Distribution, biodiversity, and function of glass sponge reefs in the Hecate Strait, British Columbia, Canada

by

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Abstract

Reefs of glass sponges (Porifera, Hexactinellida) off western Canada were recently established as a marine protected area (MPA), however effective management and monitoring of this MPA is hindered by a lack of baseline data about reef distributions and biodiversity. MPA boundaries were established around reef polygons mapped using multibeam acoustics. Multibeam technology does not differentiate between live, dead, and buried portions of sponges. To ground-truth past multibeam mapping, a remote operated vehicle (ROV) was used to conduct fine-scale photographic surveys at three reef sites in the Hecate Strait, British Columbia. I performed semivariogram analyses and spatial interpolations to produce maps of reef distributions. The relationship between glass sponges and associated megafauna (> 2 cm) was analyzed from ROV images. Polygons mapped by multibeam acoustics represented the densest areas of sponge with ~10% of live and dead sponges found outside these polygons, while the remaining area was bare substrate (i.e. buried sponge or patches of mud). Glass sponges were patchily distributed in the reefs and spatially dependent at 28 to 36 meters. Although total megafauna density was significantly higher in the presence of glass sponges, glass sponges did not correlate with an increase in all taxa. Megafauna associations in the reefs occurred at a taxon-specific level and sponge reef structural complexity was found to be an important influence on reef community structure. The reefs also hosted numerous non-reef forming sponges, which until now have been previously overlooked. Molecular analyses and taxonomic classification were used to identify multiple encrusting sponges in the reefs, of which one was a new cryptic sponge in the genus *Desmacella*. This study garnered baseline data for Fisheries and Oceans Canada to improve their capacity for monitoring changes in the status and health of sponge reef ecosystems in Canada.

Preface

Research conducted for this thesis forms part of a national contribution to the Canadian Healthy Oceans Network (CHONe) projects. Data was collected in collaboration with Fisheries and Oceans Canada (DFO), in which ship allocation time was secured through DFO and field work using the remotely operated vehicle ROPOS was shared with DFO colleagues.

Chapter Two of this thesis was conceived by L.K. Law and S.P. Leys and is being prepared as a manuscript for journal publication. LKL contributed to implementation of methodologies and was responsible for all data collection and analyses. Map files for geospatial analysis were obtained from A.S. Kahn, courtesy of K.W. Conway (NRCan) and the Canadian Hydrographic Service. SPL was the supervisory author involved with developing field work methodologies, manuscript composition, and editing.

Chapter Three of this thesis was conceived by L.K. Law, L.J. Vehring, and S.P. Leys and is being prepared as a manuscript for journal publication. LJV contributed to some initial observations for cryptic speciation in the genus *Desmacella* and offered spicule slides and scanning electron microscopy images of *Desmacella* samples collected in 2015. LKL was responsible for all data collection and analyses of *Desmacella* and other non-reef forming sponge samples collected in 2017. C.S. Davis and S. Dang from the Molecular Biology Facility at the University of Alberta (MBSU) assisted with genetic analyses of *Desmacella* samples. SPL was the supervisory author and helped with sponge collection, manuscript composition, and editing.

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Chapter 1

A General Introduction

1.1 An unexpected discovery

The ocean is the largest but least explored ecosystem on Earth. Although oceans cover over 70% of the Earth's surface, research has focused on shallow-water environments, with much remaining to be discovered in deeper oceanic systems (Sogin et al. 2006, Brandt et al. 2007, Danovaro et al. 2010). Only in recent years have advances in submersible technologies enabled the first discoveries and manipulative experiments to be conducted in some of the most remote marine habitats on the planet, including hydrothermal vents (Corliss et al. 1979), cold seeps (Olu-Le Roy et al. 2004), and trenches. Among these remote habitats, ancient glass sponge reefs (Porifera, Hexactinellida) are one of the latest scientific marine discoveries of the latter twentieth century.

Glass sponge reefs off western Canada were first discovered in 1987 using sidescan sonar and video surveys (Conway et al. 1991). Prior to this work glass sponge reefs were presumed to have gone extinct. In recent years, mapping with multibeam acoustics has revealed an extensive network of reefs covering several hundreds of kilometers of seafloor on the Canadian Pacific continental shelf (Conway 1999, Conway et al. 2005). Today, these reefs represent the only living modern-day examples of extinct reefs that once occurred during the Jurassic approximately 160 million years ago (Conway et al. 1991, Krautter et al. 2001). Prehistoric glass sponge reefs were the largest reefs to have existed on Earth, forming a 7000 km belt of sponges in the Tethys Sea, a region now covered by parts of Europe (Krautter et al. 2001, Conway et al. 2005). Modern hexactinellid reefs exist off the coast of British Columbia, Canada in the southern Strait of Georgia (SoG) and Hecate Strait and Queen Charlotte Sound (QCS).

Past studies over the last two decades have predominantly focused on understanding glass sponge ecology in the SoG reefs (Cook 2005, Chu and Leys 2010), while reefs of the Hecate Strait and QCS remain less understood. Given the Hecate Strait and QCS reefs were recently designated as a marine protected area (MPA) (Fisheries and Oceans Canada 2017), there has been growing interest in acquiring better biological data about the distribution and densities of sponges and other animal associations in these reefs. Research presented in this thesis provides the first description of live and dead sponge distributions and faunal associations in the Hecate Strait and QCS reefs, which will aid in informing future management planning of sponge reef MPAs in Canada.

1.2 Glass sponge biology: a unique animal

Hexactinellid or 'glass' sponges are one of the four classes of sponges in the Phylum Porifera (Figure 1-1) characterized by skeletons composed of a framework of siliceous 6-rayed spicules (Leys et al. 2007). Glass sponges feed on suspended particulates by pumping water through a series of canals that culminate in an excurrent vent called the osculum (Leys et al. 2007). Although glass sponges appear as sessile organisms on the seafloor, they are known to display responsive behaviours at speeds too slow to be detected by the human eye (Leys and Meech 2006). Glass sponges stand apart from other sponges in having syncytial tissue that arises from the fusion of blastomeres (Leys and Ereskovsky 2006, Leys et al. 2007). This unusual tissue structure maintains cytoplasmic continuity and enables glass sponges, which lack both true nerves and muscles, to respond to mechanical disturbances and environmental and chemical stimuli (Leys and Mackie 1997, Leys and Meech 2006). The hexactinellid sponges *Rhapdocalyptus dawsoni* and *Aphrocallistes vastus* both show cessation and gradual declines in their pumping activity in response to touch or clogging by sediment (Tompkins-MacDonald and Leys 2008). Syncytial tissue allows electric signals to propagate unimpeded through the glass sponge, causing arrests in their filter feeding apparatuses to prevent further intake of suspended particulates (Leys and Mackie, 1997; Leys et al. 1999). The function of the arrest-response, similar to a 'sneeze', is presumably a defensive strategy against prolonged exposure to sediments (Tompkins-MacDonald and Leys 2008). Sources of increased sedimentation may arise from river sediment inputs or sediment plumes generated by deep-sea trawling (Johannessen et al. 2003, Puig et al. 2012).

1.3 Communities of glass sponges worldwide

Around the world, glass sponges are dominant members of deep water (> 500 m) communities, but their existence in shallower waters up to 20 m occur in only four locations - in Antarctica, fjords in southern New Zealand, submarine caves in the Mediterranean, and on the continental shelf in the northeast Pacific (Leys et al. 2007). Distributions of glass sponges in many deep and shallow regions are generally found as scarce assemblages; however, there are several locations where glass sponges form dense habitats on spicule mats. At depths of 1000-1300 m, the hexactinellid *Pheronema carpenteri* grows in high densities (1.5 individuals m^{-2}) on spicule mats that cover approximately one-third of the seafloor in the Porcupine Seabight off southern Ireland (Bett and Rice 1992). Abundance of total megafauna was observed to be higher on spicule mats than in the surrounding area, and may be related in part to the presence of *P. carpenteri*, which provides substrate for a variety of benthic animals to colonize (Bett and Rice 1992). Shallow water spicule mats (100-230 m) off Kapp Norvegia in the Weddell Sea, Antarctica also harbor high abundances of hexactinellids (Barthel 1992, Barthel and Gutt 1992). Seven hexactinellid species were identified on these mats and of these *Rossella racovitzae* was found as dense as 23 individuals per 10 m^2 (Barthel and Gutt 1992).

