extended parental care (Thiel, 2000). Thiel (2000) concluded that direct development and extended parental care developed due to longevity and stability of the ascidian host.

While there is limited information on the larval stages of many of the animals hosting associated communities, the organisms discussed in this review tend to have multiple modes of reproduction (Fell, 1979) including brooded, lecithotrophic larvae with limited dispersal distance which have been suggested as mechanisms to increase survivorship in clonal organisms (Jackson 1986). Lindquist and Hay (1996) examined the

palatability of larvae of several tropical species of sponges, corals, hydroids, ascidians and bryozoans and found that species with large, conspicuous larvae are avoided by bottom feeding fishes. The significance of reproductive mode and larval survivorship of hosts in relation to community establishment is the tendency of larvae to settle near parent animals hence creating patches of habitat for associated species. This leads to the establishment of persistent habitat structure which can influence the evolution of direct development in associated species. Scott (1987) found that the most abundant coral species were among those most frequently inhabited by associated fauna, indicating that reproductive success and longevity in the host is mimicked by associated species.

As host species provide habitat and nursery areas for associated fauna, the behaviour of associate species can similarly improve the survivorship of the host. Crustacean associates living within the polyp tentacles of the tropical coral *Pocillopora* sp., have been observed defending the coral against predation by echinoderms (Glynn, 1976). Crustacean and echinoderm commensals living within sponges often act as "cleaners" of the sponge surface and canals, removing particles and maintaining water flow, thus facilitating host feeding and broadcast spawning activity (Hendler, 1984). The consequences of living within a host species can also involve trade-offs, for example, as the densities and relatively sedentary life styles of host-specific shrimp can make them vulnerable to disease and parasites. For example, parasitism of synaphelid shrimp by isopods was ~15% higher than that of free living shrimp (Duffy, 1992).

While many associates appear adapted to live within or on another animal, there are relatively few obvious examples of morphological adaptation to living within a host. One of the better studied examples is the reduction in gill numbers, reduced exopods and loss of

spination on all body parts in the stenopod shrimp *Spongicola japonica* which resides within deep-water glass sponges, predominantly of the *Euplectella* genus (Saito and Takeda 2003). The filtration activity of the sponge wall removes microorganisms and potential foulers from the water column and renders grooming appendages useless within the sponge walls. In contrast, shallow-water, free-living members of the Spongicolid family have retained spination and grooming appendages (Saito & Takeda, 2003)

The relationships between associates and their hosts can result in both positive and negative interactions for the associated or the host species. Regardless of the interaction, each contributes to the functioning of the community and creates something greater than the host animal itself or the associates without the host. Habitat engineering by ascidians, bryozoa, corals, hydroids and sponges results in integrated communities that are subject to the forces of evolution. These forces can manifest themselves through life history strategies or adaptations in behaviour or morphology that facilitate the maintenance of the community.

2.5 Conclusion

This is the first review of the communities associated with the habitat structure provided by ascidians, bryozoans, corals, hydroids and sponges and confirms that these host animals form important marine habitat. All of these taxa have the ability to influence species richness and community structure in the surrounding ecosystem through indirect interactions, be they a result of a particular behaviour or due to their emergent morphologies. This review confirms that the physical structure of these organisms provides

significant habitat for a wide range of species, across a range of latitudes, from the intertidal to the deep-water. Corals and sponges are well studied and known to host a variety of fauna and the inclusion of ascidians, hydroids and bryozoans as hosts broadens the consideration of biological habitat and its role in maintaining marine diversity.

Many factors contribute to the differences between host groups, including but not limited to host morphology (Koukouras et al., 1996), depth (Fielding et al., 1994), bottom substrate (Cinar et al., 2002, Santucci 1922), seasonality (Biernbaum, 1981, Davis & White, 1984, Lorz, 2001) and secondary metabolite production (Betancourt-Lozano et al. 1998). Population density of the host species has also been shown to influence dominance patterns of associated fauna of sponges (Duarte & Nalesso 1996) and ascidians (Monteiro et al., 2002). Research on the habitat value of epifaunal species in the deep-water is clearly needed. Examination of brad scale patterns of diversity of these associated communities reveals contrasting patterns with species living in non-biological habitats. The unimodal relationship with latitude suggests that symbiosis and species dominance in the tropics results in limited niche availability. Despite the broad pattern of decreased species diversity with latitude for a wide range of taxa, studies that examine whole community patterns with latitude have not found the latitudinal decrease for all species in the community (Virnstein et al. 1984, Buckley et al. 2004) and unimodal patterns have been found for other marine taxa {Angel, 1997 #6; Rutherford, 1999 #113; Worm, 2003 #32; Hillebrand, 2004 #126; Tittensor, 2010 #741}. The decrease in species richness, number of individuals and Shannon-Wiener diversity of associated communities with depth can only be confirmed or disputed with increased research of structural species in the deep-water. Regardless of the pattern of diversity, biological hosts will contain different species complexes than those

found in soft sediment or chemotrophic environments, and hence contribute to the functional diversity of the deep-water. While host volume is a factor in determining species richness and diversity, inter- and intra- specific interactions within the host, as well as host morphology and defence mechanisms can offset the advantages afforded by spatial extent of the host animal.

The concept of ecosystem engineering, like "keystone species" or "apex predators", allows ecologists and managers to assign an ecological value to species or species complexes, relative to other species and to predict the possible effects of the loss of that species. If the goal is to maintain marine biodiversity, then clearly the habitat provided by structural marine invertebrates should be considered. Increasingly, managers must decide what species are most important to maintaining ecosystem function and biodiversity and where species redundancies exist (see Karieva & Levin, 2003 for examples). Threats to sessile invertebrate populations include, but are not limited to, coral reef bleaching {Bellwood, 2006 #742; Hughes, 2003 #129; Pandolfi, 2003. #163}, direct harvesting, particularly in the case of ascidians (Fairweather, 1991) and for some species of sponges, and on a broad scale for all sessile invertebrates, removal and destruction by industrial fishing activity {Watling, 1998 #744; Turner, 1999 #348; Thrush, 2002 #91} Bioprospecting for potentially useful pharmaceuticals is also a potential threat to marine invertebrates, specifically those that produce secondary metabolites. Newman (1989, in Kamaltynov 1993) claimed that the loss of a single species of tropical tree can result in the extinction of up to 30 associated species. Given the species richness and diversity associated with the animals discussed here, the same analogy can be made for marine

invertebrates. The failure to consider the effect of host extinction on associated species can result in a vast underestimation of potential biodiversity loss (Pin Koh et al., 2004).

Table 2.1. Ecosystem engineering properties of ascidians, bryozoans, corals, hydroids and sponges.

Organism	Activity	Affect on physical environment	Source
Allogenic Engin	eering Activities		
Coral	Mucous production	Creation of particle aggregates and subsequent sedimentation and nutrient transfer to the benthos; aggregates can provide between 10-20% of the organic carbon to coral reef sediments	Wotton 2004, Wild et al. 2004
Clionid sponges	Bioerosion of calcareous substrate	Creation of coral rubble and alteration of coral structure, carbonate removal rates are estimated at 0.2-24.0 kg/m²/yr, providing support for other coral species	Wulff, J. and L.W. Buss 1979, Wulff 1999
Hydroids, sponges and corals	Egestion of fecal matter and prey debris	Alteration of sediment structure and content, creating habitat for colonization by bacteria and deposit feeders. Deposition of faecal pellets by sponges is estimaged to contribute 0.5 and 2.0 mg C/m²/d in northern waters.	Vopel 2001
Sponges	Sloughing of external spongin and spicules	Deposition of spicules and associated fauna on the sediments, alteration of sediment structure	Barthel and Wolfrath 1989
Autogenic Engi	neering Activities		
Ascidians, bryozoans, corals, hydroids and sponges	Provision of habitat for other species within	Creates additional physical structures and substrate, enhancing niche availability	Castilla et al., 2004, Kligaard 1995, Bradstock & Gordon 1983,

Table 2. Continued.

Activity	Affect on physical environment	Source			
Skeletal deposition upon death of live tissue	Alters substrate and provides habitat for other species	Jensen and Frederiksen 1992, Barthel 1992			
Creation of topographical complexity in the	Provides refuge from predation	Lindholm et al. 1997, Stoner & Titgen 2003			
benthic environment	Encourages settlement of other species Affects small scale current	Smith & Witman 1999			
	patterns	McKinney & Jaklin 2001			
	Affects sedimentation patterns	s Conway et al. 1991,			
	and processes	Hovland et al. 1994, Kenyon et al. 2003			
	Skeletal deposition upon death of live tissue Creation of topographical complexity in the	Skeletal deposition upon death of live tissue Creation of Provides refuge from topographical complexity in the benthic environment Encourages settlement of other species Affects small scale current patterns Affects sedimentation patterns			

Table 2.2. Diversity measures for associated faunal communities of ascidians, bryozoa, corals, hydroids and sponges. Data calculated or obtained from sources is listed in Appendix 1.

Index		Ascidians	Bryozoans	Corals	Hydroids	Sponges
Species Richness	No. of Studies	6	2	8	3	65
	Range	59-212	25-92	46-309	8-155	1-184
	Mean(SD)	102 (116.8)	41.7 (47.4)	123.6 (101.1)	84 (73.6)	38.7 (41.8)
Shannon Weiner Diversity (H')	No. of Studies	6	2	8	2	58
,	Range	3.7-5.8	1.8-2.3	2.36-5.5	1.55-2.65	0.13-5.19
	Mean(SD)	4.54 (0.67)	2.06 (0.36)	4.26 (0.92)	2.1 (0.78)	2.35 (1.36)
Fishers Alpha	No. of Studies	5	2	2	2	51
-	Range	10.52-16.85	1.12-2.07	12.5-27.8	0.79-2.46	0.54-67.63
	Mean	12.32 (2.55)	1.6 (0.67)	20.15 (10.8)	1.6 (1.18)	10.6 (14.9)
Species Evenness (J')	No. of Studies	5	2	6	2	43
, ,	Range	0.63-0.91	0.64-0.77	0.39-0.76	0.51-0.63	0.004-0.96
	Mean(SD)	0.76 (0.101)	0.71 (0.091)	0.66 (0.13)	0.57 (0.085)	0.61 (0.24)
No. of	No. of Studies		_			
Species/L	Dange	6	2	4	na	47
	Range	0.4-4053	4.46-38.09	3.21-43.6		0.048-227.64
	Mean(SD)	2.25(1.75)	21.27(23.77)	20.12(21.44)	na	16.59(40.023)
No. of Individuals/	No. of Studies					
L		3	2	3	na	43
	Range Mean(SD)	13.47-76.37	39.7-101.2	30.28-664	na	1.24-5683 489.9(1079.2
	, ,	36.4(34.7)	70.5(43.48)	261(350.03)	na	3)

Table 2.3. Summary of Generalized Linear Model (GLM) results for species richness (SR), species diversity (H' and Fisher's Alpha) and species evenness (J) as a function of number of individuals, latitude, depth and host volume for ascidians, bryozoans, coral, hydroids and sponges.

D	Б. 1				D: :		D 4				Analysis of
Response Variable	Explanatory Variable	Offset	Distribution	Link	Dispersion Parameter	Intercept	Parameter Value	SE	df		Deviance p-value
Variable	Log	log	negative binomial	Link	1 ai ainetei	пистери	v aruc	SL	uı	varue	p-value
SR	Individuals/L Log		(theta=1)	log	1.56	-0.95	0.65	0.099	47	6.57	0.000002
J'	Individuals	Tot.vol	quasi	logit	0.76	0.87	-0.09	0.025	62	-3.68	0.00056
		log	negative binomial								
SR	Latititude	Tot.vol	(theta=1)	log	2.96	-0.95	0.185	0.0556	53	3.32	0.937
	Latitude ²	log	negative binomial				-0.0021	0.0006	53	-3.45	0.00074
Individuals	Latititude	Tot.vol	(theta=1)	log	4.16	4.31	0.1279	0.067	46	1.9	0.013
	Latitude ²						-0.0016	0.0007	46	-2.25	0.008
Η'	Latititude	None	Gamma	log	0.298	0.81	-0.026	0.0089	48	-3.02	0.034
	Latitude ²						0.00034	0.0001	48	3.53	0.0002
Fishers											
Alpha	Latititude	None	Gamma	log	1.12	1.9	0.007	0.009	40	0.78	0.43
J'	Latitude	None	quasi	logit	0.047	-0.966	0.025	0.0123	66	2.04	0.78
	Latitude ²						-0.0002	0.0001	66	-2.04	0.036

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											Analysis
Response	Explanatory	,			Dispersion		Parameter			t-	of Deviance
Variable	Variable Variable	Offset	Distribution	Link	Parameter	Intercept	Value	SE	df		p-value
G.D.	5 1	Log	negative binomial		1.05		0.000	0.0001			0.000
SR	Depth	Tot.vol	(theta=1) negative binomial	log	4.96	2.75	-0.0026	0.0001	53	-1.36	0.0028
Individuals	Depth	Tot.vol	(theta=1)	log	4.6	6.54	-0.004	0.001	50	-2.47	0.05
H' Fishers	Depth	None	Gamma	log	0.31	0.335		0.00014	74	2.21	
Alpha	Depth	None	Gamma	log	18.41	2.26	0.0003	0.0007	59	0.52	0.6
J'	Depth	None	quasi	logit	0.049	0.506	0.0002	0.0005	66	0.51	0.9
			negative								
SR	Log Volume	None	binomial negative	log	1.35	3.64	0.147	0.077	54	1.91	0.03
Inidividuals	Log Volume	None	binomial	log	3.13	7.127	0.4337	0.172	51	2.52	0.05
H' Fishers	Log Volume	None	Gamma	log	0.33	0.457	-0.02	0.012	44	-1.65	0.37
Alpha	Log Volume	None	Gamma	log	1	1.21	0.234	0.07	41	3.32	0.03
J'	Log Volume	None	quasi	logit	1.99	0.3693	0.0036	0.088	44	0.041	0.93

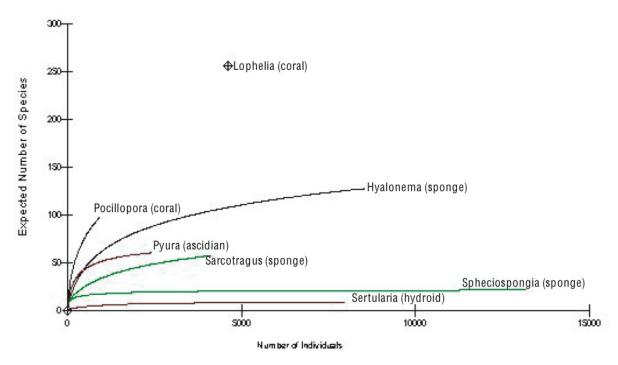


Figure 2.1 Rarefaction curves for selected communities for a variety of host species as extracted from the published literature. Corals host the highest diversity of species, while the deep-water sponge, *Hyalonema* containing a more diverse community than several shallow water, tropical hosts. The barrel sponge, *Spheciospongia vesparia* and the hydroid *Sertularia operculata* contained communities highly dominated by crustaceans.

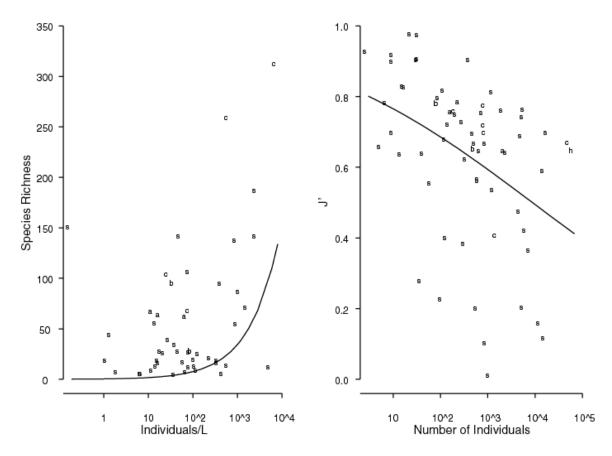


Figure 2.2 (a) Species richness vs the number of individuals per liter of host organisms. The line is fit using the median of the offset of log (volume of host) p<0.0001). (b) Relationship between species evenness (J') and the number of individuals associated with a particular host species (p<0.0001). Model parameters and sample sizes are listed in Table 3. Data sources are included in Appendix 1.

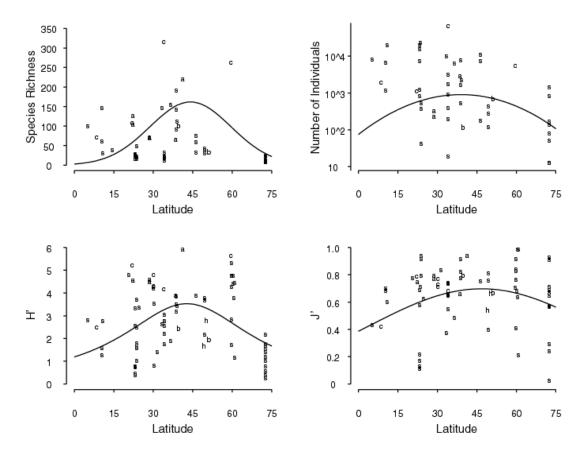


Figure 2.3. Latitudinal patterns of species richness (a), number of individuals per host community (b) and species diversity (H') (c) and species eveness (J') (d) of associated communities of ascidians, bryozoans, corals, hydroids and sponges. Lines indicate second order polynomial fits, with the quadratic term significant (p<0.05) in all cases. See Table 2.3 for parameter estimates and Appendix I for data sources.

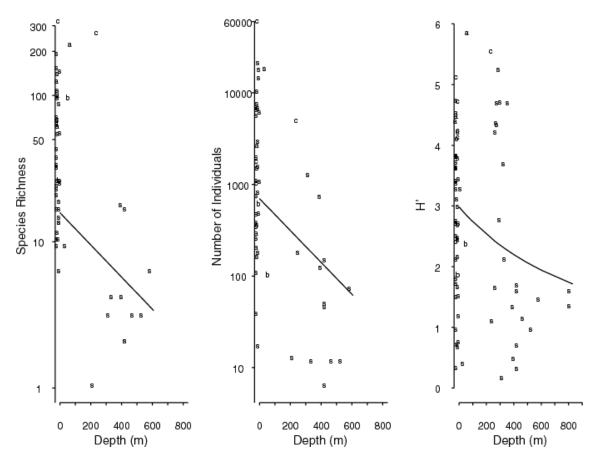


Figure 2.4 Species richness (SR) (a), number of individuals (b) and species diversity (H') (c) of communities associated with acidians, bryozoans, corals, hydroids and sponges. Lines indicated fitted generalized linear models. The effect of depth is significant (p < 0.05) in all cases. Parameter estimates are listed in Table 2.3 and data sources in Appendix I.

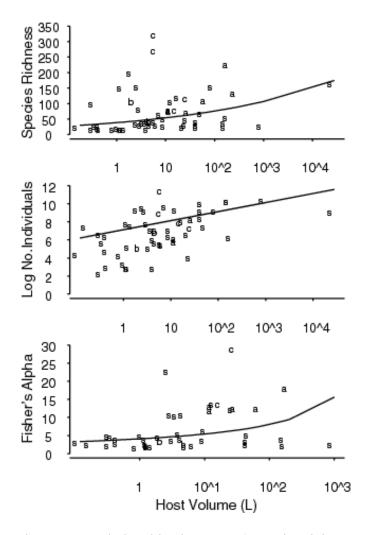


Figure 2.5. Relationships between a) species richness, b) number of individuals and c) Fisher's Alpha with host volume. Lines are fitted to generalized linear models and all relationships are significant (p = 0.05). Parameter estimates are included in Table 3.

Chapter 3

Distribution and Ecosystem Function in Deep-water Structural Species, Based on Local Ecological Knowledge: Implications for Conservation and Management

3.0 Introduction

"When targeting redfish, we'd get a tonne of Russian Hats. It must have been good feeding ground." Respondent #20.

Fishermen's knowledge of the marine environment has been recognized as a fundamental and important component of marine management (Neis & Felt, 2000) (Berkes et al., 2001; Murray et al., 2006). As fishing involves going to sea throughout the seasons, year in and year out, and adjusting to environmental change, fishermen are often able to recognize and describe spatial and temporal ecological patterns that have occurred over comparatively long periods of time, particularly regarding their target species (Hutchings & Ferguson, 1999; Hutchings & Ferguson, 2000; Wroblewski et al., 2005; Boudreau & Worm, 2010). The body of information held by fishermen about the marine environment fits within the knowledge system commonly referred to as Local Ecological Knowledge or LEK. While there is no universally accepted definition of LEK, it is generally accepted to encompass three elements, including "a shared system of knowledge about environment and ecosystem relationships, developed through direct experience with a specific physical setting and transmitted between or among generations" (Davis and Ruddle 2010 and references therein). In areas where there is little natural science research or where explanations provided by natural science are lacking, LEK can be collected to help fill these gaps.

While the collection of fishermen's ecological knowledge in the Northwest Atlantic has focused largely on commercial species, and the Atlantic cod (*Gadus morhua*) fishery in particular

(Hutchings & Ferguson, 2000; Ames, 2004; Wroblewski et al., 2005; Murray et al., 2006), fishermen also hold valuable knowledge about non-commercial species collected incidentally in fishing gear. In their efforts to increase catches or find new grounds, fishermen are frequently the first to reach areas that have not been fished before, and where scientific research has yet to occur, and hence have first-hand information of both commercial and non-commercial species caught in fishing gear. Where research surveys have historically failed to collect information on non-commercial species, fishermen's knowledge can be collected to better understand ecological phenomena, and in some cases lead to conservation efforts (Martin, 2005).

As ecosystem-based fisheries management evolves from theory to practice, a more thorough understanding of the marine ecosystem is necessary. Because most fisheries science relates primarily to commercial species, there are gaps in our understanding of how fishing activity can affect the ecology of many marine species. Non-commercial species have historically been undersampled. For example, systematic sampling of incidental catch in the inshore scallop fisheries surveys in the Bay of Fundy occurred only twice in 30 years (Kenchington et al., 2007). The need to understand the impacts of fishing on marine diversity in Canadian waters, in addition to the contribution of benthic communities to fisheries productivity and population recovery, has highlighted the relative lack of data on cold-water corals and sponges in particular. As inshore fisheries have been depleted and new areas and species sought, fishing activities have necessarily expanded to offshore and deeper waters (Roberts, 2007). Prior to the late 1990's, information on cold-water corals in Canadian waters was reported only in natural history observations (Goode, 1887; Whiteaves, 1901) and in mid-century seafloor maps produced by Russian fisheries investigations through benthic grab samples (Litvin & Rvachev, 1963). Fishermen's concern and descriptions of "trees" being caught in the bottom trawl and bottom long-line fishery off Nova

Scotia resulted in the first documentation of fishermen's knowledge being used to better understand both the nature and spatial distribution of these organisms. Initial interviews and subsequent literature reviews lead to the first species list of cold-water corals found in the Northwest Atlantic and the first mapping of corals off the coast of Nova Scotia (Breeze, 1997). Fishermen's information has been used in mapping coral beds in the Northeast Atlantic, where fishermen were instrumental in directing scientists to particular concentrations of cold-water corals (Fossa et al., 2002).

Unlike cold-water corals, marine sponges are distributed much more ubiquitously on the seafloor and consequently the collection of information on sponges in the Northwest Atlantic has had a more detailed history, primarily due nearshore investigations (Proctor, 1933; De Laubenfels, 1949; Hartman, 1958), in addition to collections made in early faunal inventories collected through dredge sampling (Lambe, 1896, 1900). In other regions, fishermen's information has lead to scientific research in specific areas noted to have high sponge abundance. For example, fishermen's descriptions of "cheese bottom" or "ostur" lead directly to scientific investigations of the marine sponge fauna of waters surrounding the Faroe Islands (Bruntse & Tendal, 2001).

In Canada, there has been significant progress over the last decade to better understand the distribution of cold-water corals and subsequently efforts have also been made to introduce ecosystem-based management practices through the development of the Sustainable Fisheries Framework (DFO, 2011). This Framework contains policies on the precautionary approach, forage fish, and protection of sensitive benthic areas, however these have yet to be put into practice (D. Osbourne, DFO Fisheries and Aquaculture Management, Ottawa, Ontario personal communication) and the impacts of fishing gear on the seafloor continue as unmanaged impacts on the marine environment. Marine ecosystem science is moving beyond a single-species approach, partially as a response to the need to better understand the impact of biodiversity loss on marine ecosystem

function (Stachowicz et al., 2002; Worm et al., 2006) and, more specifically, to better manage human impacts on the marine environment upon which humans depend for a wide range of ecosystem services (Palumbi et al., 2008). Understanding how resource users perceive the value of diversity can be of use in fostering stewardship and in gaining support for conservation initiatives, particularly those that require a change in harvesting behaviour.

Studies that have included fishermen's knowledge in the Northwest Atlantic have typically endeavoured to fill in missing information on the ecology and / or population trends of commercial species (Hutchings & Ferguson, 1999; Ames, 2004; Davis et al., 2004; Wroblewski et al., 2005; Boudreau & Worm, 2010), but have not investigated fishermen's knowledge or perception of the value of marine diversity in providing fisheries resources. The ecosystem function of cold-water coral and sponges is becoming better understood by scientists (Stone, 2006; Levin & Dayton, 2009; Buhl Mortensen et al., 2010), and the inclusion of fishermen's information into this framework could enhance conservation efforts.

This chapter presents the results of fisherman's interviews on the distributions of cold-water corals and sponges in the Northwest Atlantic, building upon the work by Gass & Willison (2005) on the former group of species. Fishermen's information on deep-water sponge populations in the Northwest Atlantic is presented here for the first time. The purpose of reporting data on both corals and sponges here is to include information on the function of these structural species, as perceived by fishermen. The role that fishermen's knowledge can play in providing baseline information for conservation purposes is discussed in the context of involving resource users in management decisions.

3.1 Methods

Information on the locations of cold-water corals and sponges was collected through a series of interviews with fishermen in Nova Scotia, New Brunswick, and Newfoundland. An effort was made to cover as much geographical territory as possible to ensure that an adequate sampling of fishing practices and experiences was included (Figure 3.1).

Interviews were collected during two different time periods, with reports included from 27 fishermen interviewed between May and July 1998 and 36 fishermen interviewed between June and November 2001 for a total of 63 (2 interviewees identifying themselves as fisheries observers).