There are rare occurrences of glass sponges in some of the most isolated regions of the ocean. Stalks of the glass sponge *Hylonema* are found at 4100 m off California in densities of ~1 stalk every 5 m (Beaulieu 2001a, Beaulieu 2001b). The landscape at abyssal depths is often barren, hence these stalks serve as 'habitat islands' providing hard substrata for a diversity of encrusting epibenthic fauna. Calcarea foraminifera, serpulid polychaetes, tunicates, bryozoans, and other sponges were some of the taxa found growing on *Hylonema* stalks (Beaulieu 2001b). Submarine caves in the Mediterranean share many characteristics with deep-sea habitats, such as near total darkness, low temperatures, poor food availability, and low hydrodynamic energy (Vacelet et al. 1994). Yet, a tiny 3 to 7 cm long hexactinellid sponge *Oopsacus minuta* has adapted to living in these extremes, forming large populations (100 individuals m^{-2}) on the wall and ceiling of the cave.

1.4 Canadian Pacific coast reefs

1.4.1 Reef distribution and formation

Although glass sponges can occur in high densities worldwide, the Canadian north Pacific is the only location where glass sponges aggregate in dense assemblages to form unusually large reefs (Leys et al. 2007). Unlike glass sponge communities found in other oceans, Pacific coast reefs are comprised of reef-building glass sponges with a fused skeleton of siliceous spicules termed dictyonine (Leys et al. 2007). Reasons for why glass sponge reefs occur here remain a mystery, however reef distributions are suspected to be limited to water conditions of low suspended sediments, high dissolved silica concentrations, low light, and temperatures between 9 and 10^{o}C (Maldonado et al. 1999, Leys et al. 2004).

During reconnaissance seafloor mapping, acoustic anomalies in sidescan sonar images were first observed in 1986 by K.W. Conway, J.V. Barrie, and J.L Luternaur (Geological Survey of Canada) (Conway et al. 1991). Photographs and sediment cores obtained on ship cruises in 1987 and 1988 confirmed these anomalies to be sponge mounds (Conway et al. 1999). Subsequent surveys were conducted using multibeam bathymetry and backscatter to map reef extents (Conway et al. 2005). Sponge reefs were identified as the darkest shaded regions in multibeam acoustic images, while the surrounding or underlying sediments were typically observed as the lightest shading in images. This difference in backscatter was due to the low acoustic reflectivity of sponge reefs compared to the high acoustic reflectivity of boulders and gravel glaciomarine sediments. From these images, four massive reef complexes were found at 150-250 m depth in the Hecate Strait and QCS (Figure 1-2 A), and numerous smaller reef complexes were found at 90-200 m in the southern SoG (Figure 1-2 B) (Conway et al. 1991, Conway et al. 2005). Although multibeam technology has been a useful tool for delineating reef extents, this technique is unable to differentiate between reef areas that are live, dead, and buried portions of sponge.

Glass sponge reefs occur in relict iceberg-furrowed troughs created during the Late Wisconsinan deglaciation (25,000-13,000 years ago) (Conway et al. 1991, Krautter et al. 2001). Isostatic rebound caused the seafloor to rise after glaciers retreated and resulted in extensive glacial scouring. A hard substrate with a network of scars and sills was left behind that provided the first settlement sites for juvenile reef sponges (Conway et al. 1991, Krautter et al. 2001). The main reef-building dictyonine sponges in the Hecate Strait and QCS reefs are *Aphrocallistes vastus, Heterochone calyx*, and *Farrea occa*, whereas reefs in the SoG are comprised of only *A. vastus* and *H. calyx* (Figure 1-3 A-D) (Conway et al. 2005). The fused spicule skeleton of these species remains intact after the death of the sponge and reef structures can cause baffling effects that cause suspended sediments to drop out of the water column (Krautter et al. 2006). Reefs develop over time as sediment buries dead sponge skeletons, upon which sponge larvae eventually settle and grow on previous generations of sponge. Reef structures may form into ridges, biostromes (beds or sheets), or bioherms (mounds) that can reach up to 21 m high (Conway et al. 1991, Conway et al. 2005).

1.4.2 Ecosystem function

Glass sponge reefs play a major ecological role in deep ocean environments. Sponges in the SoG reefs are efficient suspension feeders, removing up to 90% of bacteria from the water column whilst releasing waste in the form of ammonia out their oscula (Kahn et al. 2015). This grazing activity forms a strong link between the pelagic microbial foodweb and the benthos in a process termed benthic-pelagic coupling (Bell 2008, Kahn et al. 2015). Glass sponges are also known to be important silicon sinks (Chu et al. 2011). The sponge skeleton is formed through the deposition of amorphous hydrated silica that is highly resistant to dissolution (Chu et al. 2011). Biological silicon remains in the reefs for long periods of time and forms the siliceous skeletal framework, which provides three-dimensional habitat thought to increase benthic biodiversity (Buhl-Mortensen et al. 2010). The Pacific coast reefs offer animals refuge from predation, spawning and nursery grounds, and attachment substrate for other sessile invertebrates (Cook et al. 2008, Marliave et al. 2009, Chu and Leys 2010, Miller et al. 2012). Common sponge associates in the reefs include commercially important species of rockfish, crustaceans, and flatfish (Jamieson and Chew 2002, Cook et al. 2008, Chu and Leys 2010, Du Preez and Tunnicliffe 2011). Organisms may inhabit the sponge osculum and aquiferous canals, or animals may feed on the glass sponge itself (Beazley et al. 2013). Fragments of glass sponge spicules have been observed in the gut contents of the dorid nudibranch *Peltodoris lentiginosa* (Chu and Leys 2012). Furthermore, communities of non-reef forming sponges such as the demosponge *Desmacella austini* have been found encrusting dictyonine sponges (Lehnert et al. 2005, Kahn et al. 2016). Currently, it remains unknown whether *D. austini* is an invasive or symbiotic sponge in the reefs.

1.4.3 Threats to the reefs and conservation strategies

The delicate siliceous skeletons of glass sponges make them particularly vulnerable to damage from human activities such as deep-water trawling (Jamieson and Chew 2002). The oldest reef is dated at 9,000 years old and recovery of a destroyed reef is expected to take hundreds of years given glass sponges are slow-growing (Krautter et al. 2001, Conway et al.

2005, Kahn et al. 2016). Over the last decade, impacts of bottom trawling have been well documented in the reefs, which prompted calls for some degree of protection for this unique habitat (Jamieson and Chew 2002). Sidescan sonar surveys completed in 1988 and 1999 indicated intensive trawl scouring in and around sponge reef complexes (Figure 1-4 A, B), with the worst afflicted areas in the southern QCS (Figure 1-5 A-D) (Conway 1999). Voluntary fisheries closures were enacted in 2002 to temporarily protect the reefs from bottom trawling, but only recently in February 2017 has the Minister of Fisheries and Oceans Canada formally designated the Hecate Strait and QCS reefs as a MPA (Fisheries and Oceans Canada 2017).

Canada and other signatory countries committed under the Convention on Biological Diversity, *Aichi Target 11*, to protect 10% of our oceans by 2020 through ecologically representative and connected systems of protected areas (Rochette et al. 2014, MacKinnon et al. 2015). The Hecate Strait and QCS Glass Sponge Reef MPA contributes to achieving this target; however Canada remains well behind in its quantity of MPA establishments. To date, less than 5% of marine habitats are protected in Canada (Figure 1-6) (Rochette et al. 2014, MacKinnon et al. 2015) with several factors driving this lag including jurisdictional limitations, challenges of ownership and governance, and lack of scientific knowledge (Agardy et al. 2003, Rochette et al. 2014, Agardy et al. 2016). The Hecate Strait and QCS reefs are currently the only protected area in Canada for glass sponge habitats, therefore studying this region is essential for improving our scientific understanding about glass sponge ecology, which will aid in future decision-making around management and monitoring of sponge reef MPAs.