Interview participants were chosen using purposive sampling, where fishermen were selected based on the number of years they fished and the types of gear fished, to ensure that their breadth of experience would allow them to respond to the questions. We then asked those individuals to provide the names of additional fishermen who might be willing to be interviewed. This method is referred to as "snowball" sampling (Babbie, 1992) and has been found to be a useful method to collect information in instances where the subject matter may be sensitive (Browne, 2005). Given that we were asking fishermen to identify vulnerable marine species, for which their only experience would have necessarily been in the destruction of these organisms, "snowballing" was useful in ensuring that the people we contacted would be willing to be interviewed. To offset any potential bias introduced by snowball sampling, where participants with similar opinions might be selected as a result of peer recommendations (Maurstad 2000), names of potential interviewees were also obtained from the Maritime Fishermen's Union (MFU), the Eastern Fishermen's Federation (EFF) and the Fishermen and Scientist Research Society (FSRS) in Nova Scotia and the Fish Food and Allied Workers Union (FFAW) in Newfoundland,.

The selection of participants focused on vessel masters who had been fishing with bottom gears for at least 10 years. Given the goal of the present study to obtain information on temporal changes in the abundance of corals and sponges, we targeted fishermen having at least one decade of experience. We also made an effort to interview retired fishermen and those nearing the end of their careers, based assumptions that these fishermen have information collected over a longer time period; and would be more likely to share location-specific data..

An initial questionnaire was developed for the first set of interviews in Nova Scotia and New Brunswick and tested with three resource users to ensure that we were able to collect the information needed and that the questions were clear. We revised the questionnaire according to the feedback received. The information obtained from these interviews was first presented by Fuller & Cameron (1998); these interviews were re-sampled for information that pertained to the aims of the present study. The questions were modified for the second set of interviews in Nova Scotia and Newfoundland, given that the aims of each study were slightly different. Prior to conducting interviews in Nova Scotia and Newfoundland, questionnaires were approved by the Ethics Committee of Dalhousie University (interview questions are included in Appendix 1). In all interviews, participants were required to sign a consent form that clearly explained the goals of the study and the purpose for which the information was being collected.

A semi-directive interview technique was used, as described by Mailhot (1994) and by (Huntington, 1998, 2000) This is an effective way of gathering specific information that allows for the inclusion of additional information that is not necessarily requested directly but may be considered important to the interviewee. During the initial review of interview questions by fishermen, it was clear that most fishermen did not want to be digitally recorded. Interviews were intensive and directed, lasting between half an hour and four and a half hours. The length of the

interview was dependent partly on whether or not the fisherman's wife was present and on the level of comfort the fisherman felt with the questions being posed. A basic questionnaire was followed, with additional information and comments not related to the questions directly also recorded.

Information or responses were often provided relating to a question further along in the interview and, as such, interviews and the timing of questions were modified accordingly.

Each interview began with several short-answer questions regarding the fishing history and experience of the participants. These questions were then followed by questions about deep-water corals and sponges to determine whether the participants were in fact familiar with these organisms and if they recognized particular species or types. Field guides and photos of species, where available, were shown to help determine species identities, particularly for corals. At the time when the interviews were conducted, photographic examples of deep-water sponges did not exist. Finally, participants were asked about their fishing grounds, the areas in which they had caught structural and target species, and the types of gear they had fished. To obtain spatial information, the appropriate nautical chart was chosen and the participant was asked to mark the locations of coral and sponge catches on the chart. Participants were also asked about any changes they had observed in the locations and abundance of coral and sponges they had caught throughout their careers.

The majority of interviews took place in fishermen's homes, but in several cases the interview took place on the wharf, and in one case on a fishing vessel. In several interviews, fishermen's wives were present or nearby and would clarify information or offer additional detail. As all interviews were recorded by writing down fishermen's responses, we endeavored to have two people present during the interviews; one individual would ask questions for half the time and the other recorded and roles were switched half-way through each interview. Following the interview,

we discussed our written comments and amended them when perceptions of the interview were different between interviewers. Interviews were then transcribed from notes immediately.

In compiling information for this study, the interviews recorded by Fuller and Cameron (1998) were re-sampled for information on specific locations of sponges and corals in addition to fishermen's information on changes to the benthic environment over time. Detailed notes for all interviews were compiled and organized by theme, with information always linked to the original interviewee.

3.2 Results

3.2.1 Selection of Interview Participants

Not all fishermen who were contacted or recommended by peers as good candidates were interviewed. In Newfoundland, where interviews were collected over a one-week period, 13 fishermen were interviewed out of 41 contacted. More fishermen were interviewed in Nova Scotia where 52 were interviewed out of 86 on the contact list. Only nine fishermen were contacted in New Brunswick, primarily because the focus area for those interviews was the Bay of Fundy and Scotian Shelf, with the goal of covering as much of that area as possible, hence no fishermen were interviewed who fished in the Gulf of St. Lawrence, although this area is also know to have both corals and sponges as part of the benthic fauna found in the area (Brunel et al., 1998). In total, four fishermen from New Brunswick were interviewed, resulting in a total of 67 interviews.

3.2.2 Fishing History: Gear Type, Target Species and Area Fished

The majority of fishermen interviewed had spent between 20 and 40 years in the fishery and their mean age was 33.7 yr (+/- 1.2 SD) (Figure 3.2). Fifteen fishermen possessed more 40 years of

experience and eight had been fishing for less than 20 years. Almost all participants who had spent more than 20 years in the fishery started as inshore fishermen, targeting commercial species within 12 miles of shore. Forty-five percent of the interviewees had fished bottom longlines at some stage of their career, with gillnets, lobster traps and otter trawls being the next most frequent gear types (Figure 3.3).

As inshore fisheries declined, particularly in the late 1980's and early 1990's, fishermen either continued to fish groundfish and moved to offshore waters, switched target species from groundfish to invertebrate fisheries and stayed on the inshore grounds, or switched species and moved to offshore waters. Fishermen in Nova Scotia and New Brunswick who had targeted groundfish early in their careers switched to lobster, crab and scallop. Fishermen interviewed in Newfoundland who had targeted groundfish switched to shrimp, crab and turbot after 1992. While fishermen in Nova Scotia remained in the same general fishing area, but switched species, fishermen in Newfoundland targeted new species in areas where they had not previously fished, thus expanding the range of their fishing experience, and hence knowledge on coral and sponge locations. Among all fishermen interviewed, those who had fished in offshore waters more frequently encountered corals and sponges than those who had fished exclusively in inshore waters. Most fishermen did not fish outside the 200-mile limit on a regular basis.

Fishermen who were active fishermen at the time of the interviews generally fished more than one species, although historically they had fished an even greater range of species across a greater range of fishing seasons. Most fishermen identified groundfish as being their major target species during at least one stage of their career (Figure 3.4a). When referring to groundfish, fishermen generally also referred separately to cod (*Gadus morhua*) and haddock (*Melanogrammus aeglefinus*) and sometimes pollock (*Pollachius virens*) (Figure 3.4b). When mentioning a specific

species, fishermen referred most often to cod, frequently in the past tense. Fishermen fishing off Nova Scotia reported a greater diversity of fish species targeted throughout their careers, while fishermen in Newfoundland referred almost exclusively to cod and turbot (*Reinhardtius hippoglossoides*) as their targeted groundfish.

3.2.3 Knowledge of Distribution of Corals and Sponges

Seventeen percent of fishermen had not seen or recognized corals during the course of their fishing career. Fishermen who did not see corals either fished out of New Brunswick, and mainly in the Bay of Fundy, or were inshore fishermen targeting lobster (*Homarus americanus*). Several fishermen referred to "coral bottom", but this was identified in shallow water and was most likely the calcareous red algae, *Lithothamnion* sp. Forty-one percent of fishermen interviewed did not see sponges, with the majority of these individuals fishing out of Cape Breton in Nova Scotia. Fishermen who fished with longlines, traps or gillnets were less likely to report collecting sponges.

Fishermen provided locations of where they caught corals and sponges by the description of specific area or name, and by locating the areas of catches on nautical charts provided (Figure 3.5-3.7, Table 3.1 (corals) and Table 3.2 (sponges). Corals are found from Georges Bank to off of Cape Chidley in Labrador, with the majority of locations identified along the continental shelf break or edges of fishing banks (Figure 3.5). Fishermen were able to identify specific species of coral if asked, by using photographs provided and Gass & Willison (2005) provide detailed information on where specific species of corals were located according to fishermen's interviews. Six species or species groups were recognized, including *Paragorgia*, a large gorgonian coral, which was frequently referred to as bubble gum coral; *Acanella*, a smaller gorgonian found typically in muddy

substrate; *Flabellum*, or "cup coral"; *Keratioses*, or gold band coral; *Paramuricea*; popcorn coral; and *Primnoa* (Table 3.1). Fishermen also simply identified corals as trees and "strawberry bottom" was mentioned in the interviews and likely refers to the soft coral, *Gersemia rubiformis*, found in inshore locations.

Fishermen identified areas of sponges, both on the shelf in the Scotia Fundy area and along the edges of the banks in the Newfoundland Labrador area (Figure 3.7). When identifying specific locations of sponges on charts, fishermen noted "Russian Hats", which is the glass sponge, Vazella pourtalesi, (see Chapter 5) and distinguished between sponges and glass sponges in general. "Glass sponges" as a specific group were identified by fishermen in Nova Scotia only and were located on charts by fishermen in the Northeast Channel, the Emerald Basin / Sambro Bank area and on the Stone Fence at the entrance to the Laurentian Channel. Of the 16 fishermen who reported seeing sponges off Nova Scotia, six specifically mentioned "Russian Hats". Fishermen in the fishing off of Cape Breton spoke of "finger sponges", fitting the common description of *Haliclona oculata* and *Isodicyta* spp. Those fishing in the Bay of Fundy with scallop dredges reported sponges described as the "bread crumb sponge" and the "mattress sponge," which are thought to be *Halichondria* panicea and Mycale lingua, respectively. These sponges are known from Nova Scotian waters, and in the Bay of Fundy in particular, with identities confirmed in faunal surveys of scallop by catch in the lower Bay of Fundy (Caddy et al., 1970; Fuller et al., 1998). Fishermen in New Brunswick (both of whom fished with scallop gear) gave conflicting statements with one fishermen saying that he captured sponges in every tow and another stating that he captured sponges only occasionally. In Newfoundland, fishermen described sponges coming up in "sheets", which is similar to trawl survey collections of the glass sponge Asconema foliata (see Chapter 4). Fishermen also described "ball"

sponges along the Labrador shelf, which are most likely the demosponge, *Geodia* spp. (Table 3.2) (Chapter 4).

3.2.4 Ecological Observations of Corals and Sponges

Fishermen targeted different types of fish when hauling in corals and sponges (Table 3.1 and 3.2). In Nova Scotia, fishermen reported catching halibut in the "trees", particularly on the Scotian Shelf, on the Stone Fence and in the Sable Island Gully. "Trees" were also noted as being important for pollock. In Newfoundland, corals were caught in the turbot fishery, both by gillnets and otter trawls. One respondent linked the presence of fish in corals to "eyebait", i.e., the shrimp (*Pandalus* spp.) that are often associated with cold-water corals.

The presence of Russian Hats on the Scotian Shelf was linked to the targeting of redfish (Sebastes spp.) and pollock (Pollachius virens). When asked about the smell or texture of sponges, fishermen gave specific answers which can be used to identify sponges to the genus level. For example, fishermen noted a "garlic" smell, which is often attributed to the genus Suberites.

Fishermen did not make any specific reference to the importance of sponges for a particular target species, although one fisherman suggested the importance of "havens" created by sponges and rockweed (Fucus vesiculosus). These collective observations suggest that fishermen are potentially able to identify ecological features that can assist in identifying species in addition to recognizing the importance of "structure" for ecological functions, such as the provision of food and habitat.

3.2.5 Fishing Impacts and Changes to the Marine Environment

Among the more sensitive aspects of the interviews were those that pertained to fishermen's observations of changes over time, their thoughts on the importance of the seafloor, and specific

conservation concerns they might hold. For this reason, we attempted to interview retired fishermen to ensure could be more openness about perceptions of fishing impacts, as there is a tendency in the fishing communities to attribute environmental damage to gear types that are fished by others. Several interviewees, in fact, did not want to discuss conservation concerns or perceptions about changes over time. One interviewee in particular said that he did not encounter corals at any time during his fishing activity, although he had observed a gillnet on a wharf to be full of small *Acanella*, a species associated with muddy bottoms. He then was willing to speak more about where he found coral, but not about the impacts of fishing.

In response to the question about changes over time, fishermen reported capturing fewer corals and having to move into deeper waters and further offshore (Table 3.3). Only one respondent made a comment about sponges, and he stated that there had been an increase over time. This individual fished in the NAFO Area 4T (Southern Gulf of St. Lawrence) where there has been an increase in sponge over time, according to research trawl surveys (Hughes Benoit, DFO Gulf Region pers. comm.) The move from inshore to offshore water was particularly evident in Newfoundland. Changes in the fishery was conducted were also seen as important, as fishermen noted introduction of computer technology, such as depth sounders and high resolution fish finders, was viewed by two individuals as being a negative development in the fishery as both have meant that fish have fewer places to hide.

Fishermen had conflicting views about the importance of the seafloor to fish populations.

One respondent claimed that the entire seafloor was important, while others noted that it was important for spawning in particular. The "good fishing" in the coral areas was noted, with fishermen returning to these areas year after year, despite losing fishing gear. When discussing impacts to the seafloor in particular, fishermen who had fished with bottom longline gear tended to

blame the otter trawl gear for problems associated with the fishery and damage to the bottom. A few fishermen who had fished with trawl gear also acknowledged the impact of that gear on the seafloor.

Fishermen were wary of discussing conservation measures, as to many fishermen "conservation" meant closing areas to fishing, which was experienced by fishermen in Nova Scotia and Newfoundland following the cod collapse and subsequent moratorium on the groundfish fishery in much of Atlantic Canada. The decline of the inshore fish stocks and subsequent move to offshore has resulted in a shift in traditional fishing grounds and effective closure of areas formerly fished. Nevertheless, fishermen did refer to specific areas that were important for Atlantic cod spawning and areas known for coral abundance when discussing conservation measures.

3.3 Discussion

LEK has increasingly been used to augment natural science and inform management strategies, as large-scale environmental change needs to be understood by policy-makers more rapidly than can be accommodated by the time demanded of scientific research. The majority of LEK research has focused on terrestrial ecosystems with farmer and hunter information being collected far more frequently than that of fishers (Brook & McLachlan, 2008). Interdisciplinary methods, when combined with the natural science information, can be particularly useful in the field of applied ecology, where scientific information must be used to address problems of practical importance, as has been shown in the integration of fisher's knowledge with the design of marine protected areas and marine reserves (Neis, 1995; Scholz et al., 2004). LEK in conservation biology is again equally important as natural science as human impacts are more frequently the greatest

threat to biodiversity. Including a human component in the data collection phase can facilitate the implementation of ensuing management plans (Neis et al., 1999).

3.3.1 Fishermen's Contributions to Sponge and Coral Ecology

We demonstrate the existence of fishermen's information in spatially describing the locations of corals, extending and building upon the data gathered by Breeze et al., (1997) (Breeze, 1997), and report for the first time fishermen's records of marine sponges in the Northwest Atlantic. Fishermen who fished in offshore waters more often reported seeing corals and sponges, and fishermen who fished with bottom-tending gear also were more likely to have seen corals and sponges in their fishing gear. Bottom trawls, dredges, bottom gillnets and bottom longlines are much more likely to encounter and catch epifaunal species than traps (Fuller et al., 2008). Using fishermen's information to examine biogeographical patterns of species distribution provides an important baseline for species and groups of organisms that are both difficult and expensive to study. Our decision to interview fishermen with extensive experience in the fishery meant that we did not interview fishermen who had recently entered the fishery and, therefore, may have had more experience going to new fishing areas, particularly areas in the Arctic. As a result, we collected more historical information on where corals and sponges were caught in the past, and slightly less on current distribution. This was more pronounced in Newfoundland where, until the cod moratorium in 1992, fishing was primarily on the banks, with few vessels fishing deeper than 600 m.

Fishermen were able to identify particular species and the areas and bottom types on which they were found, leading to spatial information on the locations of particular hotspots of coral and sponge abundance. Fishermen's knowledge, at least at the scale it was collected here, does not lend

itself to fine-scale habitat mapping of a wide range of coral and sponge species. Rather, fishermen are able to confirm areas where corals and sponges were caught in abundances that affected their fishing behaviour. Fishermen are also able to identify commercially targeted fish species that prefer complex structural habitat.

Fishermen's observations of the importance of habitat structure, exemplified by the common reference to corals as "trees" is consistent with scientific knowledge where others have found specific associations of fish species with corals (Husebo et al., 2002; Stone, 2006). Fishermen specifically noted that halibut, turbot and pollock were found in corals, while cod was not. In the Northwest Atlantic, Edinger et al., (2007) did not find strong statistical associations of fish with corals, however they used datasets that were not collected simultaneously and relied solely on trawl survey information, which does not allow for *in situ* spatial analyses, such as those completed by Stoner & Titgen (2003). Others have recorded fishermen's information and commercial species associations with sea pens in the Gulf of St. Lawrence (Colpron et al., 2010).

In describing the importance of bottom type in their fishing practices and specifically regarding structural species, fishermen tended to refer to sponges and corals as being more of nuisance, in that they would frequently tear up gear, or have to untangle lines and nets. At the same time, however, fishermen also reported that these areas were where the bigger fish were, particularly halibut and pollock. A limitation to fishermen's ecological knowledge is that they will only know about places where they have fished, and hence the larger scale distribution of structural species or habitat cannot be inferred, unless a broad enough scale of interviewing is done.

3.3.2 Linking Fishermen's Knowledge and Scientific Research

Given the scale, detail and amount of fishermen's knowledge, and the relative difficulty in putting the information into a format where it lends itself to statistical testing, there remains reluctance to use such knowledge in scientific study. However, it is also likely that observations from fishermen have indeed provided the basis for many scientific questions, but that these initial observations have been infrequently recorded or credited, particularly if they were gathered outside of directed information collection. Fishermen's knowledge is generally communicated in informal settings whereas most fisheries scientific information sessions are structured in such a way that the scientists are presenting the information and that the fishermen are asked to comment on what is being presented. There are examples in the Northwest Atlantic where fishermen's concerns about the impacts of one species on another have been specifically tested. Concerns about the impact of white hake (*Urophycis tenuis*) on the recruitment of American lobsters (*Homarus americanus*) in the Gulf of St. Lawrence lead to the design of a detailed scientific study to investigate this implied effect. Subsequent analysis of the stomach contents of white hake revealed that, in fact, very few juvenile lobsters were being consumed (Davis et al. 2004).

In the Northwest Atlantic, with the exception of the collection of fishermen's knowledge following the cod collapse (Hutchings & Ferguson, 2000; Ames, 2004; Wroblewski et al., 2005; Grabowski et al., 2007), arguably fishermen's information on corals has lead to the greatest expansion of a line of scientific inquiry. Following the information collated by Breeze et al., (1997), the first international cold water coral conference was held in 2000 (Willison et al. 2001), which has ultimately resulted in the establishment of a biannual cold-water coral conference. Secondly, following this first meeting, the Canadian government allocated significant research funds over the past decade in support of scientific studies of the corals on the east coast of Canada, which

collectively have increased the knowledge on the distribution and ecology of corals in eastern Canadian waters (Buhl-Mortensen & Mortensen, 2003; Mortensen & Buhl-Mortensen, 2005; Mortensen et al., 2005; Edinger et al., 2007; Wareham & Edinger, 2007; Watanabe et al., 2009; Edinger et al., 2010). Thirdly, fisheries research surveys and observer programs began to record the presence and absence of corals on a regular basis (see compiled results in Kenchington et al., (2010). Fishermen's information has been valuable in locating areas for scientific research on sponges and corals in the Northeast Atlantic as well (Bruntse & Tendal, 2001; Fossa et al., 2002). Likewise, initial interview data presented in this study were used to determine video transect locations of "Russian hat" sponges on the Scotian Shelf with particular target areas on the edge of Sambro Bank, as well as remote-operated vehicle dive locations in the Northeast Channel, during which an active fishermen participated in the 2001 R/V Hudson Research cruise. Records from fishermen, including a sample of "Spiders Hazard", provided the basis of the scientific investigation of the reef forming coral, Lophelia pertusa, on the Stone Fence. Our interviews from Newfoundland formed the basis of a comprehensive research program on deep-water corals in that province Newfoundland and an extensive mapping of research survey and observer records (Edinger et al., 2007; Wareham, 2007).

In both the Northwest and Northeast Atlantic, the information held by fishermen on deepwater corals and sponges preceded the collection of data through scientific research surveys. From their inception in the late 1950's, trawl surveys conducted by fisheries scientists have been limited to quantifying species of commercial concern. As of 2002 and 2003, respectively, research trawl surveys in the Scotia / Fundy Region and the Newfoundland Region have collected and identified coral species. Total biomass of sponges has been recorded in the Southern Gulf of St. Lawrence research surveys since 1986, with some species information being collected since 2005; in the Scotia Fundy Trawl Surveys since 2006 and in the Newfoundland trawl surveys since 1995. Since 2008,

Newfoundland research surveys have collected individual sponge samples for identification (see Chapter 4 for preliminary analysis of that data). Fisheries observer programs began in the late 1970's, with varying degrees of coverage depending on the target fishery and gear type, with systematic reporting of corals in the Newfoundland Fisheries Observer Program since 2004 (Wareham & Edinger, 2007). Since 2010, the Newfoundland Fisheries Observer Program includes photographic information as collected by observers (V. Wareham, DFO Newfoundland Region, personal communication).

3.3.3 Using LEK in Fisheries Management and Marine Conservation

In order to use fishermen's knowledge, management systems need to be established to incorporate this knowledge into fisheries management plans. As fisheries science and management broadens to incorporate an ecosystem approach, fishermen's knowledge should be incorporated into the management process and include fishermen as part of the ecosystem (Martin et al., 2007). Fishermen's information exists within the complex social and ecological network of fisheries and fishing communities (Murray et al., 2006) and as such, can have important contributions to ecosystem based management (Leslie & McLeod, 2007), adaptive management (Berkes et al., 2000) and co-management (Noble, 2000).

As fisheries management plans evolve to take into account ecosystem impacts of fishing, and the impact that the ecosystem itself has on the dynamic nature of wild fish populations, there is a need to incorporate data that have not necessarily been collected by traditional scientific methods. In the oyster dredge fishery in New Zealand, for example, where concerns about impacts of the fishing method on the target population, as well as the seafloor, have been raised, fishermen's information has been incorporated into the fishing plan (Hill et al., 2010). The authors compared recent

fishermen's information to interviews collected from fishermen in the same area and documented by Cranfield et al., 2003). They found diverging views on the impacts of the directed oyster fishery on benthic habitat, as well as the dependence of a healthy oyster population on the health of the complex benthic structure known as "molluk". The reasons for the divergence between the two sets of interviews, were explained partially by a shifting baseline, and partially by a obtaining a more comprehensive view of the fishery, by including both existing and retired fishermen in the interviews. The resulting incorporation of fishermen's information into the fisheries management plan, and subsequent evaluation of that plan lead to the inclusion of fishermen's information, the resolution of a conflict between different viewpoints and in time, perhaps better fisheries management.

In Canada, fishermen's information on the location of benthic species has not been explicitly incorporated into fisheries management, nor has the information collected by scientific surveys of the seafloor, although this information has been used to close areas to fishing activity in the Atlantic (Breeze & Fenton, 2007) and the Pacific (Cook et al., 2008). In some cases, voluntary closures by industry have been instigated as a precursor to a *Fisheries Act* closure (Ardron et al., 2007). Protection of both sponges and corals, and particularly those in the deep-water, has received increasing attention due in large part to international policy developments (specifically the United Nations General Assembly Resolutions 61/105 and 64/72), and subsequent protocols for protecting vulnerable marine ecosystems in areas beyond national jurisdiction (Kuemlangan & Sanders, 2008; FAO, 2009). Individual fishermen's knowledge, however, has not been used to establish protection, as management processes in Canada tend to involve government staff and industry representatives, rather than fishermen themselves. It can be argued that the distance between holding the knowledge

and being able to take part in stewardship processes in an inclusive way has only served to further distance fishermen from conservation initiatives.

The increase in the use of local ecological knowledge, quantified by (Brook & McLachlan, 2008) over the past two decades and across ecosystems is now drawing criticism from social scientists concerned with the lack of standardized methodology (Davis & Ruddle 2010) as well as concerns by conservation practitioners that the collection of information without the involvement of communities at the outset of a particular research question may hamper applied conservation efforts. Natural sciences tend to want to use information collected from resource users as point data, to establish trends or to determine a previous ecosystem state, particularly when scientific information is lacking. The incorporation of resource users' knowledge is often tested against or coupled with additional research data. From a pure information perspective, this does not seem problematic, and in fact fishermen's knowledge has been helpful in establishing scientific hypothesis and filling data gaps. Social scientists tend to insist on the inherent value of local knowledge and that its collection and incorporation into decision-making be used to empower the resource users (Brook & McLachlan, 2005). Likewise, conservation scientists have argued that it is the responsibility of the scientist to use information towards the protection of biodiversity and ecosystems (Noss, 2007).

Here, we have presented important information held by resource users on the distribution of corals and sponges, where the data were used to map concentrations of these organisms for the ultimate purpose of protecting them. It is obvious that information held by resource users has an important place in primary research, particularly in the establishment of baseline information and the formation of hypotheses upon which to test further scientific questions. The relationship of the resource users to the use of their information will change depending upon where along the spectrum of natural science local ecological knowledge is incorporated. Is the knowledge important for simply

identifying biodiversity – or is it important for use in applied science, and in particular conservation science. More recent experience by Copron et al., (2010) indicates that fishermen continue to be willing to share their information on coral distribution in the Atlantic Canadian waters, and appreciated that their opinions were being collected. The information presented here and in Gass & Willison (2005), as well as that in Copron et al., (2010) suggests that fishermen are willing and able to contribute knowledge, data and ideas that can be used in ecosystem-based management, and in particular, the protection of marine benthic habitats.