1.5 Thesis objectives

The focus of my thesis was to describe the distribution of sponges and biological patterns of associated fauna in the northernmost reef complex in the Hecate Strait, British Columbia. My first objective was to determine the amount of live and dead sponge present in reef areas that were mapped from multibeam acoustics. The second objective was to determine megafauna abundances in the reefs and describe how reef structure and complexity influences benthic faunal diversity. The third objective was to determine species composition and abundances of non-reef forming sponge associates on glass sponges. The fourth objective was to determine if various colour morphotypes of an encrusting sponge in the reefs represented different species within the genus *Desmacella*. Results of this work provide the first baseline descriptions of sponge distributions and faunal compositions for glass sponge reefs in the Hecate Strait and QCS.

In Chapter Two, the amount of live and dead sponges was quantified and mapped at three sampling sites in the Hecate Strait northern reef. Reef complexity was quantified using optical intensity measures and species abundance was compared between areas of live sponge, dead sponge, and buried sponge. Mapped sponge areas closely matched the reef extent previously described by multibeam bathymetry and backscatter. Optical intensity was a useful tool for characterizing reef complexity, and biodiversity in the reefs was strongly structured by the presence of live and dead sponges. These findings demonstrate the importance of glass sponge habitat in deep water landscapes for supporting higher megafauna abundance.

In Chapter Three, the Hecate Strait and QCS reefs are shown to support a diverse assemblage of non-reef forming sponges. The most conspicuous sponge observed growing on and around glass sponges was the demosponge *D. austini*. Until now, this was the only species of *Desmacella* described for this region (Lehnert et al. 2005), but I revealed a new species of *Desmacella* present in the reefs using taxonomic description of spicule morphology and DNA sequences. The density of non-reef forming sponges was affected by the presence of dead glass sponge skeleton, suggesting dead sponges serve an equally important role as live sponges in supporting benthic megafauna. These results provide the first evidence of cryptic sponge diversity in glass sponge reefs and shows how non-reef forming sponges proliferate in these habitats.

In Chapter Four, I reflect on my findings by discussing their implications and suggest directions for future research with our current understandings about the Hecate Strait and QCS reefs.

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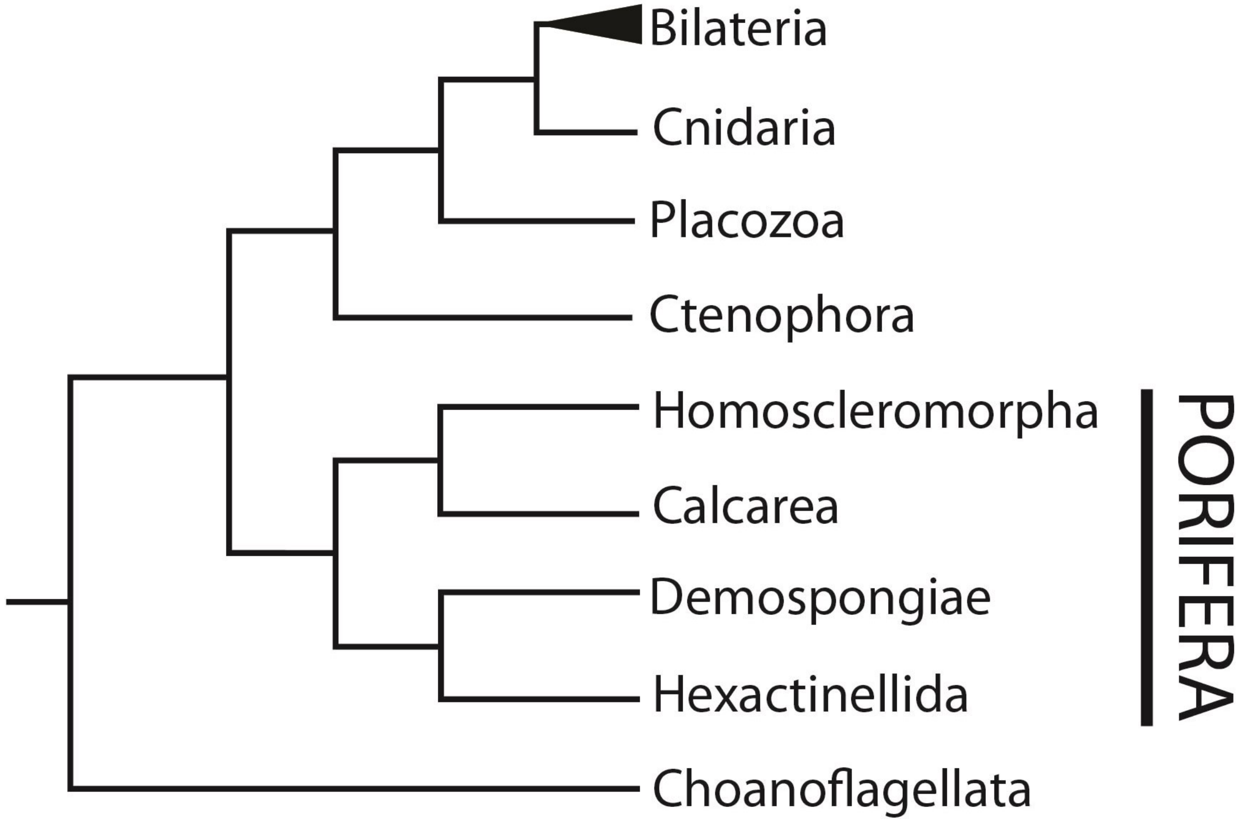


Figure 1-1. Phylogenetic relationships of early branching animals. Hexactinellida is one of four classes within the phylum Porifera that stands apart from other clades in having syncytial tissue. Topology of the tree is based on Feuda et al. (2017).

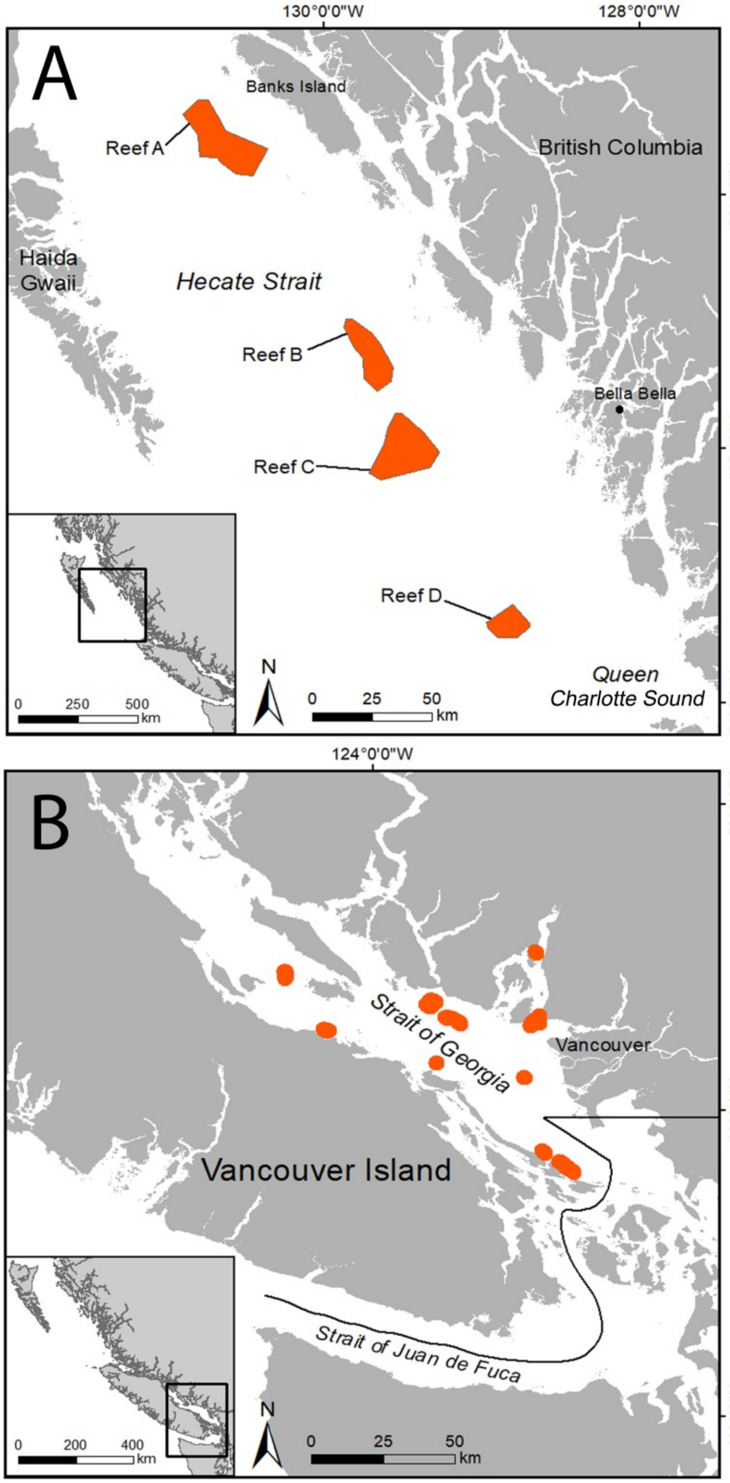


Figure 1-2. Locations of all known glass sponge reefs on the western Canadian continental shelf. (A) Four large reef complexes occur in the Hecate Strait and QCS. (B) Thirteen smaller reef complexes occur in the southern SoG. Map files from the Canadian Hydrographic Service and the Geological Survey of Canada, courtesy K.W. Conway.

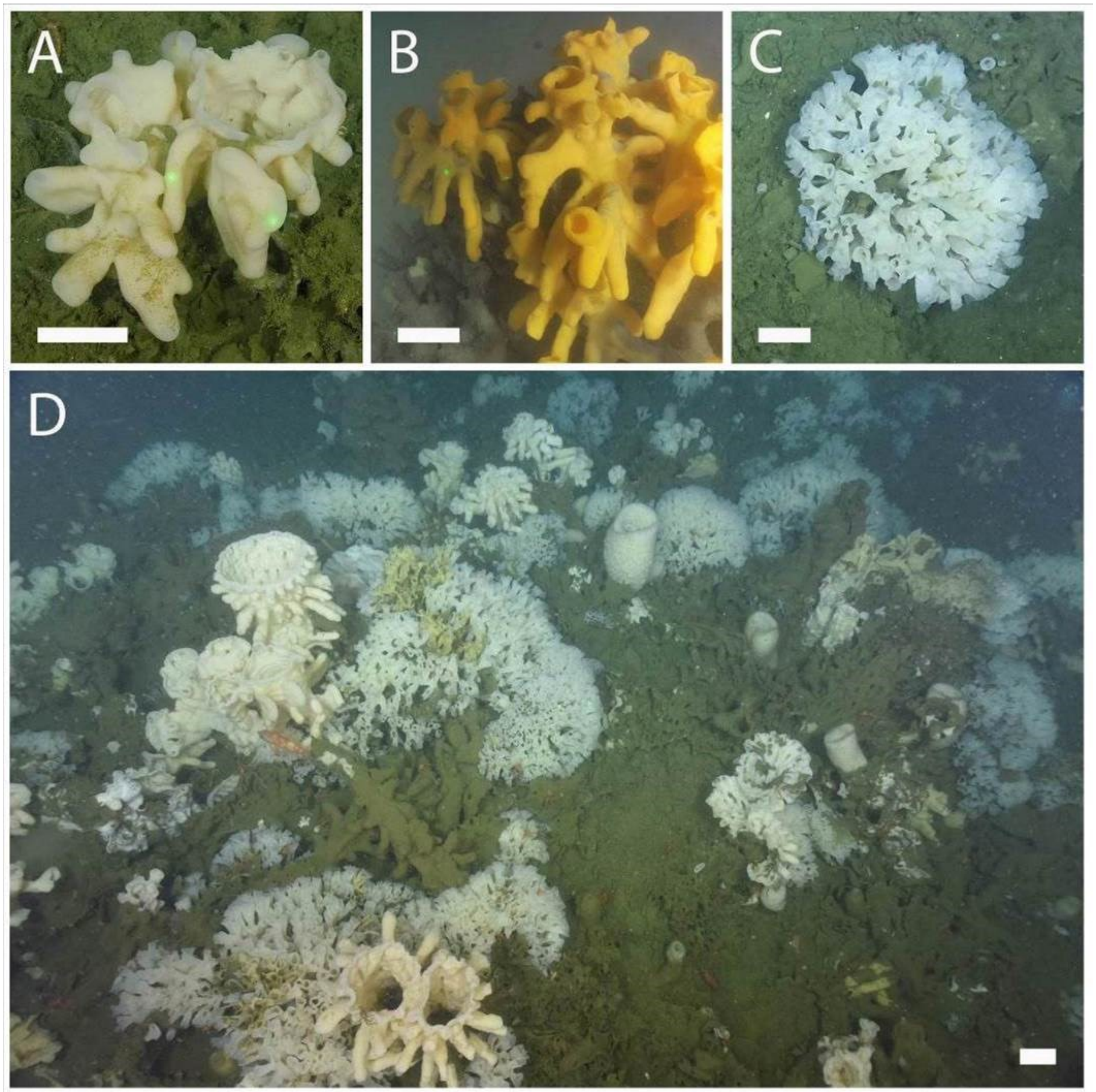


Figure 1-3. The three species of hexactinellid sponges that form the glass sponge reefs on the continental shelf off western Canada. (A) *Aphrocallistes vastus* showing mitten-like projections, (B) *Heterochone calyx* showing finger-like projections, and (C) *Farrea occa* with bush formation. (D) All three glass sponge species form the reefs in the Hecate Strait and QCS. Scale bars 10 cm.