3.4 Conclusion

In the Northwest Atlantic, fishermen's knowledge has contributed to the initial understanding of distributional patterns of sponges and corals and has been used to further scientific research that has greatly expanded knowledge of benthic structural species. Fishermen tend to have more species-specific information regarding corals, however this could be a result of the fact that they were given an identification guide as part of the interview process. In this study, fishermen were willing to provide information on the role that corals and sponges play in the marine environment, particularly as they related to providing fish habitat. Fishermen are aware of and willing to share information on the impacts their activities have on structural species. Unlike the process of collecting fishermen's knowledge on commercial species, where much has been written regarding the incorporation of this information into management processes, the current practices of ecosystem based management do not lend themselves to the incorporation of spatial information on seafloor species.

Table 3.1. Observations by fishermen of areas where corals were caught and fishermen's perspectives on relationships between corals and commercially targeted species, as well as other marine species observed in the fishing nets.

Participant	Species / Description	Gear /Species	
New Brunswick			
28	There are trees in between Browns [Bank] and Georges [Bank]	otter trawl / groundfish	
Nova Scotia			
2	Trees in the astern and western gully, fished halibut in the trees, the Stone Fence area off Quereau used to be full of trees	longline & otter trawl / groundfish	
4	There used to be coral off Grand Manan	longline / groundfish	
8	When longlining, there were piles of them [trees] on the Stone Fence, also lots in the Sable Island Gully	catch halibut in the gully with the corals	
9	Trees on Georges [Bank] and Browns [Bank]; there is "eyebait" in the coral and the pollock would follow it	otter trawl / groundfish	
11	Corals around the Stone Fence. Lots of gear lost in the corals on the edge of Georges [Bank]	otter trawl / groundfish	
13	Would get trees off Georges [Bank]	otter trawl / groundfish	
15	Used to get a lot of pollock in the trees, we cleaned them up	otter trawl / groundfish	
16	Trees in the North East Channel	longline / groundfish	
17	Trees were off the deep end and in Hell's kitchen	longline / groundfish	
18	Corals are at the east end of Sable Island gully, at 250-300ft, halibut go in the corals for protection	longline / halibut	
20	Trees follow the continental shelf, eastern end of Georges [Bank] and heel of Browns; halibut was good in the coral	otter trawl / groundfish	
21	Trees in the gully, and in hell's kitchen, used to be on Romney's peak, halibut are in the trees	longline / groundfish	
22	Get trees in the Sable Island Gully, just brought on up the other day.	longline / groundfish	
201	Referred to antler corals, doesn't get them anymore	danish seine & longline / groundfish	

Table 3.1. continued.

	G : /B : /:	G 10 ·	
Participant	Species / Description Gear /Species		
203	Observed coral on the back of crabs	trap / crab	
204	" <i>Primnoa</i> " recognized, find it out past the Bay, in by St. Pauls Island	longline / groundfish	
216	Would get trees in the gear when fishing for redfish, but not when targeting cod in shallower water. Also got them when halibut fishing	otter trawl /redfish longline / halibut	
217	Didn't fish in there [Stone Fence area] a lot because the gear got tangled in the coral, but there was good fishing there. Targeting redfish.	otter trawl / groundfish / redfish	
218	Both <i>Primnoa & Paragorgia</i> on the Stone Fence	longline / groundfish	
221	Recognized Paragorgia	longline / halibut gillnet / pollock	
223	Recognized both black coral and <i>Paragorgia</i> , around the holes	longline / groundfish	
224	Recognized Keratoises, Primnoa and Paragorgia	longline / halibut	
225	Colour pale red, orange, (<i>Primnoa</i> , <i>Paragorgi</i> a), <i>Lophelia</i> (only on the corner (Stone Fence), <i>Keratoises</i> Stone fence, saw some in the Gully. Saw <i>Keratoises</i> in the Gulf of St. Lawrence, of Southwest Newfoundland fishing for redfish. Used to save pieces, remembers the gold bands. Also glowed (bioluminescence when it came out of the water).	longline & otter trawl / pollock & halibut	
226	Recognized <i>Lophelia</i> , trees in the Gully and Stone Fence.	longline / halibut	
210	Bubble gum coral along the 50' line, at 400 to 600 fathoms	gillnet / turbot & shrimp trawl	
211	Trees, find them in 150-200 fathoms, off Labrador	longline & gillnets / turbot otter trawl / shrimp	
215	Several species recognized including <i>Paragorgia, Primnoa, Lophelia</i> , black coral and <i>Acanella</i> . Couldn't get your trawl over it [coral[]	otter trawl / groundfish	
427	Caught bits of strawberries (<i>Paragorgia</i>), while fishing for turbot	otter trawl / turbot	

Table 3.1 continued.

Participant	Species / Description	Gear /Species	
428	Lots of <i>Paragorgia</i> in the area fishing for turbot by the 200 mile line, Nets would get caught in the coral, Red corals caught almost every nets were hauled in while fishing turbot on rough bottom.	otter trawl / turbot	
431		otter trawl / turbot	
432	They are like trees, growing up like a tree on the bottom.	otter trawl / turbot	
433	Recognized Primnoa	Gillnet / turbot	
434	Would get bubble gum coral on hard bottom while gillnetting for turbot	Gillnet / turbot	
435	Got cup corals in the shrimp trawl	otter trawl / shrimp	
436	Get coral on edge of hard bottom, most of the time while targeting for turbot	Gillnet / turbot	
437	Get all corals in gillnets, found it around the Funk Islands	Gillnet / turbot	

Table 3.2. Observations by fishermen of areas where sponges were caught and fishermen's perspectives on relationships between sponges and commercially targeted species, as well as other marine species observed in the fishing nets.

Participant	Species / Description	Gear / Species	
New Brunswick			
2	7 Get it, but not a lot. It smells bad.	Dredge / scallop	
2	Not much sponge in the Bay of Fundy, sometimes gets the odd piece.	Dredge / scallop	
2	<u> </u>	Dredge / scallop	
3	O Get sponge in almost every tow, there is more in the rocky areas, not much of the branching stuff	Dredge / scallop	
Nova Scotia			
	5 Recognized the importance of havens, especially sponge and rockweed habitat.	dredge / scallop	
1	Sponge in some areas on the hard bottom, sponge used to fill the rake but now it is gone, we called it cheese bottom.	dredge / scallop	
1:	9	dredge / scallop	
1	<u>c</u>	otter trawl / groundfish	
1		otter trawl / groundfish	
1	6 Russian Hats in the Patch.	gillnet & longline / groundfish	
1	Russian Hats off Sambro, that is the only place you'll find them. Eastern side of Emerald basin, on the hard bottom.	gillnet & longline / groundfish	
1	9 Get Russian hats when trawling for redfish and pollock.	otter trawl / redfish	
2	±	otter trawl/ groundfish	
20		danish seine & longline	

Table 3.2. continued.

Participant	Species / Description	Gear / Species	
202 Eyed finger sponge, branching sponge on the edge of rough bottom.		gillnet / groundfish trap / lobster	
215	Would get sponge in the same place as corals.	otter trawl/ groundfish	
216	Stinky sponges on Scatterie Bank and Artimon Bank, shallow water 12-15 fathoms when targeting redfish.	otter trawl / redfish	
217	In shallow waters of Banquereau Bank, and on St. Pierre Bank.	otter trawl / groundfish	
220	They don't stink, come in different shapes and sizes and sometimes look like fingers on the hard bottom areas including Scatterie Bank, Smokey Bank and north of there.	otter trawl / groundfish	
224	They are in the shape of watermelons and turnips, and they were right spongy, full of water and jelly (mucous) and very smelly.	longline / groundfish	
Newfoundland			
207	Round, flat, thick or thin also finger sponges, at all depths, to 200 fathoms, finger sponges from 150 fathoms.	gillnet / shrimp trawl	
213	Torn up, beige in colour.	gillnet / groundfish	
2 , 2		otter trawl / skate & monkfish	
428	Get them occasionally in gillnets, very smelly. Glass sponges on the Stone Fence.	gillnets / otter trawl	
430	Get them scattered in nets, they are pretty much scattered over the ocean floor, get coral / sponge most of the time when targeting turbot.	gillnets / turbot	
431	Sponges caught in shrimp grid in NAFO area 2JF, soft bottom, very smelly, sheet-like - almost like sheets of foam, sometimes in balls.	otter trawl / shrimp	
432	Patches of them, all along Labrador coast, in deep water >1000 m, sponge in the otter trawl caught both when fishing for turbot.	otter trawl / turbot	

Table 3.2. continued.

Participant	Species / Description	Gear / Species	
433	Not in every net, some nets there were a dozen individuals or so, for every tonne of "product" would get 50-100lbs of sponge.	gillnet / turbot	
434	Would get it in bits and pieces, in gillnets looks like styrofoam, most of it is on the side of cliffs.	gillnet / turbot	
435	Gets sponges the same shape as the Russian Hat, but they are orange, sometimes on shrimp grate by not very often.	otter trawl / shrimp	
436	Get it in the gillnets and in shrimp grate, the size of a chart, smells bad, brownish in colour and comes in sheets.	gillnet / turbot , otter trawl / shrimp	
437	Get scattered pieces of sponge in the shrimp nets, gets in the grid and gillnet when turbot fishing at 250 fathoms.	gillnet / turbot , otter trawl / shrimp	

Table 3.3. Fishermen's observations of changes over time to the seafloor and the fishery; the importance of the seafloor to commercial fish populations and conservation concerns.

Participant	Perceptions of Change Overtime	Importance of the Seafloor for Commercial Fish Species	Conservation Comments	Gear / Species
Nova Scotia				
201	Sees as many sponges now if not more.	Don't know how important, but it is part of the whole.	Walk a fine line making it protectable and fishable at the same time.	danish seine & longine / groundfish
203		There is a crane off Cape St. Lawrence, it is like a reef. I fish as close to it as possible.	Cod are coming back a little but not enough to open it up	danish seine / crab trap
204	The whole Bay (Bay St. Lawrence) is bare compared to what it used to be.		I would ban all draggers if I could.	longline / groundfish
215	Saw corals in the 1970-1990, in the early 80's you wouldn't get the big corals you would years ago. The Stone Fence is now as level as a table, it's a desert compared to what it used to be.		Sydney Bight, is a spawning ground, all juvenile fish are found there. It should be protected.	otter trawl/ groundfish

Table 3.3. continued.

Participant	Perceptions of Change Overtime	Importance of the Seafloor for Commercial Fish Species	Conservation Comments	Gear Fished
216	I guess there was a whole lot more out there compared to what there is now. Technology had a lot to do with it, navigational technology fooled the whole party, you don't have to use your judgement anymore.		Would have put quotas on in the earlier years, eliminated the draggers. Fish were dead in the draggers, they had a lot more discard. I was on it so I helped them do it.	otter trawl /redfish longline / halibut
222		Feeding grounds on the bottom were tore up by the draggers. When fishing with the danish seine, would get 5 legged brittle stars and round stars with spikes. By the end, I wasn't getting any more stars at all.		longline & otter trawl / groundfish / danish seine / Groundfish
223	realized it too fate.	Bottom is important for spawning, not sure if it is important for food		longline / groundfish
224	I the later years, didn't see that many corals	1	Should have protected the Gully years ago.	longline / halibut

Table 3.3. continued.

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Participant	Perceptions of Change Overtime	Importance of the Seafloor for Commercial Fish Species	Conservation Comments	Gear Fished
226	There wasn't a rock left for anything to grow on. Fished along all good hard bottom areas, eastern Banquereau, Western St. Pierre, both sides of gully, St. Paul's Island. Draggers ruined the bottom for fish, nothing for them to feed off.	Would lose a lot of gear, [in the trees], but it was worth going back because there was a lot of fish there.		longline / halibut & groundfish
Newfoundlar	nd			
207	Moved out into deeper water after 1992. Big turbots are in the deeper waters. People in Fogo are gillnetting in deeper water.	Habitat destruction doesn't have an effect on fish numbers, it is overfishing that does it.		shrimp trawl / gillnet / turbot
209			Spawning grounds should have been closed down to draggers, would have saved the cod fishery.	gillnets / groundfish

Table 3.3. continued.

Participant	Perceptions of Change Overtime	Importance of the Seafloor for Commercial Fish Species	Conservation Comments	Gear Fished
211	Have to keep going further because there are no fish left			longline & gillnets / turbot otter trawl / shrimp
213	Never blame the collapse on the draggers alone, but also on computers. When draggers were given computers the fishery collapsed.	Every bit of stuff that grows on the ocean floor is important for fish.		handlining & gillnets / groundfish
427	Not much change in the bottom, except more garbage. Plastic and twine are the worst, they don't break up.			otter trawl / turbot
430	Started inshore with cod traps off St. John's, fished offshore for the past 10-15 years. Moved offshore and needed larger boat.			gillnets / turbot
432	We are going deeper and further; we can take twice as much and stay twice as long and fish four types of gear at once			otter trawl / turbot

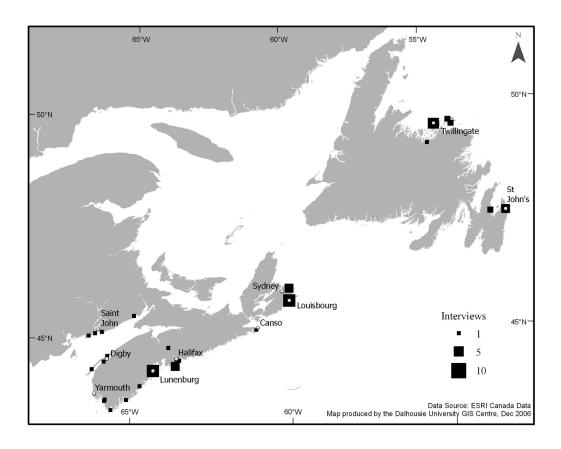


Figure 3.1. Locations and number of interviews with fishermen in Atlantic Canada who provided information on the locations of corals and sponges in the Northwest Atlantic in interviews collected between 1998 and 2001.

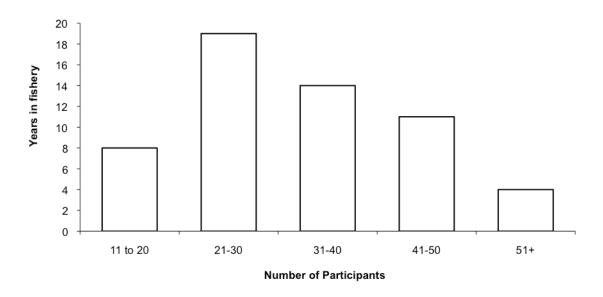


Figure 3.2. Number of years spent actively fishing for interview participants who provided years fished (n = 56, mean = 33.7).

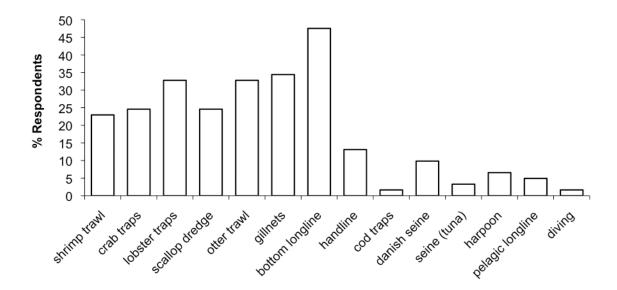


Figure 3.3. Fishing gear used by interview participants over their lifetime.

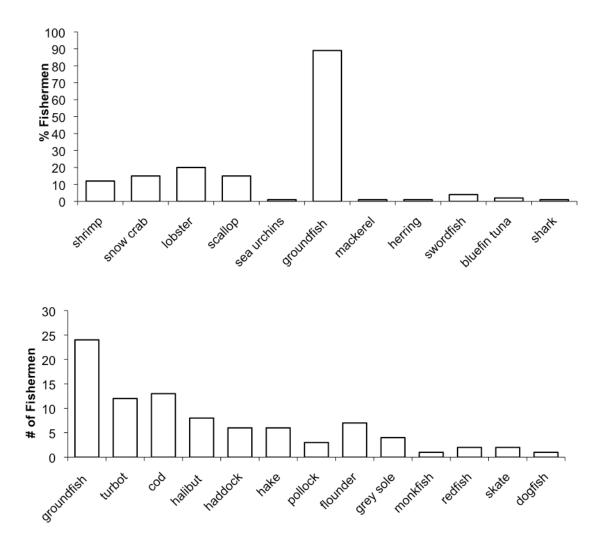


Figure 3.4 Species targeted by interview participants (a) and specific species of groundfish targeted (b).

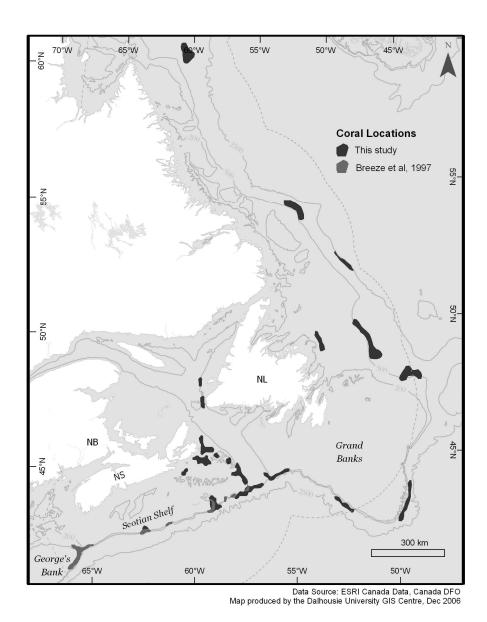


Figure 3.5. Fishermen's knowledge of coral locations in the Northwest Atlantic, previously reported by Breeze et al 1997 (Scotian Shelf) and Gass & Willison (2005) Eastern Scotian Shelf and Newfoundland.

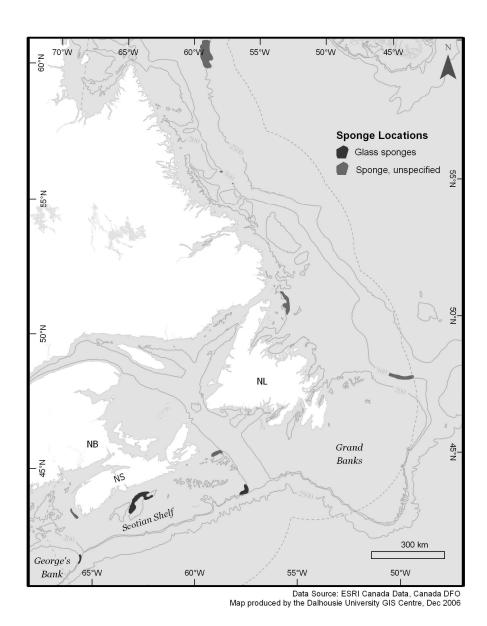


Figure 3.6. Fishermen's identification of sponge locations in the NW Atlantic, with the only reference to any species being "glass sponges" identified on the Scotian Shelf.

Chapter 4

Sponge Distribution and Diversity in the Northwest Atlantic: Analysis of Fisheries Observer and Research Trawl Data

4.0 Introduction

Information on sponge species distribution in the Northwest Atlantic has been limited to investigations carried out over half a century ago (Lambe, 1896, 1900; Proctor, 1933; Old, 1941; Hartman, 1958) and the majority of ecological research on sponges in this region has focused on sublittoral populations in the Gulf of Maine (Witman & Sebens, 1990; Ginn et al., 2000). Given that sponges are ubiquitous in the marine environment, and often comprise a significant proportion of benthic biomass, it is assumed that the lack of information on Northwest Atlantic sponges illustrates a lack of investigation, rather than an impoverished sponge fauna.

Sponges attach to the seafloor, on hard substrates or anchored in muddy areas, and frequently have branching or massive morphology, making them susceptible to capture by bottom tending fishing gear (Wassenberg et al., 2002). An assessment of bycatch in the inshore scallop grounds in the Bay of Fundy (Fuller et al., 1998) indicated that sponges often constituted the majority of the non-target catch, yet no recent or regional comprehensive identification guide on these animals existed, nor were there any comprehensive studies of sponge species distribution in the Northwest Atlantic. When the results of the assessment were compared to a similar study completed by Caddy et al., (1970), community structure had changed significantly over time, as a result of 30 years of fishing activity (Kenchington et al., 2007).

Research on the impacts of mobile fishing gear in the Northwest Atlantic, and particularly in Canadian waters, has taken place in areas of muddy or sandy sediments (Kenchington et al., 2001; Gilkinson, 2005; Gordon et al., 2005) or in heavily fished areas (Henry, 2006; Kenchington et al., 2007). The closure of the Atlantic cod fishery in 1992, and the subsequent moratorium on directed groundfish fishing in much of the Northwest Atlantic, resulted in a shift of fishing effort to new species and new areas, including deeper waters. The impacts of this shift on the marine ecosystem have not been well studied, however it can be inferred from other studies, that significant impacts particularly on sessile species occurred (Fossa et al., 2002; Roberts, 2002; Roberts & Hirshfield, 2004).

The majority of information on sponge fauna in the deep-water has been collected through the use of research trawls (Bruntse & Tendal, 2001; Klitgaard & Tendal, 2004; Janussen & Tendal, 2007). Because sponges below the littoral zone are difficult to sample, the most accessible information is often gathered through the collection of sponges in fishing gear, either from research vessels or through commercial fishing data. While an imperfect method of collection, as sponges are often collected in pieces and it is difficult to infer any information about patch size and distribution, general information on species assemblages can be obtained (Klitgaard & Tendal, 2004). Fisheries observer information has been used to examine catches and distributions of cold water corals in the Northwest Atlantic (Gass & Willison, 2005; Wareham, 2007), and for coral and sponge distribution in the North Pacific (Witherell & Coon, 2000; Shester & Ayers, 2005; Ardron et al., 2007).

Information on sponges collected by research trawls cannot be assessed in the same manner as information on fish species, primarily because there is no data on the relative catchability. As such it is difficult to estimate total biomass (as is done in for fish stock assessment), as sessile species are not distributed evenly, and are highly dependent on

substrate and currents. However, information gathered by fishing gear can be used to identify hotspots that can then provide the basis for *in situ* research. In an attempt to understand patterns in distribution, as well as make use of existing data and opportunistic sampling, I requested information on sponge bycatch from trawl surveys and fisheries observer data in the Northwest Atlantic from Fisheries and Oceans Canada (DFO) and requested samples to be collected where possible in the 2002 Newfoundland trawl surveys. The information presented here provides analysis of (1) the spatial and temporal distribution of catches particularly in commercial fisheries, (2) trawl survey information with a focus on large catches in the Newfoundland Region, and (3) preliminary species identification of sponges collected in Newfoundland trawl surveys. Other's have recently combined additional information on sponges from research surveys (briefly by (Campbell & Simms, 2009) and in more detail by Kenchington et al., (2010)).

4.1 Methods

4.1.1 Data Availability

A preliminary investigation was completed to identify which research surveys conducted in the Northwest Atlantic by Fisheries and Oceans Canada collected information on sponges. As of 2000, the multi-species trawl surveys conducted by Scotia Fundy Region of Fisheries and Oceans Canada had not collected information on sponges historically, and only began to do so, in 2001. Research trawl surveys in the Newfoundland Region contained records on sponges dating back to 1973, and covered area not included in the Scotia Fundy Observer data set. Data sources analysed in this Chapter are reported in Table 4.1.

4.1.2 Fisheries Observer Data

Observer programs were begun in Canada in the late 1970's primarily as a method to record and enforce catches and catch quotas, particularly in the foreign otter trawl fishery. The Scotia Fundy Fisheries Observer Program began in 1977, and data collected include records of catch and incidental catch for a variety of fisheries occurring in the Scotia Fundy Region, as well as for fisheries in the Newfoundland and Labrador Region, when vessels originating in Nova Scotia would travel to fish in more distant waters. Observer data has generally been underutilized for gathering information on non-commercial species. In the last decade, observer information collected in the Northwest Atlantic has provided important information on species distribution on cold-water corals (Gass & Willison, 2005; Wareham & Edinger, 2007) and has been used to assess fisheries discards (Gavaris et al., 2010). Observer records cannot be considered equivalent to that gathered by trawl surveys, which occurs on an annual basis using stratified random designs. However, because it is fisheries dependent, observer data can be very useful in understanding the impacts of specific fisheries on sessile, structural species, such as corals and sponges.

Date were received from the Virtual Data Centre house at Bedford Institute of Oceanography received in September 2001. The request included all sets using mobile bottom tending gear (including shrimp and groundfish otter trawls), target species, target species catch, location data for all sets, and all observations of sponges recorded since 1979. Because there is no requirement to report sponges, not all reports of "no catch" can be considered true zeros. To achieve some standardization of the data, reports from individual observers who never reported sponges were eliminated from the data set. Catch per unit effort (kg/set) was mapped using SPLUS version 6.2.1.

4.1.2 Research Trawl Survey Data

Data from the Newfoundland Region of Fisheries and Oceans Canada multi-species research trawl survey was provided for the years 1973-2001. A subsequent request resulted in the provision of only the trawl sets where sponges had been recorded from 1997-2005 (Table 4.1, 4.2). Both sets of data were used in this analysis. DFO multispecies stock assessment surveys consist of an annual spring and fall survey aboard the Canadian Coast Guard Ship (CCGS) Wilfred Templeman for shallow water tows < 700 m, and the CCGS Teleost conducted both shallow and deep-water tows < 1500 m, both following a stratified random design.

Collection of Sponge Samples

Individual sponge samples were collected during the Newfoundland research trawl surveys in the fall of 2008, which covered NAFO (Northwest Atlantic Fisheries Organization) Divisions 2HJ (Southern Labrador) and 3KLMNOP (northeast-southern Newfoundland, and the Grand Banks). Research vessels were equipped with a Campelen 1800 shrimp trawl with rockhopper footgear which is outfitted with tight rubber disks (102 °— 35 cm diameter) with spacers along the footrope. The 16.9 m wide net had four panels constructed of polyethylene twine with wing panel 80 mm mesh size, the square and first belly 60 mm mesh size, the second belly and cod end 40 mm mesh size with a 12.7 mm liner in the cod end. Tow duration was 15 min at 3 kt (± 1 kt); average tow length was 1.4 km (0.79nmi), and tows were conducted along a consistent depth contour, wherever possible.