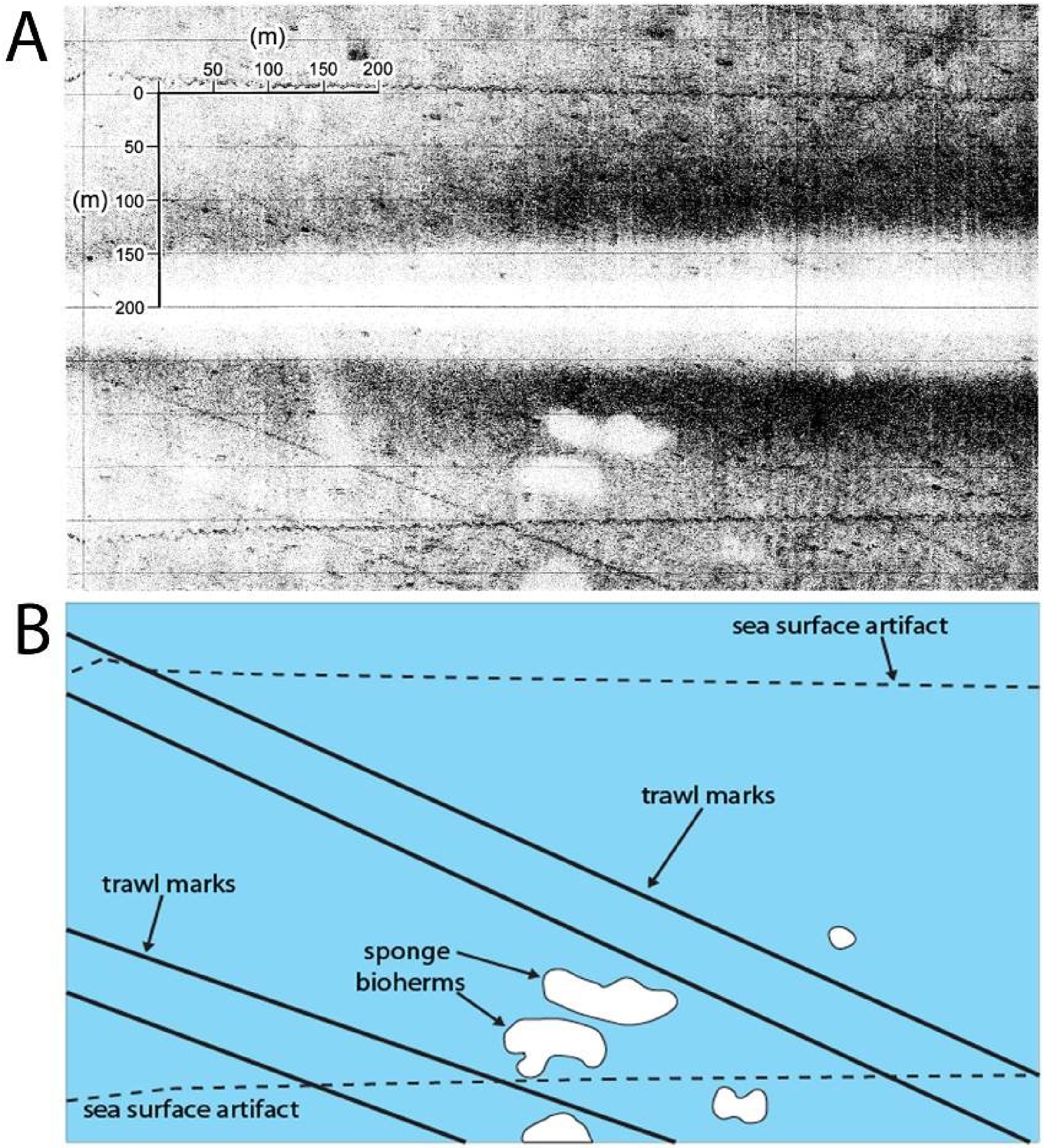


Figure 1-4. Sidescan sonar image and schematic drawing of trawl damage. (A) Sidescan sonar image of trawl marks (parallel dark tracks) across sponge reef areas in the southern QCS. Sponge reefs are circular to irregular shaped white areas in the image. Image from Conway (1999). (B) Simplified schematic drawing of the sidescan sonar image (redrawn from Conway (1999), Fig. 7b).

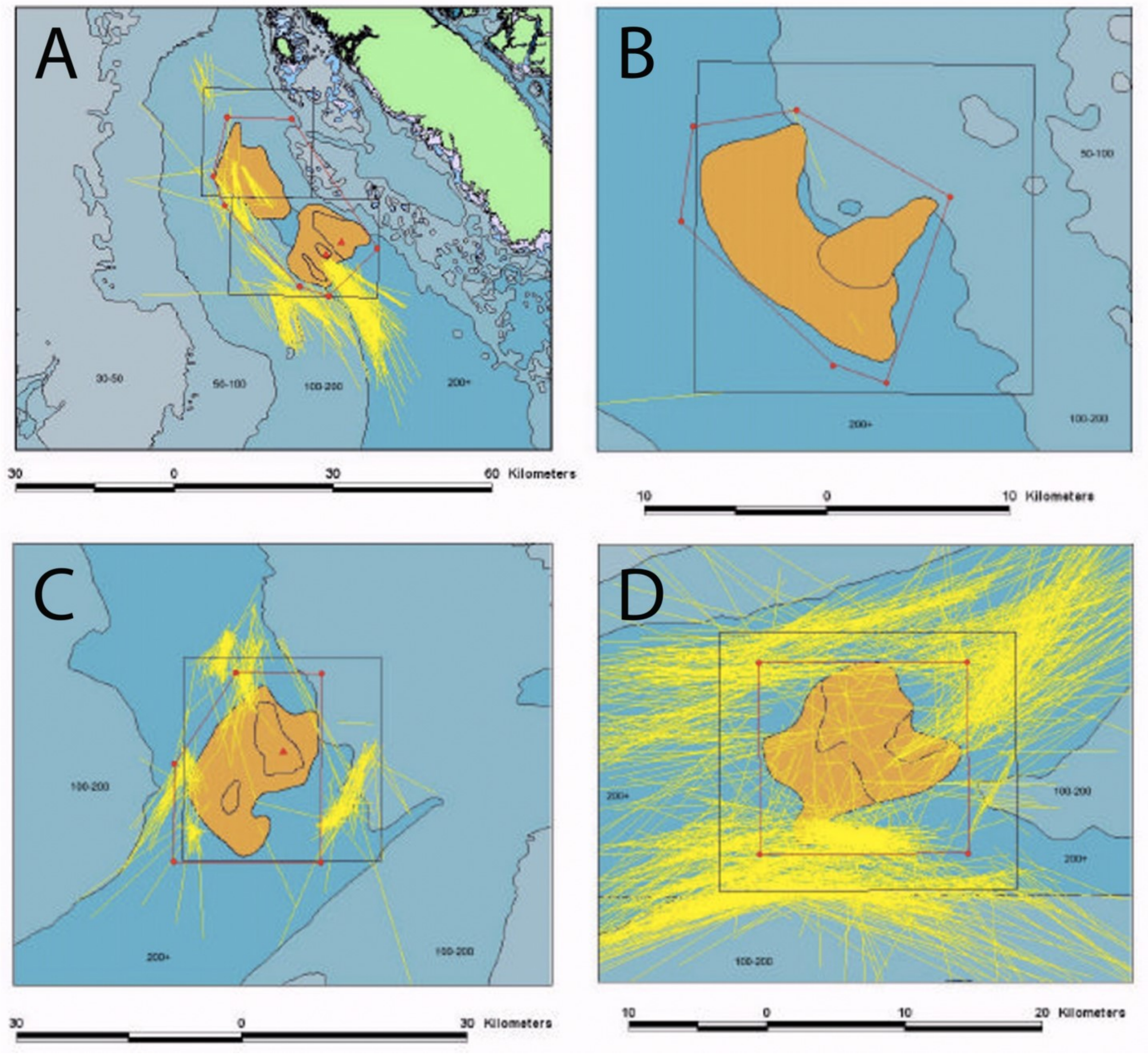
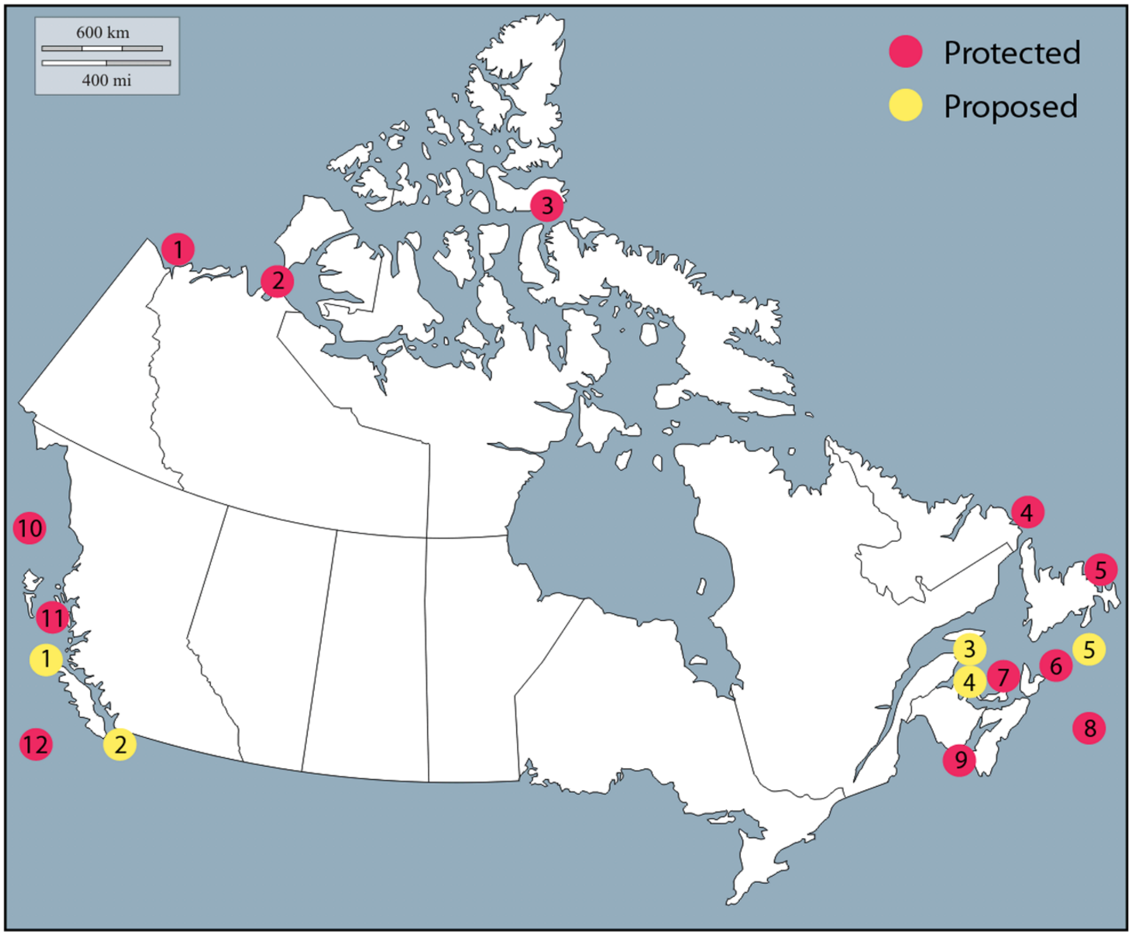


Figure 1-5. Bottom trawling activities in the Hecate Strait and QCS reefs. Trawl tow lines (yellow) that occurred between 1996 and 2000, intersecting sponge reefs (orange). (A) Reef A, (B) Reef B, (C) Reef C, and (D) Reef D (see Figure 1-2 A for reef locations). Sponge Reef D suspected to the most damaged reef in the Hecate Strait and QCS based on trawling activities. Voluntary shrimp trawl closure boxes (black) and groundfish trawl closure boxes (red) were enacted in 2002. Maps from Jamieson and Chew (2002).