4.1.3 Identification of Sponge Samples

Sponge samples were frozen upon collection, and thawed for identification. Notes

were made on all observations of associated fauna and evidence of spawning. Photos were taken of all samples, and portions of samples were preserved in 70% ethanol and in some cases whole specimens were dried. Species identifications were made based upon the classification scheme in Hooper et al., (2002), as well as with the assistance of Eduardo Hadju of the University of Rio Di Janeiro, and Rob Van Soest at the University of Amsterdam for Demosponges and Henry Reiswig at the University of Victoria for Hexactinellida. A comprehensive report on species identification and photographs of sponge specimens and spicules is in progress (Fuller & Wareham, in prep).

4.2 Results

4.2.1 Fisheries Observer Data

A total of 381510 fishing sets using otter trawl gear were observed between 1977 and September 2001. Approximately half, 47.s8% of observers recorded sponges as part of the catch, and there were 8820 observations of sponges, which amounts to 4.3% of all sets.

Depending on the target fishery, observer coverage (the number of total trips where an observer was on board) ranged from 5-15% (Table 4.2). Individual observers often began reporting sponges after a particularly large catch (> 500kg).

Sponge catch

The cumulative distribution of sponge catch between 1979 (the year of the first sponge record in the observer database) and September 2001 illustrates the fishing pattern of vessels fishing out of the Scotia Fundy Region (Figure 4.1). Vessels carrying an observer from Scotia Fundy Region (277 sets were observed on non-Canadian vessels) fished from Georges Bank to Davis Strait and Baffin Bay, and outside the 200 mile limit on the Nose and Tail of the Grand

Banks. Maximum catches were reported in 1992 at ~86,000 kg (Table 4.3). An increasing trend in sponge catch over the fishing period reflecting an expansion of fishing effort and an increased level of recording by fisheries observers.

Sponge distribution with depth

Cumulative sponge catches were concentrated in two depth strata (Figure 4.2), with the first between 100 and 250 m on the continental shelf and the second between 900 and 1250 m on the continental shelf break. The shallow water catches are all on the Scotian Shelf, where a maximum catch of 5900kg / set was reported in 1988. These sponges are "Russian Hats" (see Chapter 5); glass sponges of Class Hexactinellida identified as *Vazella pourtalesi* (Schmidt 1870) following the examination of samples collected through *in situ* sampling. The second depth stratum, with catches as high as 5000kg / set represents reports from fishing activity along the Labrador Shelf and in the Davis Strait. These large catches are most likely sponges in the Order Astrophorida (i.e. *Geodia* spp. *Stelletta* sp.) ,which have been identified from the Northeast Atlantic as forming large patches or sponge fields on the sea floor, and have been referred to "ostur" or "cheesebottom" (Klitgaard & Tendal, 2004; ICES, 2008; Hogg et al., 2010). Samples collected in the 2008 Newfoundland multi-species trawl survey confirm that the same species composition exists in the Northwest Atlantic.

Impacts of fisheries expansion

The increase of sponge catch with time, is a direct result of the expansion of fishing to deeper areas and areas further north following the cod collapse in the early 1990's (Figure 4.3). Large sponge catches on the Scotian Shelf, in the "Russian Hat" patch occurred in the late 1980's during the pollock fishery. The expansion of the Canadian Greenland halibut

fishery into the eastern Arctic fishery, resulted in fishing in new areas and large sponge catches (Table 4.4). The relationship of fisheries expansion is evident (Figure 4.4 a-e). Observer reports from 1977-1981 show low sponge catch (7 kg/set) (4.4 a), which is likely partially a factor of a lack of reporting, with most of the fishing activity taking place on the shelf and few sets in the eastern Arctic, along the western coast of Greenland. During 1982-1986, slightly higher catches occurred (35kg / set, with a total of 37 records of sponges reported) when averaged out over all sets indicates catches in on the Scotian Shelf in the area of the "Russian Hats" (4.4 b). Table 4.3 shows a total catch for the years 1982-1986 to be ~10000kg. From 1987-1991, large catches of "Russian Hats" were recorded in the pollock fishery on the Scotian Shelf, and fishing activity increased in the shrimp and turbot (Greenland halibut) fisheries in the Labrador Shelf and Davis Strait area (Figure 4.4 c). Following the cod collapse and subsequent moratorium, fisheries for shrimp and turbot further expanded, resulting in high catches of sponge (up to 5000kg)/ set (Figure 4.4 d, e). Total sponge catch (000 kg) and turbot catch (MT), as reported only by Scotia Fundy Observers (i.e. not total landings), of > 80 MT of sponges corresponds to 2000 MT of turbot catch (Figure 4.5)

4.2.2 Trawl Survey Data

Sponge distribution

Trawl surveys conducted by the Newfoundland Region of Fisheries and Oceans Canada also sporadically record sponge catches, with high catch rates showing a similar geographic distribution to that of the observer data, except on the Scotian Shelf. The difference between the distribution of sponges caught between 1973-2001as recorded in the observer data and the trawl survey data, is on the continental shelf break of the Grand Banks, and on the Northern edge of the Flemish Cap, both outside the 200 mile limit (Figure 4.6).

These large catches identified both on the shelf break and in the Davis Strait area are predominantly comprised of sponges from the Geodidae family (Figure 4.7 a, b).

Both observer data and trawl survey data, when plotted together, (Figure 4.8) show the significant concentrations of sponges from the Scotian Shelf to the Eastern Arctic, and clearly identify hotspots of sponge abundance. There is a clear delineation of sponge community composition in high concentration areas (Fuller et al., 2008) with Geodids rarely occurring on the Scotian Shelf, but clearly forming large patches (if trawl contents can be considered a proxy for seafloor communities) from the slopes of the southeastern Grand Banks, and extending along the Labrador shelf to the eastern Arctic.

Sponge species identification

A total of 603 individual samples were examined, and 37 species identified to the genus / species level (Table 4.5). Sixty-five individual samples were identified to the family level only. For the purposes of this thesis, only those sample identified to genus level are used to describe the sponge fauna of Newfoundland waters. Species that identified that are unique to the sponge grounds in the Northeast Atlantic, as described by (Klitgaard & Tendal, 2004) include the Astrophorids *Stryphnus ponderosus, Stelleta normani, Geodia barretti, G. macandrewii, G. phlegraei*, and the Poecilosclerid, *Mycale lingua*. With the exception of *Mycale lingua*, the sponges considered to be vulnerable are all found along the shelf edge and slope area (Figure 4.9), which is consistent with distributions of these species in other areas (Klitgaard & Tendal, 2004). Several specimens of carnivorous sponge, *Cladorhiza abyssicola* were collected, all occurring along the shelf edge. The glass sponge, *Asconema foliata* is reported for the first time in this region, and was collected in large volumes, with one report of

400kg. The community of sponges on the shelf were dominated by *Biemna varantia*, various *Polymastia* species, *Mycale loveni*, *Mycale lingua*, and *Hemigellius arcofer*.

4.3 Discussion

4.3.1 Data Availability and Limitations

Over the past decade there has been significant progress in collection of information on corals and more recently sponges, in research trawl surveys in particular. Efforts made to collect cold-water corals in the trawl surveys in 2000 and 2001 (Gass & Willison, 2005); the subsequent development of a Newfoundland coral collection program in both the research trawl surveys and fisheries observer program (Wareham & Edinger, 2007); and the direction from the Northwest Atlantic Fisheries Commission to identify vulnerable marine ecosystems within the NAFO Regulatory Area in 2007 (Fuller et al., 2008) have collectively lead to a significant amount of knowledge on the distribution of sponges and corals in the Northwest Atlantic (Kenchington et al., 2010). When this research began, there was no systematic collection of sponges in either trawl surveys or observer programs in Canadian waters in the Northwest Atlantic. Surveys in the eastern Arctic have collected information on sponges since 2006. The information from those surveys is not included here as it was not available at the time of the original data request.

Fisheries observers in Scotia Fundy recorded sporadically sponges since 1979, with however fisheries observers in the Newfoundland Region, did not collect information on sponges historically. While a program to engage observers and collect information on cold water corals in the Newfoundland Region was began in 2004 (see overview of Canadian coral and sponge conservation efforts in Campbell & Simms 2009), such a program has yet to be

started for sponges, although the publication of a sponge guide specifically for the NAFO Regulatory Area may inspire observer reporting (Best et al., 2010).

4.3.2 Sponge Research in the Northwest Atlantic

While a significant amount of research has been done on cold water coral distribution and diversity in the Northwest Atlantic over the last decade (Breeze, 1997; Mortensen & Buhl-Mortensen, 2004; Gass & Willison, 2005; Bryan & Metaxas, 2006; Wareham & Edinger, 2007; Wareham, 2007; Kenchington et al., 2010; Murillo et al., 2010), only recently has there begun to be interest in marine sponges, primarily as a Canadian response to the international obligation to protect corals and sponges from destructive fishing, as outlined in the 2006 United Nations General Assembly Sustainable Fisheries Resolution 61/105. The research presented here shows that sponges are an important part of the benthic community in the Northwest Atlantic, and that existing information included in fisheries observer reports and trawl survey databases can be used to identify important areas of sponge biomass.

4.3.3 Impacts of Fishing on Sponges

Fisheries observer data can be used to identify important areas of sponge occurrence, and can shed light on the relative impact of different target fisheries on sponges. As fisheries have expanded to new areas, previously unexploited sea floor areas are being impacted evidenced by the high catches of sponges. Fishing activity has been shown to have a negative impact on sponges (Collie et al., 2001) and relatively little information is available on recovery or regeneration of sponges that have been removed as a result of fishing. Sainsbury (1987) compared trawl data from 1963 and 1979 in Northwest shelf of Australia. During the 1960's, sponge catch rates were as high as 1600 kg/hour with a maximum individual catch of

794 kg, but during re-sampling in 1979, sponges were absent in the majority of trawl surveys. In Chapter 5, a fisherman from the Northwest Atlantic describes the removal of "tonnes of Russian Hats" (Class Hexactinellida) in the late 1980's once the "dragging" fleet began to fish the grounds off Sambro Bank (Harold Potter, gillnetter, personal communication).

The importance of deep-water sponge communities globally is only now gaining attention and given consideration for conservation (ICES, 2008, 2009; Hogg et al., 2010; ICES, 2010), despite the description of unique sponge fields in the Northeast Atlantic more than a decade ago (Barthel & Tendal, 1993; Bruntse & Tendal, 2001). Recent fisheries closures of areas with high concentrations of sponges on the high seas in the Northwest Atlantic (NAFO 2009) have stimulated interest in the distribution of sponges within the Canadian exclusive economic zone (EEZ), resulting in the collation of existing information on sponge distribution by Kenchington et al. (2010).

Finally, the species identification of sponges on the Newfoundland shelf contributes to the knowledge of the benthic fauna of the area, and extends the range of species identified in the Northeast Atlantic as forming significant sponge fields, to the Northwest Atlantic. The collection of sponge samples in research trawl surveys is an important step in recognizing the need for species level information on non-commercial structural species, particularly as efforts to manage human impacts on the marine ecosystem are being implemented. Trawl surveys in Newfoundlan have collected samples in 2009 and 2010 and these samples will be identified to further extend the information on sponge community composition and species distribution. Sponges are more difficult to identify than corals, and as a result collecting species information through fisheries observers will be more problematic, and likely limited to a few species that can be easily recognized (Best et al., 2010).

Table 4.1. Data used for the determination of sponge distribution and identification of sponge

samples in the Northwest Atlantic.

Data	Location	Years	Details
Scotia Fundy Observer Data	Northwest Atlantic	1977-2001	Vessels leaving Nova Scotia fished from the Scotian Shelf to the Eastern Arctic, presence and absence data provided
Newfoundland Trawl Survey Data	Newfoundland Region, Grand Banks to Eastern Arctic	1983-2001	Presence and absence data provided
Newfoundland Trawl Survey Data	Newfoundland Region, Grand Banks to Eastern Arctic	1995-2007	Sponge presence data provided
Newfoundland Trawl Survey Data	Newfoundland Shelf	Fall, 2008	Samples collected in Fall Survey, zero catch data not provided

Table 4.2. Summary of fisheries observer and trawl survey sponge records from the Nova Scotia and Newfoundland.

	Scotia Fundy Region Observer Data (1977-2001)	Newfoundland Region Trawl Survey Data (1973-2001)	Newfoundland Trawl Survey Data Presence only (1995- 2007)
# Sets	381510*	23848	NA
# Sponge observations	8820	618	1585
# Obs. by foreign vessels	277	NA	NA
% Obs. Reporting	47.8	NA	NA
%Sponges are caught	4.3	2.6	NA
% Domestic Fishery Observed	5-15	NA	NA
Depth range (m)	15-1427	30-1416	52-1508
Sponge catch range (kg)	1-5900	0.01-5000	0.01-5000

Table 4.3. Annual sponge catch, as reported by Scotia Fundy Observers from 1979-2001; N = number of records.

Year	N	Total Catch	Mean	St. Dev (+/-)
1979	1	200	200.00	0.00
1980	2	150	75.00	35.36
1981	7	2500	357.14	419.08
1982	2	2	1.00	0.00
1983	2	230	115.00	120.21
1984	5	1855	371.00	189.22
1985	20	8801	440.05	600.12
1986	8	1585	198.13	148.01
1987	87	27160	312.18	755.14
1988	41	17676	431.12	1074.12
1989	732	32461	44.35	228.69
1990	245	19211	78.41	343.32
1991	442	33645	76.12	337.95
1992	401	85369	212.89	447.36
1993	575	86773	150.91	223.26
1994	324	34835	107.52	322.49
1995	641	24689	38.52	93.87
1996	2108	58369	27.69	61.47
1997	825	13790	16.72	110.18
1998	644	12530	19.46	35.22
1999	556	30183	54.29	175.30
2000	925	63419	68.56	242.47
2001*	209	1765	8.44	22.10

^{*} Data only collected until September.

Table 4.4. Sponge bycatch by geographic area and target fishery, with average depth, mean catch and maximum catch, as reported by Scotia Fundy Fisheries Observers (1977-2001).

Area	N (sets)	Mean Depth (+/-SD) (m)	Mean Sponge Catch (+/- SD) (kg)	Max Sponge Catch (kg)
Sponge catch by geogr	aphic area			
Scotian Shelf	296969	229 (101)	0.85 (33.44)	5900
Grand Banks/ Nfld Shelf	31132	275 (172)	0.07 (1.38)	100
Labrador Shelf	29724	382(95)	2.275(21)	1000
Davis Strait	12961	442 (237)	18 (128)	5000
Sponge catch by targe	t species			
Cod/Haddock	217114	282 (131)	2.2 (46)	1000
Pollock	21810	186(53)	7 (108)	5900
Hake	155560	233 (65.5)	0.025 (1.4)	350
Shrimp	37947	370 (62)	1.4 (15)	1300
Turbot	1827	1033 (236)	135 (305)	5000

Table 4.5. Sponge species identified in Newfoundland & Labrador Region fall 2008. Trawl Survey. * denotes species identified as vulnerable by ICES (2008.)

Class	Order	Family	Taxon
Hexactinellida	Hexactinellida	Rossellidae	Asconema foliata*
	Hexactinosida	Aphrocallistidae	Aphrocallistes Beatrix
	Lyssancinosida	Euplectellidae	Euplectella aspergillum
Calcarea		Sycettidae	Sycon sp.
Demospongiae	Astrophorida	Ancorinidae	Stryphnus ponderosus*
		Astrophoridae	Stelleta normani*
		Geodidae	Geodia barretti*
			Geodia macandrewii*
			Geodia phlegraei*
		Pachastrellidae	Thenea muricata*
	Dendroceratida	Dictyodendrillidae	Spongionella sp.
	Hadromerida	Suberitidae	Homaxinella subdola
			Suberites ficus
		Polymastiidae	Tentorium semisuberites
		•	Polymastia hemisphaericum
			Polymastia mammillaris
			Polymastia robusta
			Polymastia uberrima
			Weberella bursa
	Halichondrida	Axinellidae	Phakellia robusta*
		Axinellidae	Phakellia ventilabrum*
	Haplosclerida	Chalinidae	Haliclona sp. 1
	-		Haliclona sp. 2
			Haliclona (Haliclona)
			urceolus
		Niphatidae	Hemigellius arcofer
	Poecilosclerida	Acarinidae	Iophon sp.
		Cladorhizidae	Cladorhiza abyssicola
			Chondrocladia gigantea
			Asbestopluma
		Coelospheridae	Histodermella sp.
		-	Lissodendoryx sp.
		Desmacellidae	Biemna variantia
		Isodictyidae	Isodictya
		Mycalidae	Mycale lingua *
		-	Mycale loveni
		Myxillidae	Melonanchora elliptica
	Spirophorida	Tetillidae	Tetilla cranium*

Sponge Presence in Kg/Set Caught by Canadian Vessels (1977-2001)

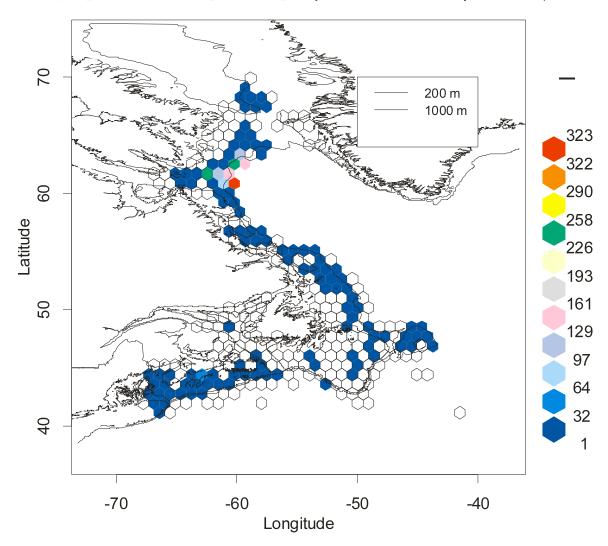


Figure 4.1. Cumulative catch of sponges as reported by fisheries observers between 1977 and 2001. Hexagons where no sponges were recorded during the entire time period of reporting are shown as empty.

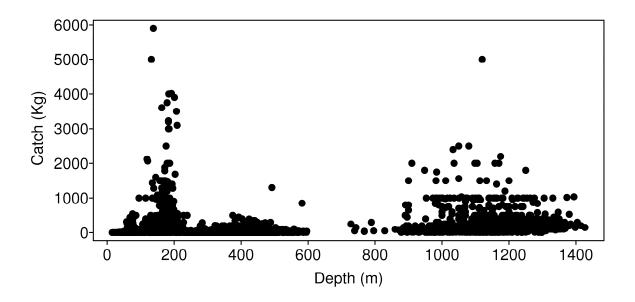


Figure 4.2. Sponge catch with depth in all observer data from 1979-2001.

Depth vs Year for All Observed Sets (1977-2001)

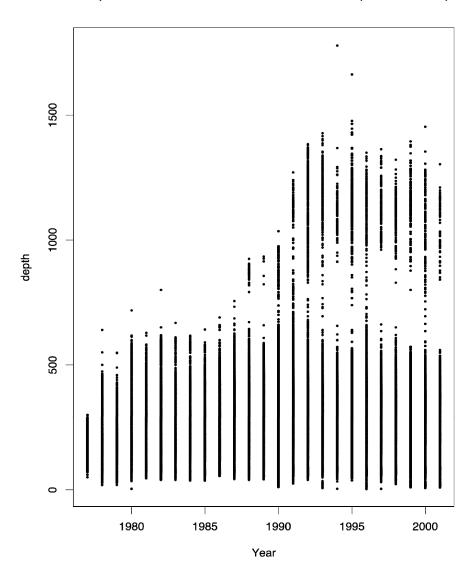
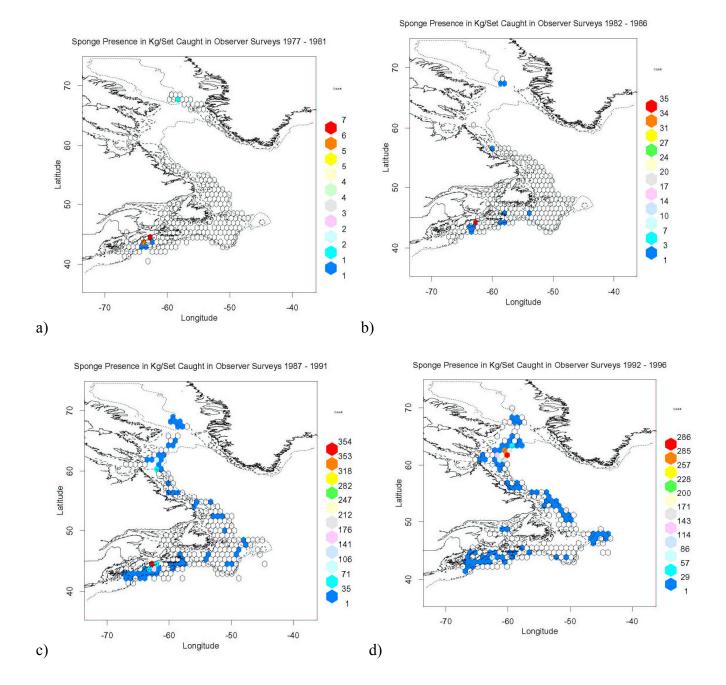


Figure 4.3. All observed sets from 1977-2001 as reported in the Scotia Fundy Observer records, and representing fishing effort from Georges Bank to Davis Strait in the Northwest Atlantic.



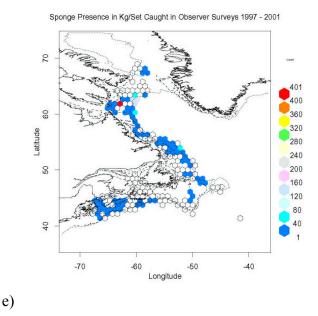
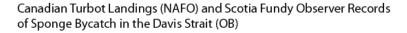


Figure 4.4. Observer catch per unit effort form 1979-2001, in five year increments illustrates the expansion of fishing effort from the Scotian Shelf to areas further north. Empty hexagons indicate zero sponge catch. Observed sets from 1977-1981 show low kg/set catches on the Scotian Shelf (a); sets from 1982-1987 indicate a similar pattern of fishing, but with higher kg/set (b); sets from 1988-1991 indicate high catches on the Scotian Shelf, corresponding with fishing activity and observer reporting of *V. pourtalesii* as well as increased fishing activity in Arctic waters (c); sets between 1992-1996 show reports of high sponge catch in Arctic waters, corresponding to the Greenland halibut fishery expansion (d); and sets from 1997-2001 are a continuation of this trend (e).



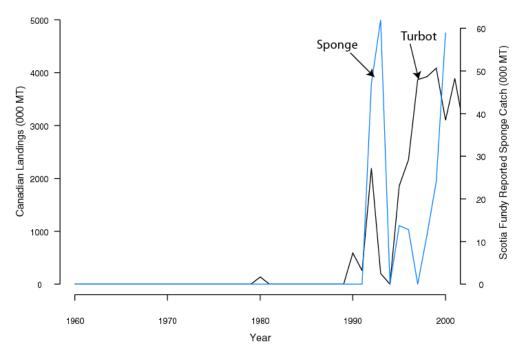


Figure 4.5. Sponge catch (000 kgs) with reported turbot catch (MT) in the NAFO Division OB.

Sponge Presence in Kg/Set Caught in Trawl Surveys (1983-2001)

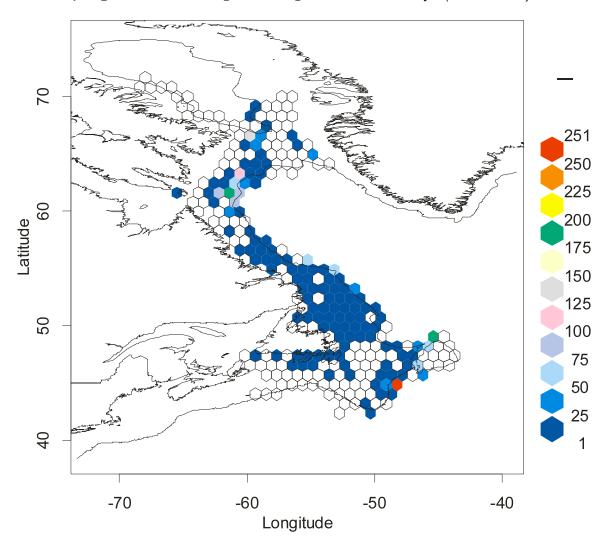


Figure 4.6. Cumulative catch of sponge as reported in the Newfoundland multi-species trawl surveys conducted between 1973-2001. Empty hexagons indicate no sponge catch reported.





Figure 4.7. Sponges collected in Newfoundland research trawl surveys (a) and the Northern Shrimp Survey in 2008 (b), both from the Davis Strait / Hatton Basin area of the Eastern Arctic, showing the dominant *Geodia* sp. sponge fauna. (Photos courtesy of Fisheries and Oceans Canada).

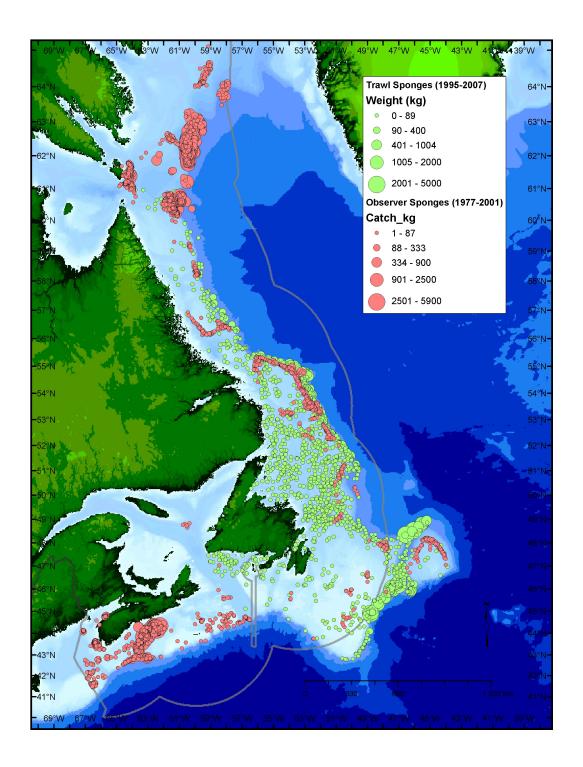


Figure. 4.8. Newfoundland multi-species stock assessment trawl survey data (1995-2007) and Scotia Fundy Observer data (1977-2001) with total sponge identified.