1 - Tarium Niryutait (1,740 km^2)
2 - Anuniaqvia Niqiqyuam (2,361 km^2)
3 - Tallurutiup Imanga (131,000 km^2)
4 - Gilbert Bay (60 km^2)
5 - Eastport (2.1 km^2)
6 - St. Anns Bank (4,364 km^2)
7 - Basin Head (9.2 km^2)
8 - The Gully (2,364 km^2)
9 - Musquash Estuary (7.4 km^2)
10 - Bowie Seamount (6,131 km^2)
11 - Hecate Strait & QCB Reefs (2,410 km^2)
12 - Endeavour Hydrothermal Vents (93.5 km^2)

1 - Scott Islands (11,546 km^2)
2 - Southern Strait of Georgia (1,400 km^2)
3 - American Bank (1,000 km^2)
4 - Iles-de-la-Madeleine (16,500 km^2)
5 - Laurentian Channel (12,000 km^2)

Figure 1-6. Existing and proposed marine protected areas in Canada managed by the Department of Fisheries and Oceans. A total area of 150,542.2 km^2 is currently protected, which makes up less than 5% of Canada's jurisdictional marine waters. Data adapted from World Wildlife Fund Canada.

Chapter 2

Patterns of sponge distribution and associated fauna in the Hecate Strait and Queen Charlotte Sound Glass Sponge Reefs Marine Protected Area

2.1 Introduction

Glass sponge reefs (Porifera, Class Hexactinellida) found off western Canada are unusual deep water habitats that were discovered in recent decades. While glass sponges themselves are not rare and occur in oceans around the world (e.g. Antarctica, the Mediterranean, and the NE Atlantic), the Canadian north Pacific is the only location where glass sponges form large reefs (Barthel and Gutt 1992, Bett and Rice 1992, Vacelet et al. 1994). The reefs were first detected as acoustic anomalies in sidescan sonar images that were collected in 1987 by the Geological Survey of Canada (GSC) during reconnaissance seafloor mapping (Conway et al. 1991). These reefs are modern-day examples of extinct fossilized reefs that were once prevalent during the Jurassic approximately 160 million years ago (Conway et al. 1991, Conway 1999, Krautter et al. 2001). In prehistoric times, glass sponges constructed the largest reefs known on earth, forming a 7,000 km belt of sponges in the Tethys Sea, a region now covered by parts of Europe (Conway et al. 1991, Krautter et al. 2001, Conway et al. 2005). Late Jurassic reefs declined in abundance during the Cretaceous and were presumed to have gone extinct after the Tertiary (Krautter et al. 2001, Conway et al. 2005). To date, modern hexactinellid reefs cover several hundreds of kilometers on the continental shelf off the coast of British Columbia, Canada.

Since the first discovery of these reefs in the late 1980s, subsequent surveys using multibeam acoustics have detailed the locations of several small sponge reefs at 90-200 m depth in the southern Strait of Georgia (SoG) (Conway et al. 2005). Four massive reef complexes were also found at 150-250 m depth in the Hecate Strait and Queen Charlotte Sound (QCS) (Conway et al. 2005). The Hecate Strait and QCS reefs are the largest glass sponge reefs in Canada, discontinuously covering over 700 km^2 of seafloor (Conway et al. 1991, Conway et al. 2005). These reefs have recently gained considerable attention since their establishment as a marine protected area (MPA). Evidence of glass sponge removal by deep-water trawling has been well-documented on the Canadian continental shelf, with the most intensive trawling having occurred in the southern QCS (Conway 1999, Jamieson and Chew 2002, Conway et al. 2005). In response to these threats, the Canadian government (Fisheries and Oceans Canada, DFO) established the Hecate Strait and QCS Glass Sponge Reefs MPA in February 2017 (Fisheries and Oceans Canada 2017). The establishment of this MPA is a cornerstone of achieving Canada's domestic and international target, under the *Oceans Act*, to protect at least 10% of marine and coastal areas by 2020. Despite its protected status, little remains known about sponge distributions and faunal associations in the Hecate Strait and QCS reefs, which presents a challenge for the effective management of this MPA.

Glass sponge reefs have garnered protection status not only for their rarity, but also for the ecosystem services glass sponges provide, including carbon sequestration, biological silica (bSi) cycling, and habitat formation. As suspension feeding invertebrates, glass sponges actively pump water through their body, feeding on large amounts of ultraplankton (<10 µm) while expelling waste in the form of ammonia out a large excurrent vent called the osculum (Leys et al. 2007, Yahel et al. 2007). Their large filtration capacity has major effects on overlying shelf water properties, and links pelagic and benthic microbial carbon in food webs through a process termed benthic-pelagic coupling (Pile et al. 1997, Gili and Coma 1998, Pile and Young 2006). Among all sponge groups, glass sponges have the most heavily silicified skeleton. This skeleton remains resilient to dissolution and allows bSi to remain assimilated in the reefs for long periods of time (Leys et al. 2007, Chu et al. 2011). Glass sponge skeletons thus represent a major Si sink, and are also the foundation for forming stable reef communities in benthic environments. When a sponge dies, the skeleton remains relatively intact and reefs accrete over time as clay-rich sediments bury dead sponge skeleton to form structures of various shapes including ridges, biostromes (sheets), and bioherms (mounds) (Conway et al. 2005, Krautter et al. 2006). Reef structures can reach up to 25 m high (Conway et al. 2005), and are comparable to old growth trees in a forested ecosystem, which provide a diverse range of microhabitats known to elevate local megafauna abundance. Commercially important species of rockfish, crustaceans, and flatfish have been observed in the reefs taking refuge from predators and using them as nursery grounds (Cook et al. 2008, Chu and Leys 2010, Du Preez and Tunnicliffe 2011). Many studies suggest topographic complexity of sponge habitat plays a role in supporting higher species diversity (Buhl-Mortensen et al. 2010, Du Preez and Tunnicliffe 2012); however, this relationship has been demonstrated more clearly between coral reefs and fish (Risk 1972, Dustan et al. 2013, Burns et al. 2015, Newman et al. 2015) than for glass sponge communities and their associated fauna. Quantifying the complexity of glass sponge habitat is therefore relevant for understanding their function in forming deep water habitats and their importance in supporting benthic biodiversity in continental shelf waters.

Over the last two decades, the GSC has conducted additional surveying in the Pacific coast reefs using multibeam acoustics to map reef distributions. Our current knowledge of reef extents in the Hecate Strait and QCS were delimited into polygons based off multibeam backscatter data that was draped over grey-scale bathymetry (courtesy of K.W. Conway). This mapping was conducted at large spatial scales (kilometres) with limited resolution of the fine-scale sponge distributions within the reefs (Conway et al. 1991, Conway 1999, Conway et al. 2005). Multibeam technology does not differentiate between reef structures that are live sponge, dead sponge, or bare substrate (i.e. buried sponge or mud patches), and so all types of bottom surfaces were included within the polygons. Furthermore, this technique does not distinguish between the different sponge species that make up the reef complexes. The hexactinellid sponges, *Aphrocallistes vastus*, *Heterochone calyx*, and *Farrea occa*, are the main reef-builders in the Hecate Strait and QCS reefs (Krautter et al. 2001, Conway et al. 2005), but their relative abundance among total live sponge cover remains unknown. Without clear identification of sponge quantities and distributions, it makes it nearly impossible to effectively and accurately monitor the status of sponges in the Hecate Strait and QCS reefs. It also constrains our ability to raise questions about how glass sponges are spatially structured in benthic environments and what their role is in supporting benthic biodiversity.

The goal of this study was to map sponge distributions and determine megafauna associations in the Hecate Strait northern reef. The Hecate Strait and QCS reefs were delimited into polygons – shapes drawn on digital files of bathymetry – based off multibeam backscatter data that was draped over grey-scale bathymetry (courtesy of K.W. Conway). Polygons representing reef extents predicted by multibeam acoustics were surveyed at fine-scales using a remote operated vehicle (ROV). I analyzed these images to determine the abundance of live, dead, and buried portions of glass sponges within these polygons. Glass sponge populations in the SoG reefs were found at narrow depth ranges and predominantly on sloped topography (Chu and Leys, 2010). Hence, glass sponges in the Hecate Strait northern reef were predicted to be distributed in a similar manner and found on elevated topographic features such as mounds. I also analyzed ROV images to determine the influence of reef structure on megafauna (> 2 cm) diversity and juvenile sponge recruitment. Topographic complexity of reef structure, referred to here as rugosity, was quantified using a technique called optical intensity, which is a purely visual method for characterizing habitat complexities from video surveys and ROV images (Shumway et al. 2007). Optical intensity values were expected to be higher for reef areas with high abundances of live and dead sponge cover, and a strong positive relationship was hypothesized between reef rugosity and benthic biodiversity. Finally, sponge oscula densities in ROV images were measured as an index of sponge abundance and can be combined with pumping rates for estimating the effects of the Hecate Strait and QCS reefs on benthic-pelagic coupling. As ocean conservation grows in the face of multiple human stressors and global climate change, my results provide insight into the ecosystem function of glass sponge habitat that may guide future protection, management, and monitoring efforts of deep water glass sponge reefs.

2.2 Materials and Methods

2.2.1 Study Site

Four major reef complexes are located in the Hecate Strait and Queen Charlotte Sound (QCS) (Figure 2-1 A). The Hecate Strait separates Haida Gwaii from mainland British Columbia and stretches approximately 220 km long with depths ranging from 300 m in the south to 50 m in the north (Thomson 1981). It is the shallowest of the two water masses with regular bathymetry (Thomson 1981). The QCS is located north of Vancouver Island and has more complex bathymetry than the Hecate Strait with three broad troughs that slice inland across the continental shelf with depths averaging 350-400 m (Thomson 1981). Oceanographic conditions for these regions are affected by winds and runoff, and dominated by semi-diurnal tidal regimes (Conway et al. 1991, Conway et al. 2005, Whitney et al. 2005). These waters also have high ambient silica concentrations and low sedimentation rates (Conway et al. 2005). Sponge reefs in the Hecate Strait and QCS occur between 150 to 250 m and are found on relict iceberg-furrowed surfaces that were formed as the result of glacial scouring during the late Wisconsin deglaciation (Conway et al. 1991, Krautter et al. 2001, Conway et al. 2005). Reef complexes in this study area are referred to as the northern, central, and southern reefs, which reflects their geographic location in the Hecate Strait and QCS seaway.

Reefs in the Hecate Strait and QCS have been heavily damaged by trawling; however, the northern reef complex was identified to have experienced less fishing activity than the other reef complexes (Conway 1999, Jamieson and Chew 2002). The northern reef was chosen for field sampling given it is one of the more intact reefs in the entire Hecate Strait and QCS.

In past multibeam mapping, sponge areas were observed to be less acoustically reflective (darker regions) with lower backscatter than surrounding areas and underlying sediments (Conway et al. 2005). Acoustic signatures from backscatter data rendered various reef shapes within the northern reef complex, with elongated ridge forms predominant in the SW sector, biostromal (sheet-like) occurrences in the northern sector, and coalescing bioherms (mounds) in the SE sector (Conway et al. 2005). The northern reef complex was described as having lower relief than reefs in the southern complex, where the largest ridges or bioherms reach 21 m high. (Conway et al. 2005).

2.2.2 ROV image surveys

Field sampling was carried out on board the Canadian Coast Guard Ship (CCGS) *John P. Tully*. The Canadian operated ROV ROPOS was used to conduct photographic surveys in October 2015 at two field sites called here *Farrea 2015* (53°11′34.3″N, 130°28′22.2″W, mean depth 170 m) and *Peloponnesus* (53°8′57.4″N, 130°25′36.4″W, mean depth 191 m) (Figure 2-1 B). During a second research cruise in May 2017, a third site was surveyed called *Sponge Ridge West* (53°11′6.20.3″N, 130°29′36.1″W, mean depth 178 m) (Figure 2-1 B). A sampling grid of stratified georeferenced points 25 m apart was overlaid on a map at each field site (Figure 2-2 A-C). The surveys involved 'flying' ROPOS at 5 m above the bottom (mab) to each grid point, hovering the ROV one to two mab, and capturing images of the reef from birds-eye view using a downward facing digital still camera (DSC, Nikon D7000). Each ROV image was 12.5 megapixels and had a pair of lasers providing a 10 cm scale.

2.2.3 Image analysis of sponge cover

Three approaches were used to quantify the amount of sponge cover within ROV images. The first approach involved a manual method for delineating live and dead sponge areas using Adobe Photoshop CS5. The manual method was applied to ROV images collected in October 2015 (*n* = 217). Live and dead sponge were traced in an image and saved as a jpeg file. Areas were calculated in pixel units and then converted to area per m^2 using the 10 cm laser dots for scale. The second approach for analyzing ROV images involved using a grid tool in ImageJ v. 1.3.3.67 (Dunham et al. In Press). The 'grid method' was applied to all images collected in May 2017 ($n = 99$). Laser dots were used for scale to generate a grid of 10 x 10 cm cells in ImageJ that was overlain onto the images using GIMP v. 2.6 (GNU Image Processing Software). Live sponge, dead sponge, and bare substrate were annotated for each grid cell when ≥ 50% of a cell was occupied by one of these cover types and the area as a percentage was calculated using the statistical program R v. 3.3.3. Finally, a third approach was used to automatically threshold sponge cover in ROV images collected in May 2017. Auto-thresholding was capable of only measuring live sponges. ROV images were first batch processed in ImageJ to remove uneven background lighting created by ROPOS' lights. Following this procedure, the Yen auto-thresholding tool was used to measure live sponge areas in pixel units and later converted into area per m^2. All data were assessed for normality using a Shapiro-Wilk's test, which indicated data for dead sponge and no sponge cover were non-normally distributed and data for live sponge cover were normally distributed. Therefore, a Wilcoxon signed-rank test and a paired t-test were used to statistically compare the accuracy of these methods for estimating live, dead, and buried sponge (STATISTICA 13.3).

2.2.4 Comparison of reef distributions to multibeam polygons

Multibeam mapped polygons delimiting reef areas were recently updated as of 2014 and obtained courtesy from K.W. Conway (NRCan). The distribution of live and dead sponge cover measured from ROV images were mapped and compared to the distribution of reef areas in multibeam polygons using a Spearman rank correlation (STATISTICA 13.3). To map reef distributions, sponge areas were interpolated by kriging for unsampled regions between ROV survey grid points. Kriging depends on mathematical and statistical models before values can be predicted for non-sampled sites (Dale and Fortin 2014). Semivariogram analyses were conducted to determine if sponge areas were spatially autocorrelated before kriging was performed. The variogram model parameters include the sill ($C_0 + C$) where the model reaches its asymptote and represents global variation of the sponge cover, the range (A_0) which denotes the maximum distance reef areas are spatially dependent, and the nugget (C_0) showing variability in sponge cover at distances smaller than the sampling interval. If spatial autocorrelation is detected, a continuous surface can be created by interpolating unsampled regions between points using the parameters from the semivariogram model. All semivariograms were created in GS+ 3.3.7 software from universal transverse mercator (UTM) coordinates (metres) and percent total live and dead sponge cover values. Semivariogram model parameters, regardless of their fit, were used to interpolate the sponge cover across the entire area surveyed by kriging. Kriging was completed in ArcMap v. 10.5 and a mask layer polygon was used to limit interpolation within the surveyed region. Percent live and dead sponge cover were interpolated in 5% isopleths. All maps and spatial analyses were completed and displayed in projection NAD 1983 UTM Zone 9.