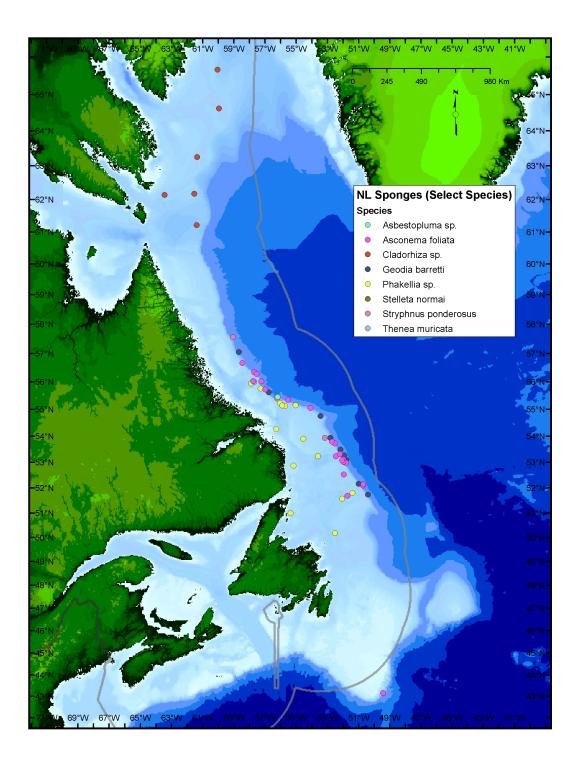


Figure 4.9. Distribution of sponge species included in a list of vulnerable species developed by ICES 2008, as identified in the 2008 Newfoundland multi-species stock assessment survey in 3JKLNO.

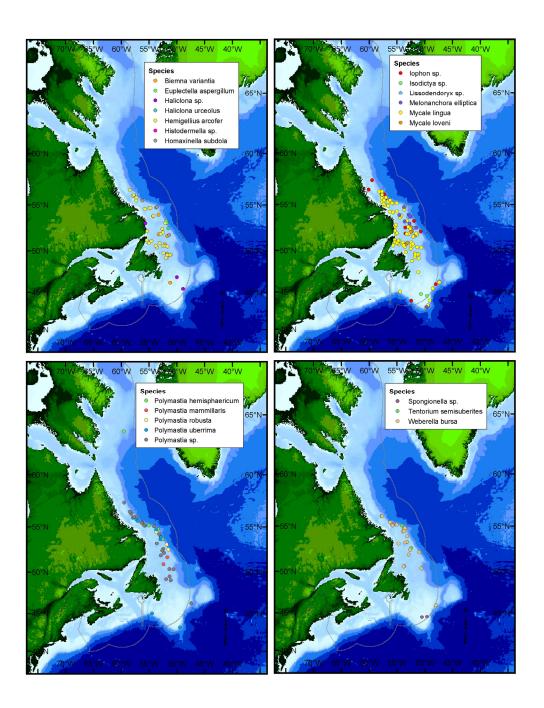


Figure 4.10. Distribution of sponges identified in the Newfoundland Fall 2008 multispecies trawl survey not included in the vulnerable list of species as determined by ICES 2008.

Chapter 5

A Unique Monspecific Population of *Vazella pourtalesi* (Schmidt, 1870) (Porifera: Hexactinellida) on the Scotian Shelf, Northwest Atlantic

5.0 Introduction

Glass sponges of the Class Hexactinellida are typically found at depths below 500 m throughout the worlds' oceans (Tabachnick, 1994), although dense populations are alsoknown from more shallow locations (Barthel & Gutt, 1992; Vacelet et al., 1994; Leys et al., 2004; Bakran Petricioli et al., 2007). Large patches of glass sponges have been found in a variety of areas globally, where their structure and biomass appears to contribute significantly to benthic habitat heterogeneity. These populations include Rossellid sponges in Antarctica (Dayton et al., 1974; Barthel et al., 1991); globally unique glass sponge reefs off the coast of British Columbia (Conway et al., 1991; Cook et al., 2008); patches of another Rossellid, *Pheronema carpenteri*, in the Northeast Atlantic, off of Morocco (Barthel, Tendal, & Theil, 1996); and sponges off the Porcupine Bight in the Northeast Atlantic (Rice et al., 1990; Bett & Rice, 1992).

Compared to Demosponges, the largest class of sponges, relatively little is known about Hexactinellid biology. Hexactinellids are the oldest known multi-cellular animals, with their origin suggested to be earlier 800 million years ago (Leys et al., 2007). Hexactinellids play a structural role in benthic communities by creating habitat heterogeneity either as individual sponges or through patch formation, as well as through spicule deposition, which alters sediment composition. For example, (Beaulieu, 2001) describes the faunal composition of *Hyalonema* stalks in the abyssal Pacific, where 135 species have been documented to make use of the hard substrate and varied current rates

along the lengths of the sponge stalks. Spicule mats left by dead individuals can structure the surface of the seafloor, altering substrate quality and, hence, the structure of the associated epifauna (Barthel, 1992; Bett & Rice, 1992). Leys et al. (2007) review the current state of knowledge of the biology, physiology and ecology of glass sponge globally, noting the increased understanding of these animals as the exploration of the marine environment expands to new locations and greater depths. Very few glass sponges have been maintained in laboratories, and the only species that has been successfully raised is one that is naturally occurring in shallow waters of the Northwest Pacific (Leys & Meech, 2006). The primary food source for glass sponges is particulate matter that is filtered from the water column, and bacteria providing the major nutrient source (Yahel et al., 2007).

Until recently, cold-water sponge grounds have received considerably less attention than deep-water corals and, with the exception of the sponge reefs off the Pacific coast of Canada (Conway et al., 1991; Cook et al., 2008), most of the reporting on "sponge fields" has generally not drawn the attention of conservation biologists. Hogg et al., (2010) review what is known about the distribution of deep-water sponges, particularly those that form large patches and the threats to these unique ecosystems.

In the Northwest Atlantic, investigations of sponge communities have been limited to those of early taxonomic records (Lambe, 1896, 1900) and species lists (Proctor, 1933; Bleakney & Mustard, 1974; Linkletter et al., 1977), in addition to ecological studies that have focused on subtidal populations in the Gulf of Maine and Bay of Fundy (Witman & Sebens, 1990; Ginn et al., 2000). Interviews with fishermen, soliciting information on the types of animals found on the seafloor off Nova Scotia and

the relative impacts of human activities on these animals, has yielded specific mention of sponge populations on the Scotian Shelf (Fuller & Cameron 1998). Fishermen described these animals as "Russian Hats" that were painful to touch and "filled the nets" when they were targeting pollock (*Pollachius virens*) and redfish (*Sebastes* spp.) (see Chapter 3). These descriptions by fishermen did not match any known sponges in the area, thus providing an impetus for the investigation presented here. The objective of this Chapter is to report all available information on the "Russian Hat" population on the Scotian Shelf, and describe the large patches of these sponges, which have not been reported elsewhere.

5.1 Methods

5.1.1 Study Area

The Scotian Shelf, on the east coast of Canada, comprises a broad continental shelf characterized by shallow banks and deeper basins. The Shelf is bounded by the Northeast Channel to the south and the Laurentian Channel to the north. The high sponge catches in the vicinity of Emerald Basin and Sambro Bank (between 42° 5 and 44° N are the focus of this study.

5.1.2 Data Collection

The collection of fishermen's information, fisheries observer data, sponge samples and finally *in situ* investigations was iterative. Interest in specific areas ws generated as a result of interviews with fishermen, which resulted in (a) a querying of the fisheries observer data for records of sponge catches from the Canadian Fisheries

Observer Program database at the Bedford Institute of Oceanography, (b) an examination of the collection of marine invertebrates at the Nova Scotia Museum of Natural History, and (c) participation in scientific research cruises for the opportunity to explore areas where high sponge catches had been recorded using ROVs and cameras. Table 5.1 outlines the data used to describe the "Russian Hat" population on the Scotian Shelf.

Local Ecological Knowledge

Interviews with fishermen conducted by (Fuller & Cameron, 1998) were resampled for specific information on the locations of "Russian Hats", as this work marked the first time that fishermen's information on sponges in the Northwest Atlantic had been recorded. Additional interviews conducted between June and November 2000, that yielded information on cold-water corals as well as sponges on the Scotian Shelf, provided additional information on the location of "Russian Hat" catches.

Observer Data

Observer records were extracted from the Virtual Data Centre at the Department of Fisheries and Oceans, Bedford Institute of Oceanography, for the years 1977 to 2001. Observers were not required to identify sponge species, and all sponges were recorded under the code "8600". As not all observers recorded the presence of sponges, given that the focus of observer reports had been on commercial species, some of the records of 'zero' sponges may not always reflect a true zero catch, but may reflect a failure to record sponges. To account for this potential bias, records from observers were used here only if the individual observer had reported observing sponges in the catches on at least

one occasion. Several variables in the observer database were analysed, including depth of tow, sponge catch and target species, to identify areas of high sponge concentration and associated fish species.

In Situ Surveys

I participated in two research surveys, the primary goal of which was to sample cold-water corals on the continental slope off the Scotian Shelf, and as such any sponge sampling was opportunistic. I could not plan a comprehensive research protocol or repetitive transects. As a consequence, sampling was undertaken along a single transect, along which two different surveying methodologies were employed.

One transect was done in August 2001, on the C/V Martha Black, using the remote operated vehicle (ROV), ROPOS. ROPOS was equipped with an ultra-short baseline navigation system (ORE Trackpoint II) which provided detailed recording of the track line as the ROV moved along the seafloor. ROPOS is also equipped with sampling equipment, a depth sensor, compass as well as two parallel laser beams set 10 cm apart. The lasers allowed for measurement of sponge height and width during analysis of the video footage. The ROPOS transect began at a depth of 277 m and was terminated at 202 m (Table 5.2). The second transect was done in September 2002 on the CGS Hudson using the underwater camera and video system, CAMPOD (at a speed of < 1nm).

CAMPOD was maintained at a level of 2 m above the seabed and photos were taken with an oblique and vertical camera. The CAMPOD transect was 200 m long and at a continuous depth of 187 m. Detailed descriptions of the ROPOS and CAMPOD transects

and equipment used, in addition to video interpretations, are included in (Mortensen & Buhl-Mortensen, 2004).

5.2 Results & Discussion

5.2.1 Species Description

This study is the first time that a monospecific population of *Vazella pourtalesi* has been documented in the North Atlantic. *V. pourtalesi* is a vase-shaped sponge, typical of many Rossellid species (Reiswig, 2006; van Soest, 2010). As characteristic of all Hexactinellids, the skeletal structure of *V. pourtalesi* is made of silicate spicules all of which have some form of "hexactine" morphology. Reiswig (1996) provides a full description of the spicules, with the deterministic characteristics being the presence of discoidal microscleres consisting of only micridiscohexasters. Reiswig (1996) reexamined four specimens collected in the Caribbean and reinstated the genus *Vazella* (Gray) to accommodate these samples previously described as two separate species in the genus *Holtenia*. The resulting reclassification is a monospecific genus, with all material examined now combined under *Vazella pourtalesi*. Common names of this species are "Russian Hats" or "Cap of Liberty."

Specimens collected and observed on the Scotian Shelf are much larger than those described by Van Soest et al. (2002) and examined by Reiswig (1996) with the material available being no larger than 92 mm in length and 10 mm in diameter. In the analysis of video footage from the ROPOS transect, *V. pourtalesi* ranged from 2 to 110 cm in height, with a mean of 21.71 cm (+/- 11.6) and from 2 to 75 cm in width, with a mean of 14.36 cm (+/- 8.23). This represents a significant increase in the previously

known size range of this species. As previous samples were collected as single specimens and there have been no other in situ observations of *V. pourtalesi*, there are no previous estimates of population density. A maximum density of 16 sponges / m² was estimated from oblique photos taken during the CAMPOD transect. Bett and Rice (1992) estimated densities of *Pheronema carpenteri* at 1.5/m² between 1000-1300 m in the Northeast Atlantic. shows *V. pourtalesi* occurs in a variety of substrates and a significant amount of flocculent material can accumulate in the spicule "fur" on the external surface of the sponges (Figure 5.2 (a-f)).

5.2.2 Geographical Distribution

Significant populations of other species in the Family Rossellidae have been found in Antarctica at ~100-300 m (Barthel & Gutt, 1992) and in the Northeastern Atlantic on the Porcupine Bight off Ireland at 1000-3000 m and on the continental slope off Morocco at 740-820 m (Barthel, Tendal, & Thiel, 1996). The population of *Vazella* on the Scotian Shelf, with the shallow boundary of its depth range at potentially ~75 m according to fisheries observer data, and extending to at least 275 m is at the shallow end of distribution for hexactinellids globally. The discovery and description of the *Vazella pourtelesi* population represents an important addition to the knowledge of monospecific populations of Rossellid sponges, which form dense patches on the seafloor, creating significant biological structure.

In their description of the genus *Vazella*, Van Soest et al. (2002) identify two locations in the Atlantic Ocean from the Carribbean to the Azores. The type specimen location, off Sombrero, Florida, sampled at a depth of 479 m and off Sand Key, Florida

at a depth of 282 m, constitutes a single Caribbean location. An additional sample was collected off the Azores in the mid-Atlantic at a depth of 845m among other glass sponges, notably the Rossellid *Pheronema* sp. which is known to form large patches in the Northeast Atlantic (Rice et al., 1990). The location of the *Vazella* population on the Scotian Shelf is within the described geographic range (Hooper et al., 2002). The incidence of *V. pourtalesi* decreases with depth (Figure 5.5).

The largest concentration of *V. pourtalesi*, as evidenced from Fisheries Observer data, is in the Emerald Basin between Sambro Bank and The Patch. Interviews with fishermen also showed this to be the area where the majority of Russian Hats were located (Figure 5.2). Fishermen also reported finding *V. pourtalesi* on the Stone Fence and in the Northeast Channel (Table 5.3), although two interviewees were adamant that the Emerald Basin / Sambro Bank area was the only place that these sponges had ever been caught. Evidently, *V. pourtalesi* is not confined to the Emerald Basin / Sambro Bank, as it has been observed in the Northeast Channel (Metaxas & Davis, 2005). However, the dense patches observed in the video transects I collected, as well as the large catches reported by fisheries observers, where up to 5900 kg of sponges were recorded (Figure 5.4), suggests *V. pourtalesi* on the Scotian Shelf is unique and represents a previously undescribed population.

5.2.3 Bottom Substrate

Based on the observations documented here, *V. pourtalesi* grows on a variety of substrates. In the CAMPOD transect, the substrate was mostly comprised of gravel covered with a layer of silt, whereas the substrate ranged from silty and hummocky to gravel habitat along the ROPOS transect. One of the differentiating features of *V*.

pourtalesi from *Pheronema carpenteri* is that it does not have an extensive basal spicular component, limiting its ability to anchor in soft substrate. *V. pourtalesi* tends to occur on hard substrate typically comprised either of stone or gravel, although in some cases, as observed here, it also occurs on the base of the cold water coral, *Paragorgia arborea*. Fishermen also reported "Russian Hats" as being found on hard substrate (Table 5.3).

5.2.4 Currents

The distribution of sessile epifauna is often related to current, which regulates food transport and availability to suspension feeders. The distribution of deep-water corals has been related to current speed (Genin et al., 1986; De Mol et al., 2002) and corals on the Scotian Shelf slope areas are most abundant in the channels between the banks, where currents are higher than those in adjacent areas. Rice (1990) postulated that the population of *Pheronema carpenteri* occurred downstream and downslope of higher current areas, and this has been confirmed by more recent current measurements (White, 2003).

Although *V. pourtalesi* have been reported, by fishermen's information and video transects, in the Northeast Channel which has high currents, the sponge does not attain the same densities found in the lower current areas near the Emerald Basin and Sambro Bank. The Emerald Basin is known to have an intermediate nephaloid layer (Azetsu-Scott et al., 1995), and a similar a phenomenon exists on the Porcupine Bank in the Northeast Atlantic (Thorpe & White, 1988). This nephaloid layer may facilitate an increased food source that contributes to the large patches of sponges in these two areas.

5.2.5 Community Structure and Associated Megafauna

The numerous dominant benthic epifauna in the Emerald Basin is *V. pourtalesi*, with 1184 individuals quantified from the ROPOS video transect. Of these, 39 sponges were dead or presumed dead given the level of sediment cover on the external surface and the lack of any visible sponge surface. Fish and other invertebrates were also observed along the transect. The ocean pout (*Zoarces americanus*) was the most frequently observed fish species (n=55), followed by redfish (*Sebastes* spp.) (n=39), hake (*Merluccius merluccius*) (n=17), more than one species of flatfish (n=15), and 5 gadoids. In addition to other sponge species (n=139), shrimp (likely *Pandalus borealis*) was the most frequently observed invertebrate (n=184), followed by rock crab (*Cancer borealis*), for which 50 individuals were recorded. Cerianthid anemones and other sponges were the only other sessile invertebrates that were observed.

Several individual sea stars, *Henricia* sp. (but presumed to be *sanguinolenta*) on the surface of *V. pourtalesi* were also observed, suggesting that *Henrica* feeds on the sponge. This has been observed in Antarctic environments (Dayton, 1979) where starfish actively prey on Rossellid sponges (Dayton, 1979). Witman and Sebens (1990) have documented predation by *Henricia* spp. on subtidal sponges in the Gulf of Maine.

5.2.6 Life Cycle and Reproduction

There is no published information on the reproduction of *V. pourtalesi*. Dayton et al. (1974) report small Rossellids adjacent to parent sponges and suggests that this is likely the result of asexual budding. Observations of *V. pourtalesi* show small sponges clustered around larger "adults" (Figure 5.5 e), however it is not known whether the smaller sponges are the result of larval settlement or asexual reproduction. Growth rates

for hexactinellids have been quantified in a handful of studies, reviewed by Leys et al. (2007), and are known to vary with species and geographic location. Dayton's (1979) estimates of growth rate ranged from 2 cm -16 cm in 10 years in two species of Rossellids, with larger sponges growing minimally or not at all. Growth rates have been measured in two species of hexactinellids found in the Northeast Pacific, with growth rates of 2 cm/ yr in *Rhabdocalyptus dawsoni* (Leys & Lauzon, 1998) and linear growth rates for *Aphrocallistes vastus* of 1-3 cm/yr (Austin, 2003). The presence of *V. pourtalesi*, between 10 to 15 cm in height on discarded fishing line observed in the ROPOS transect, also suggests that growth rates may be on the order of centimeters per year.

5.2.7 Threats and Limiting Factors

The main threat to the *V. pourtalesi* population on the Scotian Shelf is bottom trawling. Observer data from 1977-2001 show that high catches of sponges, which are assumed to be the 'Russian Hat' sponge, occurred in the pollock fishery (Table 5.4), and fishermen's information (Table 5.3) clearly indicates how the sponges were caught and the geographical areas in which they were caught. The majority of bottom trawling for pollock in the areas where *V. pourtalesi* is found occurred in the mid to late 1980's. The fact that dense patches were seen here in video transects more than a decade later suggests that not all the sponges were removed / damaged and that recovery post-disturbance is possible. Given that little is known about the ability of glass sponges to survive air exposure, and that efforts to keep glass sponges alive in the laboratory following transfer from their natural environment, have generally been unsuccessful (Leys et al., 2008), it is assumed that there is 100% mortality of these animals once

caught by fishing gear and exposed to air. While observer records provide an estimation of the amount of sponges caught, the actual damage to the population cannot be accurately estimated by trawl catch as the catchability of the sponges is unknown.

The limitations to the distribution of this species are also unknown. Further research and recording of benthic currents, food availability, and investigations into the reproduction and larval transport of these sponges is needed in order to fully understand their seemingly limited distribution on the Scotian Shelf.

Table 5.1. Data Sources for identification of *Vazella pourtalesi* distribution on the Scotian Shelf.

Data Source	Details
Nova Scotia Museum Records	Unidentified specimens collected by Honeyman in 1887, description "unattached, off Sambro Bank"
Local Ecological Knowledge (Fishermen's interviews)	15 Interviewees in Nova Scotia, 6 identified location of "Russian Hats"
Fisheries Observer Data	1977-2001
ROPOS Transect	C/G Martha Black, August 2001
CAMPOD Transect	CGV Hudson September 2002

Table 5.2. *In situ transect* location information for ROPOS and CAMPOD video transects of *V. pourtalesi* on the Scotian Shelf collected in August 2001 and September 2002 respectively.

Source	Location						
	Latitude (°I	N)	Longitude	e (°W)	Depth Range (m)	Length (m)	
	Start	End	Start	End Transect			
	Transect	Transect	Transect				
ROPOS	43.81914	43.84177	-63.0128	-63.0519	202 - 275	4021	
635 CAMPOD	44.25091	44.25199	-62.5918	-62.5887	187	201	

Table 5.3. Observations by fishermen of "Russian Hats" on the Scotian Shelf, collected through local ecological knowledge interviews.

Participant	Species / Description	Gear / Species
Number		
14	Russian hats on the end of Georges and off Halifax on Sambro Bank, you would get a load	otter trawl / groundfish
15	of Russian Hats Russian hats off Halifax, 30-40 miles SE of	otter trawl / groundfish
	Halifax in deep water, only place I've ever seen them.	
16	Russian Hats in the Patch	gillnet & longline / groundfish
18	Russian Hats off Sambro, that is the only place you'll find them. Eastern side of Emerald Basin, on the hard bottom	gillnet & longline / groundfish
19	Get Russian hats when trawling for redfish and pollock	otter trawl / redfish
20	Spiders nests and Russian Hats on the Western Edge of Sambro Bank. Would get a ton of Russian Hats when looking for Redfish	otter trawl / groundfish

Table 5.4. Fisheries observer records on the Scotian Shelf from 1977-2001, with total sets, depth and mean and maximum sponge catch.

Area	N (sets)	Mean Depth (+/-SD) (m)	Mean Sponge Catch (+/- SD) (kg)	Max Sponge Catch (kg)
Scotian Shelf Fishery	296969	229 (101)	0.85 (33.44)	5900
Pollock	21810	186 (53)	7 (108)	5900

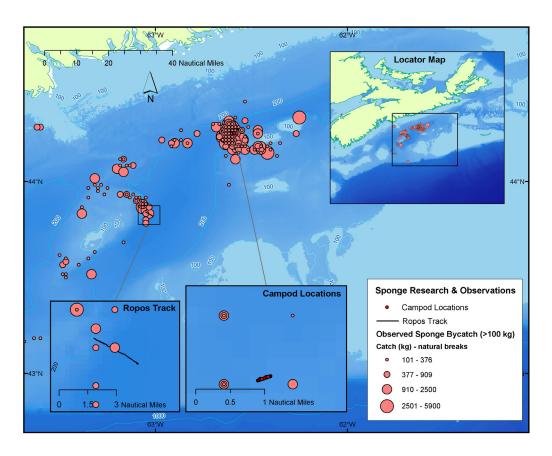


Figure 5.1 Scotia Fundy Fisheries Observer records on the Scotian Shelf from 1977-2001. Sponge catch per unit effort indicates high catches in area of the *V. pourtalesi* patches. *In situ* video transect locations with ROPOS and CAMPOD, in August 2001 and September 2002 respectively.

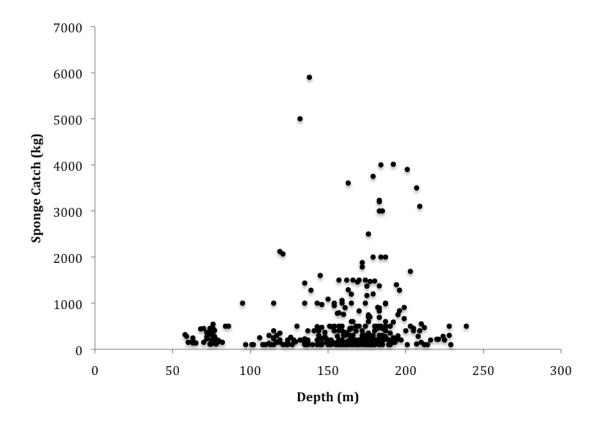


Figure 5.2. Sponge catch > 100 kg as recorded by fisheries observers, in the geographic region bounded by 42° N and 44° N and 62° W and 64° W Maximum catch recorded is 5900 kg, with several catches > 2000 kg.

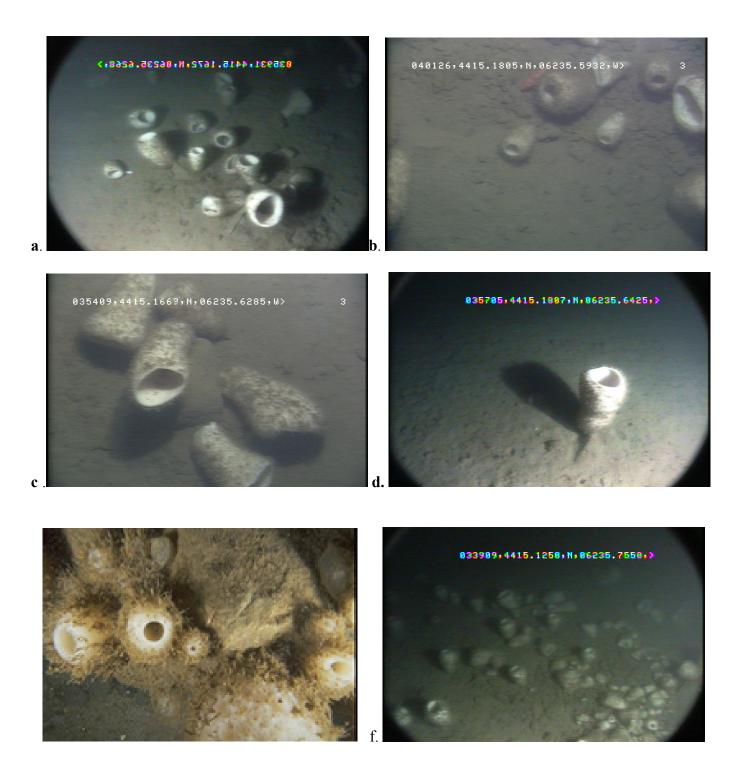


Figure 5.3. *Vazella pourtalesi* (Schmidt, 1870) from the Scotian Shelf; photographs taken using the CAMPOD system., a), d) and f) are oblique shots, with a field of view of 4m and b), c) and e) are taken with the vertically situated camera with a 2m field of view.

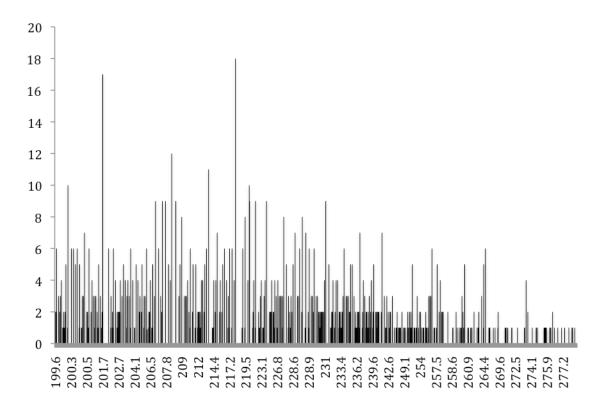


Figure 5.4. Number of individuals of *V. pourtalesi* observed with depth along the ROPOS transect.

Chapter 6

Closed Area Effects on Sponges (Porifera) in the Gulf of Maine, Northwest Atlantic

6.0 Introduction

Fishing with bottom-tending gear on the sea floor alters sea floor habitat and species composition (Dayton et al., 1995; Thrush & Dayton, 2002), resulting in changes to the benthic species diversity (Hiddink et al., 2006; Hixon & Tissot, 2007; Ragnarsson & Lindegarth, 2009), habitat complexity and community structure (Jennings & Kaiser, 1998; Auster & Langton, 1999; Ardizzone et al., 2000; Kaiser et al., 2000; Watling, 2001), benthic productivity (Hermsen et al., 2003; Queirós et al., 2006), and ecosystem functioning (Tillin et al., 2006; De Juan et al., 2007; Olsgard et al., 2008). The incidence and persistence of fishing impacts vary with substrate (Thrush et al., 2001; Kenchington et al., 2006; Hiddink et al., 2007) and intensity and frequency of fishing effort (Collie et al., 1997), as well as levels of natural disturbance (Henry et al., 2006; Hiddink et al., 2006). Both short-term (see review of experimental studies in (Pitcher et al., 2009) and long-term impacts of bottom fishing (Philippart, 1998; Hall-Spencer & Moore, 2000; Veale et al., 2000; Tillin et al., 2006) have been investigated, with some focus on cumulative impacts (Foden et al., 2010) and estimates of recovery times for benthic communities (Gilkinson, 2005; Kaiser et al., 2006; Hiddink et al., 2007; de Marignac et al., 2009).

Marine sponges (Phylum Porifera) are known to provide structure on the seafloor (Barthel 1992, Butler et al 1995, Freese et al. 1999, Lindholm et al 1999, (Cook et al., 2008) and can occupy a significant portion of the benthos at a broad range of depths.

Benthic species that provide "secondary substrates" or significant additional habitat structure and heterogeneity are of particular interest as their damage or removal necessarily affects any associated species (Dijkstra & Harris, 2009; Voultsiadou et al., 2010). Based on observations of sponges in situ, species and species complexes can occupy 10-90% of the substrate (Table 6.1).

Compared to tropical environments, and coral reef ecosystems in particular, sponges in the Northwest Atlantic have been the subject of relatively few studies. Initial biogeographic descriptions (Lambe 1896, Lambe 1900, Hartman 1958; Old, 1941; De Laubenfels, 1949) were followed by limited research on basic ecology, with a particular focus on the Gulf of Maine ecosystem (Witman & Sebens 1985, Sheild & Witman, 1993; Leichter & Witman, 1997; Ginn et al., 2000). Although experimental studies have examined the potential impact that sponges, as structural habitat, can have on the survival of fishes in the Northwest Atlantic (Lindholm et al., 1999; Scharf et al., 2006), the species composition of the sponge fauna in the Northwest Atlantic is not well understood; for example, comprehensive taxonomic keys to the area do not exist and those that do (Witman & Sebens, 1990) identify only half of the sponges to species level.

Investigations of sponges in the Bay of Fundy have resulted in the publication of several first accounts of species for the area (Ginn et al. 2000, Fuller et al., 1998), in addition to new descriptions (Ginn et al., 1998). In response to recent fisheries management requests for information on vulnerable marine ecosystems in order to more adequately address the impacts of fishing, broad-scale distribution patterns at the phylum level have recently been identified (Kenchington et al., 2010) with a notable emphasis

sensitive circumboreal sponges (Fuller et al., 2008; ICES, 2008, 2009; Kenchington et al., 2010).

As a partial response to the decline of groundfish populations in the Gulf of Maine, spatial fisheries closures have been used as management measure since the mid 1990's to reduce fishing effort (Murawski et al., 2000; Ward et al., 2001; Stokesbury, 2002) (Link et al., 2005). One of the added benefits of these closed areas is that they offer the opportunity to examine recovery of the seafloor following the cessation of fishing activity. The Western Gulf of Maine (WGOM) closed area was established in 1998 as part of efforts to rebuild groundfish populations. The closed area overlaps the boundaries of the Stellwagen Bank National Marine Sancturary which was created in 1992 primarily for marine mammal protection, albeit without restrictions on fishing activity (Brailovskaya, 1998). While there is little added protection within the Sanctuary, its establishment necessitated an increased focus on research as part of the comprehensive management plan (NOAA, 2008). Establishment of the WGOM closed area offers a unique opportunity to examine potential differences between sponge communities inside and outside of a marine area that has been closed to fishing.

While other studies have examined the impact of trawling and dredging on sponges, necessarily focusing on short-term impacts and immediate damage or removal of sponges following the passage of bottom-fishing gear (Pitcher et al., 2009), the recovery of sponge communities has been less well studied, primarily because the majority of recovery studies have examined infauna in mud habitats, and meta-analyses have tended to lump colonial epifauna (Kaiser et al., 2006). The removal and/or damage of sponges resulting from gear impact has been estimated to range from 9% to 89.9%

(Table 6.2), depending on the type of gear, sponge morphology, and disturbance history. In a meta-analysis of trawl impact studies, Collie et al (2001) predicted that sponges will be reduced by 21% when exposed to trawling.

Emergent and larger sponges have been reported to be more susceptible to trawling impacts (Freese et al., 1999; Wassenberg et al., 2002), a finding consistent with models of bottom-trawl impacts on benthic fauna, based on size (Duplisea et al., 2002). Within the Gulf of Maine ecosystem, comparisons between sites disturbed and undisturbed by fishing activity have found that benthic biomass, species richness and number of organisms (excluding colonial epifauna) can be higher at the undisturbed sites (Collie et al. (1997). Based on a video transect footage taken from Jeffrey's Ledge (located at the northeastern end of the WGOM closed area), Pugh (1999) found that sponge percent cover was significantly greater in untrawled boulder habitats than in trawled areas, and that species richness was an order of magnitude greater in untrawled areas. An analysis of video footage taken at various sites during different stages of recovery found that sponges occupied a greater percentage of the WGOM closed area 2, 4, and 6 years after trawling had ceased (Knight et al., 2006), although the relative contribution of specific sponge species to this recovery was not documented. While the study area is by no means a pristine marine ecosystem, the fact that benthic production (Hermsen et al., 2003) and species diversity (Collie et al. 1997) can be altered in a short time frame has important consequences for the maintenance of ecosystem function and in the role that structural species play on the seafloor.

The over-arching objective of the present study was to describe and compare the sponge communities on adjacent gravel habitats in the WGOM closed area and an area

open to fishing activity. This descriptive work allowed me to draw inferences pertaining to the temperate benthic communities recovering from the impacts of fishing. Specifically, I compared 1) sponge species diversity using the Shannon Wiener (H') index; (2) sponge species richness with species number as the metric; (3) sponge species composition and morphology; and (4) sponge volume per station as a proxy for biomass. Species that were associated with sponges were recorded as well. Based on the results of others, and on generally accepted ecological trends following trawling disturbance, I predict that species diversity and species richness will be higher within the closed area compared to the area being actively fished. I also predict that biomass will be higher within the closed area, assuming that sponges have had sufficient time to recover from the fishing-induced disturbance. Given that sponge morphology has been found to be a defensible proxy for sponge diversity (Bell & Barnes, 2001), I expect sponge morphological composition to be different between the closed and open areas, with closed areas supporting larger and more emergent forms. Finally, given the role that sponges can play as hosts to other species, I also expect that areas containing higher volumes of sponges, and those with branching or mounding morphologies, will be characterized by a greater number of associated species.

6.1 Methods

6.1.1. Study Area and Fishing History

The WGOM closed area is located in the southwestern region of the Gulf of Maine, running from $43^{\circ}15^{\circ}$ latitude south to $42^{\circ}15^{\circ}$, and west to east from longitude $70^{\circ}15^{\circ}$ to $69^{\circ}45^{\circ}$ (Figure 6.1). During the period from 1998 - 2000, the WGOM closed area was closed to fishing, with the exception of limited shrimp trawling in muddy

habitats during the winter months. Shrimping does not occur in the gravel habitat sampled for this study. Sampling was undertaken on hard bottom (gravel to cobble) areas on Stellwagen Bank, within the Stellwagen Bank National Marine Sanctuary (SBNMS), Gulf of Maine. The Sanctuary encompasses 1435 square kilometers 892 and was declared a sanctuary in 1992, primarily because of the marine mammal populations that frequented the area (NOAA, 2008). Both recreational and commercial fishing are allowed within the sanctuary boundaries, and the only restriction on bottom fishing is within the overlap area of the WGOM and the SBNMS.

6.1.2 Sampling Design

Samples were collected from June 12-16th, 2000, by the National Oceanographic Atmospheric Administration (NOAA) ship R/V *Ferrel*, using a 1 m wide naturalist dredge fitted with a 6 mm mesh bag. Hard-bottom sites within the Stellwagen Bank National Marine Sanctuary and the WGOM closed area were chosen based on backscatter data on USGS multibeam bathymetry maps (Valentine 1999) on either side of the closed area boundary (Figure 1). Most fishing vessels in the area have electronic Vessel Monitoring Systems (VMS) that help to enforce fishing restrictions. For the purposes of the present study, it is assumed that stations inside the protected area were unfished. Stations were chosen on the top of Stellwagen bank, which has a low topography, making sampling with the naturalist dredge possible and reducing the risk of gear loss. Twenty stations were sampled in total, ranging from 37 to 67m in depth, with twelve stations located outside the WGOM closed area and 8 inside (Table 6.2). Tow speed averaged 1.4 knots/ hour and duration of tows ranged from 1.5 to 3.0 minutes.

6.1.3 Sample Processing at Sea

The total volume of the dredge contents was shovelled into a 5 l bucket and measured in order to standardized sponge volume collected per volume of tow. Total sponge volume was measured by water displacement in a 1 L graduated cylinder. Volume of individual sponges was measured where possible and larger samples of the same species were combined for total volume. Morphological categories, including for each sponge taxon were recorded immediately upon observation on deck to avoid any effect of water loss or drying over time. These categories, as defined by Bell & Barnes (2001), were encrusting, massive, globular, pedunculate, tubular, flabellate, repent, arbourescent and papillate. All samples were preserved in 4% seawater buffered formalin solution upon collection. Fauna associated with the sponges were recorded upon collection and preserved with the host specimen.

6.1.4 Sponge and Associated Species Identification

All samples were sieved with a 0.5 mm sieve and associated macrofaunal species were identified to the lowest possible taxon. Sponge taxon identification was based on keys prepared by Arndt (1935), Ackers et al. (1992) and Van Soest et al. (2000). Spicule preparations were made as described in Ginn et al. (1998). Species associated with the sponge samples were recorded on a presence/absence basis, given that the sampling method did not lend itself to the provision of accurate quantitative results.

6.1.5 Statistical Analysis

Diversity was calculated using the Shannon-Wiener diversity index, H'. Species richness was calculated simply as the number of species found in the trawled and

untrawled areas. Sponge morphology was described for each species in accordance with Bell and Barnes (2001). Sponge volume was standardized to tow volume collected and then square-root transformed. Differences in species composition between the two sites were tested using the Bray Curtis similarity measure. Morphological differences were compared with a non-parametric chi square test. Total sponge volume for dredge tows in the trawled and untrawled area were compared using a one sided t-test and a non-parametric Wilcoxon test. Data analyses were undertaken using SPLUS and PRIMER (version 5.2.8 (Clarke & Warwick, 2001)) statistical software.

6.2 Results

Of the original 20 stations selected for sampling, 12 were used in the final analysis: 6 stations were located inside the closed area (stations 4,5,13,14,15,17) and 6 outside the closed area (stations 1,2,9,10,14,20). No data were collected at stations 3, 6 or 7 because of damage incurred by the collecting net. Stations 4, 8, 12, 18 and 19 were all on sandy substrate and hence not useful in the comparison of gravel habitats.

6.2.1 Sponges and Associated Fauna

A total of 15 species of sponges were identified from dredge samples, representing approximately one quarter of the ~70 species of sponge that have been identified in the Gulf of Maine (see Appendix III). Table 6.3 lists sponge species collected in the closed and open areas of Stellwagen Bank and their corresponding morphologies. *Haliclona oculata* and *Isodictya deichmannae*, both aborescent or branching sponges, were found in the closed area only. *Iophon* sp. was the most abundant

and most frequently collected taxon, being present in 7 out of 10 stations. (Given the need for a taxonomic revision of *Iophon* in the North Atlantic (Dr. Rob Van Soest, University of Amsterdam, Zoological Museum of Amsterdam, personal communication,), no members of the genus were identified at the species level. The collection of *Myxilla brunnea* represents a new record for the Northwest Atlantic.

Several species were observed to be associated with sponges either within the canals of the sponge itself or on the external surface (Table 6.4). *Iophon* sp., the most abundant by volume within the closed area, housed the bivalve *Hiatella arctica* the brachiopod *Terebratulina septentrionalis*, three different nemerteans and three species of polychaete, including *Amphitrite cirrata* and *Thelepus cinncinatus* both of which were within the sponge body. Two species of bryozoa, *Crisia eburnea* and *Idmidronea angulatus*, as well as the polychaete *Filograna implexa* were found at the base of the *Iophon* sponge, where it attached to the gravel substrate. Others sponges with associated fauna, which included *Psuedosuberites sulphereus*, *Polymastia infrapilosa* and *Hymedesmia* sp., did not have any infauna associated with them; rather, all species associates were located on the sponge surface.

6.2.2 Species Diversity and Community Composition

Shannon-Weiner species diversity (H') was calculated based on volumes of sponge species collected as a measure of abundance. The volume of total sponge in dredge tows ranged from 0 to 2.5 l (wet weight) with tow volume ranging from 1.0 to 72.5 l. Species diversity outside the closed area was an order of magnitude greater than that within the closed area (H' = 0.63 and 0.06, respectively). Species richness was equal in trawled and untrawled areas with 8 species sampled in each.

The Bray Curtis dissimilarity calculation resulted in a dissimilarity of species composition of 79.48 % between the trawled and untrawled sites (Table 6.5). *Iophon* sp. and *Halichondria panicea* contributed the greatest amount of between inside and outside the closed area difference (0.67 and 0.33, respectively). Morphological differences were noted between the closed and open areas, however, a non-parametric chi-square comparison did not result in a statistical difference between the two areas. Differences in sponge biomass inside and outside the closed area were compared using a one sided t-test (p<0.042, n=12 for inside the closed area and n=7 for outside the closed area) (Figure 2). Non-parametric Wilcoxon test yielded similar results. Variability in sponge catch among tows was high, reflecting the patchiness of benthic communities, and likely the method of dredge sampling. Total sponge volume collected outside the closed area was 5.8% of that inside the closed area.

6.3 Discussion

6.3.1 Sponge Species and Associated Fauna

The present study contributes to knowledge of marine sponges in the Gulf of Maine, particularly given that the sponge fauna on gravel habitats of Stellwagen Bank had not been previously investigated. With the exception of *Myxilla brunea*, all sponges identified herein have been documented previously in the Gulf of Maine. Other researchers have tended to focus their work on the more rugose boulder habitat of Jeffrey's Ledge (Pugh 1999; Knight et al. 2006) or on subtidal rock ledges (Witman & Sebens, 1990) (Leichter & Witman, 1997). When compared to gravel habitats on the nearby Scotian Shelf, the present study suggests that the sponge fauna is richer and

potentially more diverse (Henry et al., 2006) in the Gulf of Maine, although there has been no comprehensive attempt at cataloguing the sponges on the Scotian Shelf. Dredge sampling is not the most ideal method for examining benthic faunal assemblages, however, it does allow for species identification, which cannot be done for most sponge species using non-extractive methods.

Species associated with sponges in northern waters, tend to be facultative inhabitants and represent the fauna in the local geographic area rather than being host-specific symbionts (Klitgaard, 1995). A direct relationship between sponge volume and number of species and number of individuals of associated fauna has been reported for some species (Westinga & Hoetjes 1981)(Frith, 1976; Koukouras et al., 1985) while other factors, such as depth (Pearse 1949) and morphology (Koukouras et al., 1996; Neves & Omena, 2003), have been reported to have more of an effect for others. *Iophon* sp. represented the greatest biomass of any of the species collected, and also had the greatest number of infaunal species associated within its canals and on its surface, thus confirming its importance as a habitat provider on the seafloor. While the diversity of sponges was lower in the areas closed to trawling, the species richness of associated fauna was greater.

6.3.2 Comparison of Areas Closed and Open to Trawling

Basic information on sponge growth and reproductive rates of the sampled species is generally not known. Leichter & Witman (1997) reported the growth of *Halichondria panicea* on vertical rock faces in the Gulf of Maine to be, on average, 5% increase of biomass per week, which extrapolates to a 260% increase annually (although this is almost certainly an over-estimate, once seasonal effects have been accounted for)

Halichondria panicea, the second most abundant sponge, contributed to the disimmilarity between the closed and open areas which indicated that the closed area had increased in biomass during the two years after fishing had ceased. Using video analysis on Jeffrey's Ledge, Pugh (1999) observed that *Iophon* spp. are significantly more abundant in areas unaffected by trawling. As an indicator of trawling activity, Pugh (1999) included the presence of bald areas on top of boulders filled in with sponge, which suggests that sponges are among the first colonizers after disturbance (an observation also noted by J. Collie, Professor of Oceanography, University of Rhode Island, pers. comm). This conclusion is consistent with the recovery observed by Knight et al. (2006) in fished areas 4 and 6 years after the cessation of trawling.

Pugh (1999) noted a difference in sponge species richness, using presence / absence data in trawled and untrawled areas, finding 13 species present in the untrawled areas and 4 in the trawled area. In my research, species richness was similar in open and closed areas, but the species composition was not the same. It is not clear if the species difference was simply an artifact of sampling, or if some species tend to be more resilient to disturbance. While smaller and encrusting sponges are able to withstand the effects of trawling to a greater extent than larger sponges (Moran & Stephenson, 2000), I found no statistical difference in sponge morphologies in the closed and open sites.

One of the arguments used in favour of fisheries exclusion zones is the maintenance and enhancement of biodiversity, and bottom trawling and dredging has been found to reduce benthic species diversity over a variety of substrates (Thrush & Dayton, 2002). Here, I found lower sponge species diversity inside a closed area, rather than the expected result of higher diversity. This result can be attributed to the substantial

volume increase in one sponge, *Iophon* sp., an increase that has also been documented by Pugh (1999) and Knight et al. (2006).

The present study shows that it is important to consider species function, as well as species diversity, when evaluating the success of a closed area. The increase in *Iophon* sp. represents an increase in benthic complexity and habitat structure as the area studied here recovers from the impacts of disturbance. The effect of habitat structure on diversity in marine systems has been examined for several biotic features, including coral reefs (Ohman 1998), sea grass beds (Lee 2001, De-Troch 1996) and kelp forests (Edwards 1980, Dayton 1985, Smith 1996). Thrush et al. (2001) examined the importance of smallscale habitat structure in soft sediments and found important links between epifaunal presence and total species diversity. In Australia, areas with high densities of structureforming bryozoans colonies have been closed to fishing with the objective of protecting associated commercial fish stocks (Bradstock and Gordon 1983). In the Gulf of Maine sponges are the main species providing biogenic structure on the gravel habitat sampled. Removal of these species, particularly those with massive morphology, decreases habitat structure, leaving juvenile fish species more open to predation (Lindholm et al 1999). Auster et al (1996) examined three sites in the Gulf of Maine, comparing the effects of trawling on various substrates. They found that in areas of no trawling, near Swan Island, the percentage of area covered by epifaunal species was significantly different inside and outside the closed area. Areas observed on Jeffrey's Bank in 1987, prior to trawling activity, ranged from 10 to 25% sponge cover. The same areas in 1992, post trawling, had no more than 7% sponge cover.

Witman (1999) indicates that physical disturbance through natural causes is rare at depths greater than 30 m in the Gulf of Maine. The shallowest site in his study was 37 m, thus eliminating physical disturbance as a cause of lower biomass in sites outside the closed area. Predation pressure by starfish, specifically *Henricia saunguinolenta* (Muller) (Sheild & Witman 1993), can lead to a decrease in sponge biomass of the branching sponge *Isodictya* spp, however, *H. sanguinolenta* was not frequently observed in the dredge contents examined in the current research and is unlikely to be responsible for the large difference in biomass between the two areas.

One of the major obstacles in assessing recovery from fishing impacts is the lack of true controls, particularly in areas that have been fished for decades with bottom-tending gear. Recovery from the impacts of fishing gear has been investigated on soft bottoms (Pravoni 1998) and monitoring continues to take place on rocky habitats (Collie et al 1998, Freese et al 1999). Most trawl studies have taken place in areas that have been impacted by fishing at some point, so the baseline for recovery most likely does not represent a virgin state, which is problematic in assessing the true effects of fishing on natural ecosystems (Tegner & Dayton 1997). Monitoring of closed areas and of non-commercial by-catch can help develop information for both removal of structure forming species and recovery of such populations post fishing impacts.

6.4 Conclusion

The work presented here suggests that marine sponges in the Northwest Atlantic are affected by fishing and that release from fishing pressure provides necessary conditions for recovery. Although there was a relatively low biomass of sponge collected

in this study, they were the most abundant epifaunal structure. Repeated sampling over several years is needed to determine successional patterns, differences in species recovery and community composition. Simple morphological characteristics (Bell and Barnes 2001) may be used as surrogates for more direct sampling methods. This could result in simple and less labour-intensive monitoring techniques. However, monitoring of habitat recovery has not been an integral part of closed-area management.

Table 6.1. Literature information on relative marine sponge abundance at various geographical locations.

Location	Substrate	Sponge Species	Area covered or density	Depth	Source
Santa Marta, Columbian Carribean	Zoned reef	86 species in complex	10-18%	5-35m	(Zea, 1993)
Ammen's Rock, Gulf of Maine	Vertical rock surface	Halichondria panicea	43%	~30 m	(Leichter & Witman, 1997)
North Ammen's Rock, Gulf of Maine	Vertical rock surface	Halichondria panicea	46%	~30 m	(Leichter & Witman, 1997)
Florida Bay, Lower Arsnicker Keys	Rocky bottom	Speciospongia vesparium, Ircinia campana, Hippospongia laehna, Ircinia felix, Spinosella vaginalis, Vergangia longissima	9%		(Butler et al., 1995)
Cape Armitage, McMurdo Sound, Antarctica	Rocky bottom	Rossella racovitzae (most dominant, plus other species)	55%	30-60 m	(Dayton et al., 1974)
Northeast Pacific, Abyssal plain	Soft bottom	Hyalonema sp.	72.6-180.8/ha	4100 m	(Beaulieu, 2001)
Northeast Coast, New Zealand	Vertical rock surface	Encrusting & discrete sponges	46%	12m	(Ayling, 1983)
Northeast Coast, New Zealand	Flat rock platforms	Polymastia sp., Stylopus sp,	14%	18m	Ayling, 1980
Faroe Island, Northeast	Shelf and	Geodia barretti, G.	90% of benthic	200-	(Klitgaard & Tendal,
Atlantic	slope areas	macandrewi, Isops phlegraei, Stryphnus ponderosus	biomass	600 m	2004)
Hecate Strait, North Pacific	Horizontal and vertical surface face	Chonelasma calyx, Farrea occa, and Aphrocallistes vastus	700km ²	90-210 m	(Cook et al., 2008)

Table 6.2. Literature information on the impacts of fishing on marine sponges.

No. of tows / experimental	Substrate	Location	Gear Type	Results	Source
type					
1 / BACI*	Sand over rock	Georgia coast, Southeast Atlantic	Roller rigger trawl	31.7% of sponges damaged	(Van Dolah et al., 1987)
1	Sand / pebble	Biscayne National Park, Gulf of Mexico	Roller frame trawl	9% damaged or removed from bottom	(Ault et al., 1997)
5	Sand / pebble	Biscayne National Park, Gulf of Mexico	Roller frame trawl	25% of sponges damaged or torn loose,	(Ault et al., 1997)
8 weeks of shrimp fishing (10-12 boats, 5 nights per week)	Sand	Biscayne National Park, Gulf of Mexico	Roller frame shrimp trawl	50% of sponges were torn loose from the bottom	(Tilmant, 1979)
1	Pebble, cobble, silt	Eastern Gulf of Alaska	N'oreastern trawl with rockhopper discs	67% vase sponges and 14% of finger sponges were damaged	(Freese et al., 1999)
1	Coarse sand / some gravel	North West Shelf of Australia	Pair trawl	89% removal of benthic organisms (sponges were dominant taxa)	(Sainsbury et al., 1992)
1 / BACI	Coarse sand / some gravel	Northwest Shelf of Australia	McKenna fish trawl	15.5% of sponges were removed	(Wassenberg et al., 2002)
	Coarse sand	Northwest Shelf of Australia	Otter trawl	14.5%	(Moran & Stephenson, 2000)
1 / BACI	Coarse sand / some gravel	Northwest Shelf of Australia	Shrimp trawl	After 6 months, 6% difference in sponge biomass	(Pitcher et al., 2009)

^{*} BACI = before / after control/ impact

Table 6.3. Locations of sampling stations on Stellwagen Bank, inside and outside of the Western Gulf of Maine Closed Area.

Date	Stn	Tow	Depth (m)	Dredge on Bottom (Lat)	Dredge on Bottom (long)	Dredge off Bottom (Lat)	Dredge off Bottom (Long)	Tow Duration (mins)	Volume of tow contents (L)	Speed over bottom (NM)	Bottom Type	Inside / Outside Closed Area
				Data								Outside
15/06/00	1	1	69	missing				3	3	1.5-2	Gravel	
15/06/00	1	2	67	42 25 931	70 13 925	42 25 976	70 14 128	3	12	1.5-2	Gravel	Outside
15/06/00	2	1	62	42 23 786	70 14 308	42 23 861	70 14 553	3		1.2-1.9	Gravel	Outside
											Sand/ shell	Not incl.
13/6/00	3	1		42 14-717	70 14 893	42 14 694	70 15 111	3	60	2.6-3	debris	
											coarse	Inside
12/06/00	4	1	49	42 16 959	70 11 424	42 16 951	70 11 477	1.5	27	1.3-1.7	sand	
12/06/00	4	2	53	42 17 020	70 10 791	42 16 969	70 10 908	1.5	24	1.2-1.5	Gravel	Inside
4.0.16.10.0	_			40.504			=0.11.005	_			gravel and	Inside
13/6/00	5	1	51	42 19 581	70 11 774	42 19 557	70 11 802	2	7.5	1.0-2.0	rock/sand	
14/06/00	6	1	49	42 22 387	70 15 119	42 22 438	70 15 472	5	15	1.5-2.4	Sand	Not incl.
14/06/00	7	1	57	42 22 971	70 14 276	42 22 975	70 14 480	3	5	1.7-2	Sand	Not incl.
10/6/00	0		2.6	10.01.100	50 14 250	12 20 520	50 15 415	2		0015	coarse	Not incl.
13/6/00	8	1	36	42 21 120	70 14 359	42 20 539	70 15 415	3	60	0.8-1.5	sand	0 1
14/06/00	9	1		42 21 988	70 15 452	42 22 212	70 15 659	5	12	0.8-1.4	Sand	Outside
14/06/00	9	2	44	42 21 889	70 15 365	42 21 933	70 15 695	5	12	1.8-2	Rocks	Outside
15/06/00	10	1	54	42 23 970	70 15 880	42 24 004	70 16 001	3		1-1.5	Gravel	Outside
1.5.10.6.10.0				10.01.050	5 0.15.0 2 0	12 24 100	50 15 005	2		1.6	rocky,	Not incl.
15/06/00	11	1	57	42 24 372	70 15 820	42 24 408	70 15 995	3	6	1.6	muddy	NT 4 1
12/6/00	10	1	25.0	42 20 550	70 15 250	42 20 520	70 15 415	2	20	1 1 5	Coarse	Not incl.
13/6/00	12	1	35.8	42 20 558	70 15 359	42 20 539	70 15 415	3	30	1-1.5	sand	Tarai da
12/06/00	13	1	50	42 17 537	70 10 750	42 17 462	70 10 870	3		0.8-1.2	Gravel and rock	Inside
12/00/00	13	1	30	42 17 337	70 10 730	42 17 402	70 10 870	3		0.6-1.2	Coarse	Inside
12/06/00	13	2		42 17 531	70 10 907	42 17 467	70 11 041	3		1.2-1.6	sand	Histae
12/00/00	13	2		74 17 331	/0 10 90/	72 1/40/	/0 11 041	3		1.4-1.0	sand/rock/	Inside
12/06/00	13	3		42 17 506	70 10 839	42 17 449	70 10 986	3		1.2-1.4	gravel	msiac
14/06/00	14	1	57	42 17 300	70 10 839	42 17 449	70 10 986	3	1.5	1.2-1.4	rock	Outside
17/00/00	17	1	31	TZ 10 /0J	70 20 040	-T2 10 / 70	10 20 990	3	1.3	1-1.3	rocks,	Outside
14/06/00	14	2	57	42 18 905	70 21 290	42 18 947	70 21 473	3	3	1-1.5	some sand	Outside

Table 6.3 Continued.												
Date	Stn	Tow	Depth (m)	Dredge on Bottom (Lat)	Dredge on Bottom (long)	Dredge off Bottom (Lat)	Dredge off Bottom (Long)	Tow Duration (mins)	Volume of tow contents (L)	Speed over bottom (NM)	Bottom Type	Inside / Outside Closed Area
13/6/00	15	1	56	42 18 050	70 10 779	42 18 049	70 10 816	3	12	0.8-1.5	rock/sponge	Inside
13/6/00	16	1	58	42 19 033	70 10 848	42 19 019	70 10 930	2		1.0-1.5	sandy	Inside
13/6/00	17	1	54.8	42 20 062	70 11 763	42 20 041	70 11 800	2	3	1-1.5	rock/gravel	Inside
13/6/00	17	2	56	42 19 979	70 11 921	42 19 966	70 11 955	3	15	0.5-1	rock/gravel rock, small	Inside Not incl.
14/06/00	18	1	42	42 22 661	70 16 380	42 22 690	70 16 663	5	2	1.5-2	boulders	
14/06/00	18	2	42	42 22 724	70 17 115	42 22 729	70 17 230	3	10	1.5-2	sandy Mostly sand,	Not incl. Not incl.
13/6/00	19	1	37	42 21 901	70 15 867	42 21 918	70 15 971	3	30		few rocks	
14/06/00	20	1		42 13 665	70 21 772	42 13 661	70 21 811	2	3	0.9-1.2	Sand	Outside
14/06/00	20	1		42 13 667	70 22 024	42 13 661	70 20 076		2	1.0-1.5	Gravel	Outside

Table 6.4. Sponge species and species morphologies found inside and outside of the Western Gulf of Maine Closed Area.

Species	Morphology
Inside WGOM Closed Area	
Polymastia mammilaris (Mueller, 1806)	papillate
Haliclona oculata (Pallas, 1766)	arborescent
Isodictya deichmannae (DeLaubenfels, 1949)	arborescent
Clathrina coriacea (Montagu, 1818)	encrusting
Halichondria panicea (Pallas, 1766)	massive
Myxilla sp	massive
Iophon sp.	massive
Psuedosuberites sulphereus (Bowerbank,	
1866)	encrusting
Outside WGOM Closed Area	
Semisuberites sp.	encrusting
Sycon protectum (Lambe, 1896)	tubular
Iophon sp.	massive
Polymastia infrapilosaTopsent, 1927	papillate
Myxilla brunnea (Hansen, 1885)	globular
Clathrina sp.	tubular
Myxilla incrustans (Johnston, 1842)	globular
Hymedesmia sp.	encrusting

Table 6.5. Faunal associates from sponges on Stellwagen Bank, recorded as presence / absence on sponges collected in dredge contents.

Sponge Species	Associated Species	
	Faunal Group	Species
Tophon sp.	Mollusca	Hiatella arctica
		Terebratulina
	Brachiopoda	septentrionalis
	Bryozoa	Crisia eburnea
		Idmidronea atlantica
	Nemertea	Amphiporus angulatus
		undetermined sp. A
		undetermined sp. B
	Polychaeta	Amphitrite cirrata
		Thelepus cinncinatus
		Potamilla neglecta
		Filograna implexa
	Decapoda	Pandalus borealis
	Echinodermata	Ophiopholis aculeata
		Terebratulina
Psuedosuberites sulphureus	Brachiopoda	septentrionalis
Polymastia infrapilosa	Echinodermata	Ophiopholis aculeata
		Henricia sanguinolenta
	Caprellida	Caprella septentrionalis
		Caprella linearis
	Nemertea	undetermined sp. C
Hymedesmia sp.	Polychaeta	Euphrosine borealis

Table 6.6. Bray Curtis similarity analysis on the percent contribution of sponge species to communities in trawled and untrawled stations.

Species	Average Abundance Untrawled Area	Average Abundance Trawled Area	Av. Dissimilari ty	Diss / SD	% Contribution	% Cumulative
Iophon sp.	0.67	0.50	18.62	0.86	23.43	23.43
Halichondria panicea	0.33	0.00	9.59	0.58	12.07	35.50
Semisuberitie s sp.	0.00	0.17	6.71	0.41	8.45	43.95
Myxilla incrustans	0.00	0.17	6.71	0.41	8.45	52.39
Hymedesmia sp.	0.00	0.17	6.71	0.41	8.45	60.84
Sycon protectum	0.00	0.17	4.66	0.42	5.86	66.69
Myxilla sp.	0.17	0.00	3.73	0.43	4.69	71.39
Pseudosuberi tes sulphureus	0.17	0.00	3.73	0.43	4.69	76.08
Polumastia infrapilosa	0.00	0.17	2.93	0.43	3.68	79.76
Myxilla brunnea	0.00	0.17	2.93	0.43	3.68	83.45
Clathrina sp.	0.00	0.17	2.93	0.43	3.68	87.13
Polymastia mammilaris	0.17	0.00	2.93	0.44	3.22	90.35

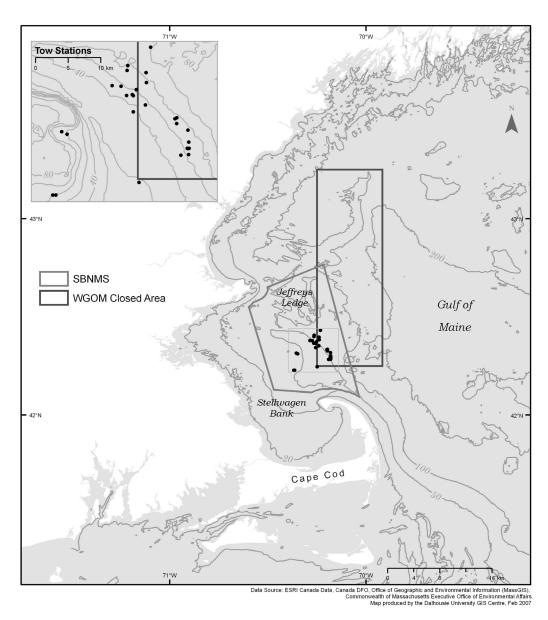


Figure 6.1. Study area, indicating the Stellwagen Bank National Marine Sanctuary, the Western Gulf of Maine Closed area and the area of overlap between the two. Stations inside and outside the closed areas are identified in the inset.

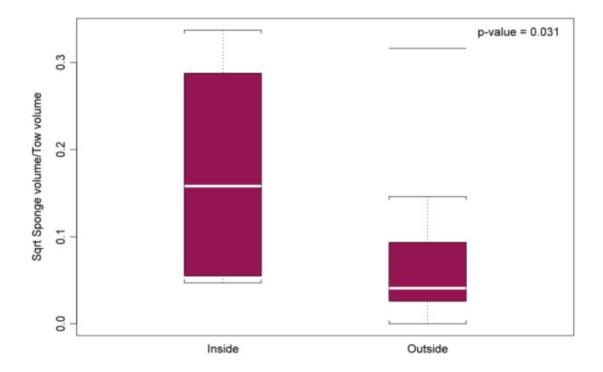


Figure 6.2 Sponge volume differences on gravel/cobble substrate inside and outside the Western Gulf of Maine Closed Area following a two year closure to fishing activity.

Chapter 7

Conclusion

7.0 Contribution to Science

This thesis contributes builds significantly on previous knowledge of marine sponge species and distribution in the Northwest Atlantic, and situates the research into the broader ecological context of ecosystem engineering in benthic environments.

The results presented in Chapter 2 contribute to the understanding of the ecosystem engineering characteristics of benthic structure forming organisms, specifically ascidians, bryozoans, corals, hydroids and sponges. These animals act as ecosystem engineers, altering the physical and chemical environment, modifying habitat for other species and influencing species distribution and abundance. The ability of these animals to host a variety of other organisms on and within their body structure increases their importance in maintaining and contributing to marine diversity. Corals host the most species rich communities, both in the deep-water and shallow water with high Fishers α (a measure of species diversity that is better at estimating rare species than the Shannon-Wiener index). Ascidians are second to corals in associated faunal richness, and exhibit higher Shannon-Wiener diversity (H') although the associated communities have the lowest density of all host groups. Sponges are the best studied of all the host organisms, and contain the most dense communities, although there is extreme variability among individual host species. The communities living on erect bryozoans and hydroids are relatively poorly studied, as compared to the other hosts. The communities associated with sponges, hydroids and corals are more likely to be dominated by a few species than those associated with ascidians and bryozoans. Communities inhabiting biological hosts occur at higher densities than communities found in soft sediments, from the intertidal to the deep-water.

Broad scale patterns of diversity of associated show that species richness and diversity of associates exhibit a unimodal pattern with latitude, with maximum diversity appearing between 30° and 45°. This finding is a departure from the typical decreasing species diversity with distance from the equator, but is consistent with patterns of species richness found in a variety of marine species. Species richness and diversity of associated fauna decreases with depth, however there is a distinct lack of information on deep-water biological habitat. Existing data indicates high species richness of associated fauna on deep-water structural species. Across all host organisms, species richness and diversity are positively correlated with host volume though volume accounts for a small amount of the variability of community composition.

The complex three-dimensional structure offered by these animals creates important oases for a wide variety of species. Destruction or removal of these animals through increased eutrophication of coastal areas, coral reef diseases, industrial fishing and direct harvesting, among other anthropogenic effects not only effects the host animal, but the complex communities living within or on their body structures. Given the widespread and ever increasing threats to the marine environment, the failure to consider the communities associated with these animals, and the indirect interactions that modify the physical environment for other species, will result in an underestimation of biodiversity loss and ecosystem function. These results and conclusions are corroborated by a recent review of the importance of structural species in the deep-water (Buhl Mortensen et al., 2010).

The combination of fishermen's local ecological knowledge, fisheries observer reports, trawl survey data and *in situ* observation provides a comprehensive information base which which to understand both the spatial and temporal distribution of sponges in the Northwest Atlantic. Fishermen often have long term knowledge of the marine environment. As presented in this thesis (Chapter 3) and also by and Breeze 1997 and Gass & Willison 2005, fishermen have been instrumental in identifying areas where deep-water corals and sponges form significant concentrations on the seafloor in Atlantic Canada. These observations have lead directly to research with undersea cameras and ROVs, which has greatly improved the understanding and knowledge of spatial distribution of these animals.

In contrast to the knowledge held by fishermen regarding their commercial species, the knowledge regarding sponges and corals is not yet used effectively in ecosystem management in Canada. While there have been area closures stemming from information provided by fishermen and subsequently verified by natural science methods, the information that fishermen hold regarding the significance of structural species as fish habitat does not inform fish habitat protection through fisheries management measures. It would be difficult to gather the same type of information today, as fishermen are less likely to share information that may be used to reduce access to fishing grounds.

The greatest contribution to science is the description of the *Vazella pourtalesi* population on the Scotian Shelf, which adds to the globally significant locations of glass sponges. Information from fisheries observer data and trawl survey data in the Newfoundland Region in particular, shows the extension of the "sponge grounds" known from the Northeast Atlantic, and consisting predominantly of Geodid sponges. These "sponge grounds" can be a distinct ecotype, occupying large areas of the seafloor at depths < 1000 m and as such

providing significant structure and habitat heterogeneity. Prior to this examination of sponges, deep-water corals were considered the primary megafaunal benthic species in the Northwest Atlantic (Breeze, 1997; Mortensen & Buhl-Mortensen, 2004; Gass & Willison, 2005; Bryan & Metaxas, 2006; Wareham, 2007).

As both the observer data and the trawl survey data constitute destructive sampling, and were collected with otter trawl fishing gear, assumptions about the impacts of fishing on sponges in the Northwest Atlantic can be made. The removal of up to 6000 kg of sponges in one trawl, and the cumulative removal of ~ 80,000 kg of sponge in the Greenland halibut fishery in the Eastern Arctic constitute the highest reported sponge bycatch globally. Until the last decade, fisheries dependent data and trawl survey data have not systematically sampled non-commercial species, and have particularly lacked in systematic sampling of non-commercial benthic species. The conservation value of deep water corals has changed this practice, and now there is a broad knowledge of the distribution of coral species in the Northwest Atlantic (Kenchington et al., 2010). This research, combined with the imperative to implement ecosystem based fisheries management, has already improved the collection and identification of sponge species in Atlantic Canadian trawl surveys (ICES, 2010).

While assumptions can be made about the effect of fishing gear on the removal of sponges, little is known about the recovery rates. In the examination of the sponge community inside and outside the Western Gulf of Maine Closed area (Chapter 6), early successional patterns can be observed, however it is clear that longer term monitoring is needed. Contrary to expectations, the diversity of sponges is higher in the area open to fishing activity, primarily as a result of increased growth of *Iophon* sp. In this case, *Iophon* sp. also had a greater number of associated species, providing shelter and access to the water column for a number of other

benthic organisms. As this study took place in a shallow water, high energy environment it is difficult to extrapolate the results to the deep-water. Much more research effort is needed to understand recruitment patterns, recovery rates and regeneration of sponges, particularly in deeper and colder environments.

7.1 Conservation and Management Implications

The 2006 United Nations General Assembly Sustainable Fisheries Resolution 61/105 called on States and regional fisheries management organizations to protect vulnerable marine ecosystems from the impacts of destructive fishing practices. As a result of this agreement, Canada developed the Policy for Managing the Impacts of Fishing on Sensitive Benthic Areas (DFO, 2009), which was adopted in 2009, to address the impacts of fishing on fish habitat. While the Canadian *Fisheries Act* prohibits the harmful alteration, disruption or destruction of fish habitat (Section 35.2), all fisheries are currently exempt from this provision as fisheries are viewed as an activity, rather than a work or undertaking as defined under the *Canadian Environmental Assessment Act*. All other impacts to fish habitat are managed under the 1986 Policy for the Management of Fish Habitat (DFO, 1986), which was adopted with the goals of conserving existing fish habitat, restoring damaged habitat and developing new habitat as part of mitigating fish habitat destruction authorized under the *Fisheries Act*.

Despite this policy framework, and a scientific understanding of the impacts of fishing gears in temperate marine ecosystems (Auster et al., 1995; Collie et al., 1997; Collie et al., 2001; Kaiser et al., 2006), Canadian waters (DFO, 2006) and in Arctic waters (Garcia et al., 2006), there has been no protection of sponges from the impacts of fishing in Atlantic Canada.

The information presented in this thesis, provides a basis for the protection of several areas where sponges form dense patches. These areas include the *V. pourtalesi* patch on the Scotian Shelf, the dense patches of "ostur" along the Labrador Shelf and into the Eastern Arctic. High densities of sponge that are found outside Canada's 200 mile limit in the Northweast Atlantic Fisheries Organization (NAFO) Regulatory Area received interim protection in 2009 through NAFO's measures to implement the UNGA Resolution 61/105.

7.3 Areas for Future Research

This study presents results of what should be the beginning of research on sponges in the Northwest Atlantic. Future research should incorporate any information that as been gathered by research trawl surveys and Fisheries Observer programs in the last decade in order to update the distributional maps of sponge catch. There is a need for taxonomic expertise and training on the sponge fauna, in order to understand species distributions more thoroughly, particularly in deep water and northern areas. With the exception of the video transects of the V. pourtalesi patch, and a cruise during the summer of 2010 led by DFO Maritimes Region using the R/V Hudson, there has been little in situ research on sponges. Results from the 2010 Hudson Cruise as well research cruises in the NAFO Regulatory Area in 2009 and 2010 lead by Spanish investigators (NERIEDA cruise) will contribute greatly to our understanding of sponge distribution and community composition in areas beyond national jurisdiction, outside Canada's 200-mile limit. Similar research should be done within Canadian waters, with a particular focus on the Newfoundland and Labrador slope and eastern Arctic waters. Further investigation into species interactions with commercial and non-commercial marine organisms is needed in order to better understand the specific role of the large patches of Geodids in the

life histories of North Atlantic fish and invertebrate species. The closed areas within the NAFO Regulatory Area and any voluntary closures should be accompanied by a management plan that allows for research on recovery, recruitment and patch formation of sponges. There is an need for increased collaboration with researchers in the Northeast Atlantic, particularly on growth rates and recruitment of sponge fields that are thought to contain long-lived species. Finally, this research should be incorporated into then be incorporated into fisheries management plans through the Integrated Fisheries Management Plans and habitat protection policies, such as the Canadian Sensitive Benthic Areas Policy, as well as marine protected area network planning and regional coral and sponge conservation strategies.

Appendix I

Literature Data on Associated Communities of Ascidians, Bryozoans, Corals, Hydroids and Sponges.

Appendix 1. Literature sources of data and variables used in Chapter 2.

Org.						Depth			Data	Biomass of Secondary Production	Species	SR		Specie		Pielou's	Fisher 's	Shannon
	Species	Source	Location	Lat.	Long.	(m)	Sample #	Volume*	Source	(g/m2)	dominance		# of Ind.	s/L	Inds. / L	Evenness (J')	Alpha	Wiener (H')
Ascidian	Microcosmu s sabatieri	Monniot 1961	Mediterranean	42.50	3.15	85	25	203.00	calculated	NA	ascidians	212.00	NA	1.04	NA	0.918	16.85	5.80
Ascidian	Pyura chilensis	Zamoran o and Moreno 1975	Coral Bay, Chile	39.85	73.50	6	4	32.00	calculated	473.36	crustacea	59.00	2444.00	1.84	76.38	0.638	11.33	3.79
Ascidan	Pyura praeputialis	Castilla et al 2004	Bay of Antofagasta, Chile	23.60	70.50	1	12	294.00	calculated	NA	gastropoda	120.00	NA	0.41	NA	NA	NA	4.43
Ascidian	Pyura praeputialis	Cerda and Castilla 2001	Bay of Antofagasta, Chile	23.60	70.50	6.5	824	71.60	calculated	246.4	polychaetes	96.00	NA	1.34	NA	0.727	11.23	4.43
Ascidian	Pyura stolonifera (intertidal)	Fielding et al 1994	Durban, South Africa	29.88	31.00	0	5	14.10	calculated	366	polychates	64.00	190.00	4.54	13.48	0.749	11.78	4.35
Ascidian	Pyura stolonifera (intertidal)	Fielding et al 1994	Durban, South Africa	29.88	31.00	2	5	14.10	calculated	670		61.00	271.00	4.33	19.22	0.776	10.54	4.49
Bryozoan	Celleporaria agglutinans, Hippomenell a varicata	Bradstock and Gordon 1983	Tasman Bay, New Zealand	41.00	172.50	75	1	2.42	given in paper, CaCo3 sg used to convert kg to L	NA	caprellids/ bryzoans	92.00	96.00	38.09	39.75	0.772	2.07	2.32
Bryozoan	Flustra foliacea	Stebbings 1971	South Wales, UK	52.5	3.5	17.5	1	5.60	given in paper (converte d from area)	NA	polychaetes	25.00	567.00	4.46	101.25	0.644	1.12	1.81
Coral	Leptogorgia virgulata	Wendt et al 1985	South Atlantic Bight	31.64	81.261 1	20	3	NA	insufficie nt data to calculate	NA	crustacea	53.00	466.00	NA	NA	NA	NA	4.20
Coral	Lophelia pertusa	Jensen and Frederiks en 1992	Northeast Atlantic	61.00	6.00	260	25	6.97	calculated from biomass	NA	crustacea	256.00	4626.00	36.75	664.08	NA	NA	5.50

Org.	Species	Source	Location	Lat.	Long.	Depth (m)	Sample #	Volume*	Data Source	Biomass of Secondary Production (g/m2)	Species dominance	SR	# of Ind.	Specie s/L	Inds. / L	Pielou's Evenness (J')	Fisher 's Alpha	Shannon Wiener (H')
Coral	Lophogorgia hebes	Wendt et al 1985	South Atlantic Bight	31.64	81.261 1	20	3	NA	insufficie nt data to calculate	NA	crustacea	60.00	964.00	NA	NA	0.690	NA	4.08
Coral	Oculina arbusculata	McClosk ey 1970	North Carolina	35.43	76.80	11	8	7.09	calculated from biomass	NA	crustacea	309.00	56 616	43.60	NA	0.661	NA	4.05
Coral	Oculina varicosa	Wendt et al 1985	South Atlantic Bight	31.64	81.261 1	20	3	NA	insufficie nt data to calculate	NA	crustacea	99.00	959.00	NA	NA	0.710	NA	4.67
Coral	Pavona frondifera	Tsuchiya et al. 1986	Gulf of Thailand	10.00	101.00	5	33	18.55	given in paper	NA	crustacea	65.00	1664.00	3.50	89.70	0.399	12.49	2.37
Coral	Pocillopora damicornis	Austin et al 1980	Great Barrier Reef	23.50	152.00	6	40	31.40	given in paper	NA	polychaetes	101.00	951.00	3.22	30.29	0.766	27.82	5.08
Coral	Titanideum frauenfeldii	Wendt et al 1985	South Atlantic Bight	31.64	81.261 1	20	3	NA	insufficie nt data to calculate	NA	polychaetes	46.00	224.00	NA	NA	0.750	NA	4.16
Hydroid	Ectopleura dumortieri	Lagardere and Tardy 1980	Gulf de Gascogne, France	44.6	1.26	62.5	NA	NA	insufficie nt data to calculate	NA	bryozoa, nudibranchs	8.00	NA	NA	NA	NA	NA	NA
Hydroid	Nemertesia antennaria	Hughes et al 1975	Torbay, UK	50.43	3.55	15	NA	NA	insufficie nt data to calculate	NA	caprellids	155.00	NA	NA	NA	0.517	0.80	1.55
Hydroid	Sertularia operculata	Round et al 1961	Lough Ine, Ireland	51.55	9.25	1	NA	NA	insufficie nt data to calculate	NA	suspension feeders on stalks, deposit feeders on holdfasts	89.00	67777.00	NA	NA	0.637	2.47	2.66
Sponge	Agelas oroides	Koukoura s et al 1996	North Aegean Sea	40.22	23.78	7.5	18	1.38	given in paper	NA	amphipoda	135.00	1408.00	97.83	1020.29	0.804	2.60	3.06

Org.						Depth			Data	Biomass of Secondary Production	Species	SR		Specie		Pielou's	Fisher 's	Shannon
	Species	Source	Location	Lat.	Long.	(m)	Sample #	Volume*	Source	(g/m2)	dominance	SIC	# of Ind.	s/L	Inds. / L	Evenness (J')	Alpha	Wiener (H')
Sponge	Anoxycalyx (Scolymastra) joubini	Kunzmann 1996	Antartica	74	20	275	4	5.46	given in paper	NA	amphipoda	NA	168.00	NA	30.77	NA	NA	NA
Sponge	Aplysina aerophoba	Koukouras et al 1996	North Aegean Sea	40.22	23.78	3	25	2.23	given in paper	NA	amphipoda	184.00	6513.00	82.51	2920.63	0.755	3.35	3.37
Sponge	Aplysina aerophoba	Voultsiadou- Koukoura et al 1987	North Aegean Sea	40.5	25	4	29	20.33	given in paper	61.79	amphipoda	104.00	1857.00	5.12	91.35	NA	NA	3.33
Sponge	Aplysina archeri	Villamizar and Laughlin 1991	Venezuela	11.80	66.60	22	98	60.20	calculated , mean volume time N	NA	amphipoda	53.00	1001.00	0.88	16.63	0.660	NA	1.14
Sponge	Aplysina lacunosa	Villamizar and Laughlin 1991	Venezuela	11.80	66.60	22	100	100.50	calculated , mean volume time N	NA	amphipoda	139.00	5694.00	1.38	56.66	0.680	NA	1.47
Sponge	Aplysina fistularis	Betancourt- Lozano et al 1998	Baja, Mexico	26	112	5	24	NA	not sufficient data to calculate	NA	amphipoda	43.00	NA	NA	NA	0.608	30.45	3.23
Sponge	Aulospongus	Pearse 1950	Bimini,	25.07	79.26	1.5	1	NA		NA	amphipoda	2.00	3.00	NA	NA	0.918	2.62	0.92
Sponge	schoenus Axinella cannabina	Koukouras et al 1996	Bahamas North Aegean Sea	40.22	23.78	17.5	21	0.37	given in paper	NA	amphipoda	84.00	448.00	227.64	1214.09	0.896	3.60	3.74
Sponge	Axociella nidificata	Kunzmann 1996	Antarctica	74	20	235	4	0.53	given in paper	NA	amphipoda	1.00	12.00	NA	22.64	NA	NA	NA
Sponge	Clathria pauper	Kunzmann 1996	Antarctica	74	20	550	4	1.44	given in paper	NA	amphipoda/gast ropoda	3.00	11.00	2.08	7.64	0.910	1.05	0.92
Sponge	Cliona celata	Wendt et al 1985	South Atlantic Bight	31.64	81.261 1	20	3	NA	insufficie nt data to calculate	NA	caprellida	89.00	2685.00	NA	NA	NA	NA	3.40
Sponge	Geodia baretti	Klitgaard 1995	North East Atlantic, Faroe Islands	61.128 3	55	322	151	NA	insufficie nt data to calculate	NA	crustacea	10.00	18.00	NA	NA	0.820	9.26	2.73

Org.						Depth			Data	Biomass of Secondary Production	Engaine	SR		Specie		Pielou's	Fisher 's	Shannon
	Species	Source	Location	Lat.	Long.	(m)	Sample #	Volume*	Source	(g/m2)	Species dominance	SK	# of Ind.	s/L	Inds. / L	Evenness (J')	Alpha	Wiener (H')
Sponge	Geodia macandrewii	Klitgaard 1995	North East Atlantic, Faroe Islands	62.011	55.5	348	42	NA	insufficie nt data to calculate	NA	crustacea	62.00	382.00	NA	NA	0.615	20.48	3.65
Sponge	Geodia sp.	Klitgaard 1995	North East Atlantic, Faroe Islands	61.128	55	291	100	NA	insufficie nt data to calculate	NA	decapod	25.00	37.00	NA	NA	0.898	33.84	4.17
Sponge	Halichondri a hentscheli	Kunzman n 1996	Antarctica	74	20	445	1	0.12	given in paper	NA	decapod	NA	47.00	NA	391.67	0.630	1.83	1.65
Sponge	Halichondri a panicea	Frith 1976	North Hayling, UK	50.82	0.95	1	116	10.96	given in paper	NA	decapod	36.00	358.00	3.29	32.67	0.376	5.14	2.07
Sponge	Halichondri a panicea	Long 1968	North East Pacific	47.755	122.75 3	1	33	3.40	given in paper	NA	decapod	68.00	6098.00	20.00	1793.53	0.734	9.60	3.76
Sponge	Halichondri a panicea	Peattie and Hoare 1981	Menai Strait	53.2	4.23	6.25	41	NA	NA	NA	decapod	50.00	32699.00	NA	NA	NA	NA	NA
Sponge	Haliclona oculata	Wendt et al 1985	South Atlantic Bight	31.64	81.261 1	20	104	NA	insufficie nt data to calculate	NA	decapod	24.00	13140.00	NA	NA	NA	NA	NA
Sponge	Haliclona rubens	Pearse 1950	Bimini, Bahamas	25.07	79.26	1.5	4	29.00	given in paper	NA	decapod	16.00	36.00	0.55	1.24	0.896	11.04	3.58
Sponge	Hippospongi a communis	Rutzler 1976	Rass Salakta, Tunisia	35.555	11.068	15	40	51.22	given in paper	106.11	decapod	25.00	2711.00	0.49	52.93	0.633	3.81	2.94
Sponge	Hyalonema bianchoratu m var. typica	Beaulieu 1998	North East Pacific	34.75	123	4100	35	3.04	given in paper	NA	decapod	139.00	8580.00	45.75	2824.23	0.356	21.51	2.49
Sponge	Hymeniacid on perlevis	Frith 1976	North Hayling, UK	50.82	0.95	1	60	5.12	given in paper	NA	decapod	31.00	238.00	6.06	46.53	0.741	9.51	3.67
Sponge	Iotrochota brotulata	Pearse 1950	Bimini, Bahamas	25.07	79.26	1.5	1	NA	insufficie nt data to calculate	NA	decapod	4.00	6.00	NA	NA	NA	NA	1.45

Appendix 1. Continued

Org.	Species	Source	Location	Lat.	Long.	Depth (m)	Sample #	Volume*	Data Source	Biomass of Secondary Production (g/m2)	Species dominance	SR	# of Ind.	Specie s/L	Inds. / L	Pielou's Evenness (J')	Fisher 's Alpha	Shannon Wiener (H')
Sponge	Ircinia campana	Wendt et al 1985	South Atlantic Bight	31.64	81.261 1	20	3	NA NA	insufficie nt data to calculate	NA NA	decapod	83.00	249314.0 0	NA NA	NA	NA	NA NA	0.71
Sponge	Ircinia fasciculata	Rutzler 1976	Rass Salakta, Tunisia	35.555	11.068	5	1	0.50	given in paper	NA	decapod	11.00	335.00	22.00	39164.00	0.719	2.69	2.66
Sponge	Ircinia fasciculata	Bacescu 1971	Cuba	25.00	90.00	15	2	1000.00	given in paper	2.53	decapod	13.00	19582.00	0.01	19.58	0.689	1.13	2.38
Sponge	Ircinia foetida	Pearse 1932	Dry Tortugas, South Atlantic	24.65	92.85	1	9	2.97	given in paper	NA	decapod	20.00	NA	6.73	NA	NA	NA	NA
Sponge	Ircinia muscarum	Rutzler 1976	Rass Salakta, Tunisia	35.555	11.068	15	4	10.84	given in paper	22.94	decapods	14.00	762.00	1.29	70.30	0.638	2.44	2.43
Sponge	Ircinia oros	Rutzler 1976	Rass Salakta, Tunisia	35.555	11.068	15	1	1.19	given in paper	1.66	echinodermata	6.00	16.00	5.06	13.49	0.627	3.49	1.62
Sponge	Ircinia retidermata	Ilan et al 1994	Haifa, Isreal	32.835	34.786	830	1	NA	insufficie nt data to calculate	NA	hydroids	3.00	20.00	NA	NA	0.817	0.98	1.30
Sponge	Ircinia strobilina	Pearse 1932	Dry Tortugas, South Atlantic	24.65	92.85	36	2	NA	insufficie nt data to calculate	NA	isopoda	23.00	NA	NA	NA	0.671	7.07	3.22
Sponge	Ircinia strobilina	Pearse 1950	Bimini, Bahamas	25.07	79.26	1.5	3	203.25	given in paper	NA	nematoda	41.00	321.00	0.20	1.58	NA	NA	NA
Sponge	Ircinia varabilis	Rutzler 1976	Rass Salakta, Tunisia	35.555	11.068	15	6	3.60	given in paper	4.677	nematoda	16.00	1471.00	4.45	408.84	0.527	2.52	2.11
Sponge	Ircinia varabilis	Pearse 1932	Dry Tortugas, South Atlantic	24.65	92.85	1	1	0.18	given in paper	NA	nematoda	9.00	1032.00	51.14	5863.64	0.094	1.18	0.28
Sponge	Isodictya setifer	Kunzman n 1996	Antarctica	74	20	445	2	0.37	given in paper	NA	nematoda	2.00	6.00	NA	16.22	0.650	1.05	0.65
Sponge	Isops phlegraei	Klitgaard 1995	North East Atlantic, Faroe Islands	61.128	55	323	104	NA	insufficie nt data to calculate	NA	nematoda	54.00	133.00	NA	NA	0.809	33.85	4.65

Appendix 1. Continued.

Org.	Species	Source	Location	Lat.	Long.	Depth (m)	Sample #	Volume*	Data Source	Biomass of Secondary Production (g/m2)	Species dominance	SR	# of Ind.	Specie s/L	Inds. / L	Pielou's Evenness (J')	Fisher 's Alpha	Shannon Wiener (H')
Sponge	Microciona prolifera	Long 1968	North East Pacific	47.755	122.75	7.5	15	8.91	given in paper	NA	no dominance pattern	52.00	9551.00	5.84	1071.94	NA	NA	NA
Sponge	Mycale acerata	Kunzman n 1996	Antarctica	74	20	420	5	1.46	given in paper	NA	no dominance pattern	4.00	116.00	2.74	79.45	0.218	0.80	0.44
Sponge	Mycale macilenta	Frith 1976	North Hayling, UK	50.82	0.95	1	29	3.98	given in paper	NA	ophiuriods	23.00	101.00	5.78	25.39	0.789	9.30	3.57
Sponge	Mycale microsigmat	Ribeiro et al 2003	Brazil	22.00	42.50	2.5	19	NA		NA	polychaeta	75.00	2235.00	NA	NA	0.753	21.08	4.69
Sponge	osa Phakellia robusta	Klitgaard 1995	North East Atlantic, Faroe Islands	62.2	42.83	265	59	NA	insufficie nt data to calculate	NA	polychaeta	43.00	661.00	NA	NA	0.193	10.29	1.05
Sponge	Phakellia rugosa	Klitgaard 1995	North East Atlantic, Faroe Islands	61.91	50.38	380	25	NA	insufficie nt data to calculate	NA	polychaeta	28.00	37.00	NA	NA	0.965	52.46	4.64
Sponge	Phakellia ventilabrum	Klitgaard 1995	North East Atlantic, Faroe Islands	62.2	42.83	297	37	NA	insufficie nt data to calculate	NA	polychaeta	22.00	26.00	NA	NA	0.968	67.63	4.32
Sponge	Pseudosuber ites nudus	Kunzman n 1996	Antarctica	74	20	608	6	0.50	given in paper	NA	polychaeta/amp hipoda	6.00	68.00	12.00	136.00	0.548	1.58	1.42
Sponge	Rossella antarctica	Kunzman n 1996	Antarctica	74	20	415	12	5.65	given in paper	NA	polychaete	17.00	689.00	3.01	122.05	0.555	0.73	1.29
Sponge	Rossella nuda	Kunzman n 1996	Antarctica	74	20	357	7	4.93	given in paper	NA	polychaete	4.00	11.00	0.81	2.23	0.890	2.62	2.07
Sponge	Rossella racovitzae	Kunzman n 1996	Antarctica	74	20	445	17	7.45	given in paper	NA	polychaete	16.00	139.00	2.15	18.66	0.671	1.03	1.56
Sponge	Sarcotragus cf. muscarum	Pearse 1950	Bimini, Bahamas	25.07	79.26	830	1	NA	insufficie nt data to calculate	NA	polychaete	4.00	8.00	NA	NA	0.774	3.18	1.55

Org.						Depth			Data	Biomass of Secondary Production	Species	SR		Specie		Pielou's	Fisher 's	Shannon
	Species	Source	Location	Lat.	Long.	(m)	Sample #	Volume*	Source	(g/m2)	dominance		# of Ind.	s/L	Inds. / L	Evenness (J')	Alpha	Wiener (H')
Sponge	Sarcotragus muscarum	Cinar et al. 2002	Aegean Sea	38	27	3	20	28110.00	given in paper	NA		148.00	5299.00	0.01	0.19	0.600	NA	2.88
Sponge	Spheciospon gia vesparia	Westinga and Hoetjes 1981	Curacao	12.16	69	20	35	179.60	given in paper	NA	polychaete	24.00	16578.00	0.13	92.31	0.582	2.76	2.67
Sponge	Spheciospon gia vesparia	Pearse 1932	Dry Tortugas, South Atlantic	24.65	92.85	12	1	50.00	given in paper	NA	polychaete	10.00	6282.00	0.20	125.64	0.194	1.30	0.67
Sponge	Spheciospon gia vesparia	Pearse 1932	Dry Tortugas, South Atlantic	24.65	92.85	18	1	50.00	given in paper	NA	polychaete	18.00	13504.00	0.36	270.08	0.151	2.05	0.63
Sponge	Spheciospon gia vesparia	Pearse 1932	Dry Tortugas, South Atlantic	24.65	92.85	55	1	185.00	given in paper	NA	polychaete	9.00	17128.00	0.05	92.58	0.107	1.03	0.36
Sponge	Spheciospon gia vesparia	Pearse 1950	Bimini, Bahamas	25.07	79.26	1.5	2	25.74		NA	polychaete	10.00	445.00	0.39	17.29	NA	NA	1.67
Sponge	Spirastrella inconstans	Fishelson 1965	Dahlak Archipelago, Eritrea	15.83	40.2	1	3	30.90	calculated as volume of a sphere with 27cm diameter (as noted in paper)	NA	polychaete	32.00	NA	1.04	NA	NA	NA	NA
Sponge	Spongia officinalis	Pearse 1932	Dry Tortugas, South Atlantic	24.65	92.85	1	12	4.56	given in paper	NA	polychaete	22.00	693.00	4.82	151.97	0.558	4.09	2.45
Sponge	Spongia zimocca	Rutzler 1976	Rass Salakta, Tunisia	35.555	11.068	15	2	0.42	given in paper	0.427	polychaete	13.00	168.00	31.33	404.82	0.714	3.29	2.64
Sponge	Stryphnus ponderosus	Klitgaard 1995	North East Atlantic, Faroe Islands	61.128 3	55	311	523	NA	insufficie nt data to calculate	NA	polychaete	122.00	845.00	NA	NA	0.746	40.53	5.20
Sponge	Suberites lata	Long 1968	North East Pacific	47.755	122.75 3	7.5	14	7.04	given in paper	NA	polychaete	25.00	150.00	3.55	21.31	NA	NA	NA
Sponge	Tedania charcoti	Kunzman n 1996	Antarctica	74	20	445	1	0.98	given in paper	NA	polychaete	2.00	43.00	2.04	43.88	0.270	0.54	0.28
Sponge	Tedania oxeata	Kunzman n 1996	Antarctica	74	20	490	6	1.41	given in paper	NA	polychaete / decapod	3.00	11.00	2.13	7.80	0.690	1.35	1.10

Org.	Species	Source	Location	Lat.	Long.	Depth (m)	Sample #	Volume*	Data Source	Biomass of Secondary Production (g/m2)	Species dominance	SR	# of Ind.	Specie s/L	Inds. / L	Pielou's Evenness (J')	Fisher 's Alpha	Shannon Wiener (H')
Sponge	Tedania trirhaphis	Kunzman n 1996	Antarctica	74	20	338	3	1.67	given in paper	NA NA	polychaete/ amphipoda	3.00	1192.00	1.80	713.77	0.004	0.83	0.13
Sponge	Thenea laevis	Klitgaard 1995	North East Atlantic, Faroe Islands	61.035 1	55.66	299	36	NA	insufficie nt data to calculate	NA	polychaete/ amphipoda	108.00	559.00	NA	NA	0.687	39.86	4.64
Sponge	Thenea valdivae	Klitgaard 1995	North East Atlantic, Faroe Islands	61.60	55.30	300	44	NA	insufficie nt data to calculate	NA	polychaete/amp hipoda	90.00	605.00	NA	NA	0.660	29.25	4.29
Sponge	Tragosia infundibulifo rmis	Klitgaard 1995	North East Atlantic, Faroe Islands	61.115	55	288	42	NA	insufficie nt data to calculate	NA	polychaetes	17.00	148.00	NA	NA	0.391	4.96	1.60
Sponge	Zygomycale parishii	Duarte and Nalesso 1996	Brazil	6.5	30	5	25	14.90	calculated (mean volume times N)	NA	zoanthid	92.00	7012.00	6.17	470.60	0.414	12.37	2.70

Appendix II

Interview Questionnaire Used to Collect Fishermen's Local Ecological Knowledge

- 1. How old were you when you started fishing?
- 2. How long have you been fishing?
- 3. Where did you start fishing and what did you fish for?
- 4. Did you always fish fulltime? If no, when did the changes occur?
- 5. Community fished from:
- 6. Current Boat: Held: Size:
- 7. What areas do you currently fish? What species do you target? How has this changed over the years?
- 8. What areas have you fished?
- 9. When we say deep-water coral or sponge do you know what that refers to?
- 10. Did you ever get sponges/ corals in your bycatch?
- 11. Where (see chart notes for details)? Was it a particular type of bottom or a particular area?
- 12. What percent of the time were corals/ sponges found? Did this change over time?
- 13. Were there any other animals that came up in areas where you caught sponges or coral?
- 14. What percent of the catch were sponges/coral? Did this change over time?
- 15. If yes, where and when did the changes occur?
- 16. Did you get the same species all the time? Were there different types in different areas?
- 17. What type of fish would you be targeting when you got sponges / corals in your gear?
- 18. What did the sponge look/smell like?
- 19. Are there any other characteristics you can used to describe the sponges / corals?
- 20. What role do you think the corals and sponges play in the marine environment?
- 21. What is your opinion of protecting parts of the bottom of the sea?
- 22. What are the traditional methods of conservation that were used before the development of today's fishing methods?
- 23. Do you think the conservation methods used today (quotas, etc) would be necessary if we still fished the traditional way?
- 24. Do you think the way the fishery is run today is better than it used to be?
- 25. What are your suggestions for protecting certain areas? Which areas would you protect and why?

Appendix III

Species List of Marine Sponges Recorded in the Gulf of Maine and Bay of Fundy

Sponges recorded in the Gulf of Maine, including the Bay of Fundy as documented in published reports. In total, 67 species have been recorded. The Gulf of Maine Census of Marine Life lists 27 species in the Bay of Fundy and 32 in the Gulf of Maine. The species list here and that in the Census are most likely not complete and more work is needed particularly on the identification of encrusting sponges.

Species	Source
Class Calcarea	
Family Clathridae	
Clathrina coriacea (Montagu, 1818)	Barthel & Tendal, 1997
Order Leucosoleniida	
Family Leucosoleniida	
	Verrill & Smith, 1874; Barthel &
Leucosolenia botryoides (Ellis & Solander, 1786)	Tendal, 1997
Leucosolenia cancellata (Verrill 1873)	
Family Sycettidae	
	Verrill & Smith, 1874; Linkletter et al.,
Sycon ciliatum (Fabricius, 1780)	1977; Barthel & Tendal, 1997
Sycon protectum (Lambe, 1897)	This study
Sycon sp.	Hartman, 1958
Class Demospongiae	
Order Homoscleromorpha	
Family Plakinidae	
Oscarella lobularis (Schmidt, 1862)	Magee et al., 2000
Order Hadromerida	
Family Polymastiidae	
Polymastia hispida (Bowerbank, 1864)	Barthel & Tendal, 1997
	Caddy 1974, Proctor, 1933; Barthel &
	Tendal, 1997; Fuller et al., 1998
Polymastia robusta (Bowerbank, 1864)	
	Caddy, 1974; Barthel & Tendal 1997;
Polymastia infrapilosa Topsent, 1927	Fuller et al. 1998
	This study, Barthel & Tendal 1997;
Polymastia mammilaris (Mueller. 1806)	Fuller et al. 1998
Weberella bursa (Mueller, 1806)	Caddy 1974
Trichostemma hemisphaericum Sars, 1872	Caddy 1984
Sphaerotylus borealis (Swarzewsky)	Caddy 1974
Tentorium semisuberites (Schmidt 1870)	Caddy 1974

Species Species	Source
Family Suberitidae	
Prosuberites epiphytum (Lamark, 1813)	Barthel & Tendal, 1997; Ginn et al. 1998
Psuedosuberites sulphereus (Bowerbank, 1866)	This study, Barthel & Tendal 1997, Fuller et al. 1998
Suberites montalibidus (Lambe, 1895)	Procter, 1933
(,	Proctor, 1933, Caddy 1974, Barthel &
Suberites ficus (Esper, 1794)	Tendal 1997, Fuller et al. 1998
Suberities concinnus (Verrill, 1873)	Procter 1933
Suberites hispidus (Bowerbank, 1864)	Procter 1933
Family Clionidae	
	Verrill & Smith, 1874, Proctor, 1933,
	Barthel & Tendal 1997, Fuller et al.
Cliona celata Grant, 1826	1998
	Hartman, 1958; Caddy 1974; Fuller et
Cliona vastifica Hancock, 1849	al. 1998
Cliona lobata Hancock, 1849	Hartman, 1958
Order Poecilosclerida	
Suborder Microcionina	
Family Iophnidae	
	Witman & Sebens 1985, Barthel &
Iophon pattersoni (Bowerbank, 1866)	Tendal 1997
Iophon scandens (Bowerbank, 1866)	Caddy 1974
Iophon chelifer (Ridley & Dendy 1887)	Proctor 1933
Iophon sp.	This study
Family Mycalidae	
Esperiopsis normani (Bowerbank, 1866)	
Mycale fibrexilis (Wilson, 1891)	Fuller et al., 1998
Mycale lingua (Bowerbank, 1866)	Fuller et al., 1998
Mycale lobata (Bowerbank, 1866)	Barthel & Tendal, 1997
Family Desmacididae	
Isodictya deichmannae (De Laubenfels, 1949)	
Isodictya palmata (Ellis & Solander, 1786)	Caddy, 1974, Fuller et al., 1998,
Family Myxilidae	
Myxilla incrustans (Johnston, 1842)	Fuller et al., 1998, Ginn et al., 1998
Myxilla fimbriata (Bowerbank, 1864)	Ginn et al., 1998
• • • • • • • • • • • • • • • • • • • •	
Lissodendoryx fibrexilis (Fristedt, 1885)	Fuller et al., 1998
	Hartman, 1958, ARC Collection
Lissodendoryx fragilis (Fristedt, 1885)	D 1022
Lissodendoryx fragilis (Fristedt, 1885) Lissodendoryx isodictyalis (Carter, 1882) Plocamionida ambigua (Bowerbank, 1866)	Procter, 1933 Caddy, 1974

Species	Source
Family Tedaniidae	
Tedania suctoria (Lieberkuhn, 1859)	Barthel & Tendal, 1997
Tedania sp.	This study
Teauma sp.	This study
Family Hymedesmiidae	
Hymedesmia canadensis Ginn, 1998	Ginn et al., 1998
Hymedesmia spp.	This study
11ymeweshild spp.	This study
Family Crellidae	
Crella sp.	Ginn et al., 1998
Crella rosea (Topsent, 1892b)	Ginn et al., 1998
Crema rosea (Topseni, 10,20)	3 mm et a n, 1996
Family Microcionidae	
Clathria (Micriciona) prolifera (Ellis & Solander, 1786)	Bleakney & Mustard 1974
Artemisina arcigera (Schmidt, 1870)	Procter, 1933
Artemisina sp.	,
· · · · · · · · ·	
Order Haplosclerida	
Family Chalinidae	
Acervchalina loosanoffi (Hartman, 1958a)	Hartman, 1958
Haliclona canaliculata Hartman, 1958a	Hartman, 1958
Haliclona oculata (Pallas, 1766)	Fuller et al. 1998
Haliclona urceolus Rathke & Vahle in Mueller 1806)	Fuller et al., 1998
Haliclona rosea (Bowerbank 1866)	Procter 1933
Thunctona rosea (Bowchoank 1800)	110ctc1 1933
Family Niphatidae	
Hemigellius sp. aff. flagifer DeWeerdt & Van Soest,	1987)Ginn et al. 1998
Hemigellius arcoferus (Vosmaer, 1885)	Hartman 1958
Tremigentus ureojerus (vosituer, 1002)	
Order Dendroceratida	
Family Darwiniellida	
Aplysilla sulphurea Shulze, 1878	Ginn et al. 1998
Aplysilla sp.	Barthel & Tendal 1997
Tipiyawa op.	Bartilet & Tellaul 1997
Family Halisarcidae	
- ····································	Witman & Sebens 1985; Barthel &
Halisarca dujardini Johnston, 1842	Tendal 1997, Harvey-Clark 1997
	/, <i> </i>
Family Dysideidae	
V V	Barthel & Tendal 1998, Fuller et al.
Dysidea fragilis (Montagu, 1818)	1998, McGee et al. 2000
2 journa j. ug (1710111115u, 1010)	1770, 1110000 01 41. 2000
Order Halichondrida	
Family Halichondriidae	
- many remonder name	Proctor 1933, Barthel & Tendal 1997
Halichondria sitiens Schmidt, 1870	Fuller et al. 1998
Transmitta strens benning, 1070	Tuner et un 1990

Halichondria panicea (Pallas, 1766)

Halichondria bowerbanki Burton, 1930 Spongosorites genetrix (Schmidt, 1870) Hymeniacidon perlevis (Montagu, 1818) Hymeniacidon sp.

Order Spirophorida

Tetillia sp.

This study, Proctor, 1933; Bleakney & Barthel & Tendal 1997, Fuller et al. 1998, Ginn et al. 1998
Verrill & Smith, 1874, Bleakney & Mustard 1974, Hartman 1958
Proctor 1933, Fuller et al. 1998
Proctor, 1933
Mcgee et al. 2000

Hartman, 1958

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