The relationship between live sponge cover and depth and slope were analyzed in ArcMap. The spatial analysis tool was used to generate slope raster layers for each field site from a 5 m cell digital elevation model (DEM). Depth (m) and slope (in degrees) values were acquired for each survey grid point by intersecting the stratified grid point layer with the DEM and slope layers. Differences in depth and slope were compared between field sites and a Spearman rank correlation was used to determine the relationship between percent live sponge cover with depth and slope (STATISTICA 13.3). Bathymetric data was obtained from the Canadian Hydrographic Service and the GSC.

2.2.5 Juvenile sponges and reef-associated megafauna

To determine the role of reef structure on juvenile sponge recruitment, the number of juvenile reef-forming sponges – with a maximum osculum diameter <5 cm – were counted in all 2015 and 2017 ROV images. No attempt was made to differentiate between juveniles of *H. calyx*, *A. vastus*, and *F. occa* since these species cannot be distinguished from photos alone at young life stages. The cover types live sponge, dead sponge, or bare substrate, to which juvenile sponges were attached was recorded. Juvenile sponges were found only on dead and bare substrate, hence densities of juvenile sponges were calculated from the total dead and buried sponge areas surveyed in each ROV image. These data were assessed for normality using a Shapiro-Wilk's test, which indicated juvenile sponge data were non-normally distributed. A Mann-Whitney U-test was used to compare juvenile sponge densities between dead and no sponge cover. The density of juveniles was also compared between field sites using a Kruskall-Wallis test to determine if juvenile sponge recruitment varies in different areas of the northern reef (STATISTICA 13.3).

To understand how sponge cover influences associated megafauna in the reefs, megafauna defined here as animals >2 cm in length, which could be readily identified from ROV images, were identified to the lowest taxonomic level possible and the cover type on which these organisms were found was recorded. These data were also assessed for normality using a Shapiro-Wilk's test, which indicated megafauna data were non-normally distributed. A Mann-Whitney U-test was used to compare average densities of organisms on live and dead sponge cover compared to buried portions of sponge. Species diversity at each field site and between reef cover types were calculated using the Shannon-Wiener Diversity Index (H') and similarities between community compositions were measured using Sorensen's index of dissimilarity. Species counts were log-transformed and a distance matrix was created using the Bray-Curtis similarity index. Similarities between species composition and the effect of high (> 60%), medium (20-60%), and low (< 20%) sponge cover were visualized using a non-metric multidimensional scaling plot (NMDS) implemented in the statistics program R using the package 'vegan'.

2.2.6 Optical intensity for rugosity analysis

Variations in the optical intensity (spectra) of ROV images were measured as an estimate of reef habitat complexity (rugosity) and used to determine how reef rugosity influences associated animal abundance. I followed the methods of Shumway et al (2007) for measuring optical intensity. A subsample of 50 image files at each field site was randomly selected and imported into ImageJ and converted into a grey-scale bitmap. The standard deviation (SD) of the spectral intensity values was determined for each image, and the mean SD was calculated. The mean SD of spectral values for each image was normalized (Z score: Zar, 1999) and used for statistical comparisons between field sites. A simple linear regression was used to examine the relationship between live sponge cover and bare substrate with optical intensity measures for testing whether optical intensity values can distinguish between reef cover types (STATISTICA 13.3). Simple linear regression was also conducted to examine the relationship between optical intensity measures and species abundance parameters.

2.2.7 Estimates of sponge oscula

An individual sponge is often difficult to identify because of their complex branching form. Instead, individual oscula that represent single sponge filtration units, can be quantified as a metric of sponge abundance. Furthermore, these oscula counts can be combined with suspension-feeding rates to determine reef-wide metabolic energetics. Although sponge grazing and excretion rates could not be calculated in this study, the densities of live sponge oscula in the Hecate Strait northern reef were quantified to be paired with pumping rates in future whole-reef metabolic analysis.

Three reef-building hexactinellid species are found in the reefs; however, oscula were measured only for *F. occa*, given this is the most prevalent reef-forming sponge in the Hecate Strait northern reef. Areas of live *F. occa* were first delineated from ROV images using the manual method described above, and the proportion of *F. occa* cover was calculated from the total area of live sponge at each survey grid point. The species *F. occa* grows as a bush with many hundreds of small oscula branching outwards and it was not possible to count every single osculum in an ROV image. Therefore, oscula in a known area of live *F. occa* were counted from a subsample of 40 randomly selected images. The relationship between oscula counts (dependent variable) and area of live sponge cover in pixel units (independent variable) was analyzed using a simple linear regression (STATISTICA 13.3), and the line of best fit was used to estimate the number of oscula per area of live sponge (pixel units) in the remaining ROV images. The number of live oscula in a continuous patch of live sponge were standardized to obtain densities per m^2. At each field site, the diameter of oscula ($n = 200$) facing directly towards the ROV camera were measured to determine oscula areas. These data were assessed for normality using a Shapiro-Wilk's test, which indicated oscula data were non-normally distributed. A Kruskall-Wallis test was used to compare all oscula measurements between field sites for determining if oscula density and sizes varied among reef locations (STATISTICA 13.3).

2.3 Results

2.3.1 Sponge cover in the Northern Reef

The manual, grid, and auto-thresholding methods were determined to be equally accurate approaches for estimating sponge cover in ROV images. Estimates of cover for dead sponge (Wilcoxon signed-rank, $p = 0.42$), live sponge (Paired t-test, $p = 0.10$), and bare substrate

(Wilcoxon signed-rank, $p = 0.08$) were compared and found to be similar between the manual and grid methods (Figure 2-3 A). At all field sites, areas of live sponge were slightly underestimated by the auto-thresholding method when compared to the manual method (Figure 2-3 B; Wilcoxon signed-rank, $p = 0.002$); however, the mean difference in percent live sponge cover estimated between the methods was negligible (1.6 ± 0.6 %, mean ± SE).

The areas surveyed by ROV at each field site were 1297.7 m^2 at *Farrea 2015*, 348.9 m^2 at *Peloponnesus*, and 730.7 m^2 at *Sponge Ridge West* (Table 2-1). Relative to the total area surveyed at each site, live sponge cover was the greatest at *Sponge Ridge West* (12.4%), followed by *Peloponnesus* (8.4%), and *Farrea 2015* (6.9%). In the northern reef complex, the total area predicted to be reef from multibeam mapping was 118.5 km^2 (courtesy of K.W. Conway, NRCan). A total of 1728.7 m^2 was surveyed within multibeam mapped polygons, while 648.6 m^2 was surveyed outside the polygons (Table 2-2). Buried sponge or bare substrate represented 63% of the area surveyed within the multibeam polygons, while dead and live sponge cover accounted for 26.8% and 10.2% respectively (Table 2-2). A small proportion of reef (5% live and 4.7% dead sponge) was discovered outside the multibeam polygons; however, most of the area beyond the multibeam polygons (90.3%) was dominated by bare substrate. Using these numbers, the proportion of live and dead sponge and bare substrate were estimated for the entire northern reef complex (Table 2-3). Exposed reef structure (live and dead sponge) constitutes 43.9 km^2 (37.0%) of the northern reef, while approximately 74.7 km^2 (63.0%) represents bare substrate (buried sponge and mud patches) with no three-dimensional structure at the surface.

2.3.2 Multibeam polygon estimates and analysis of sponge distributions

The ROV survey grid points located within multibeam polygons had greater amounts of live and dead sponge cover than grid points that were located outside the polygons (Spearman rank correlation, $\rho = 0.26$, $p < 0.001$). Semivariogram model parameters showed sponge reef distributions were spatially autocorrelated with 94 to 97% of the structural variance within the reefs explained by the models (Table 2-4). Semivariogram models also showed sponge areas at each sampling site were spatially dependent at range distances of 30.0, 36.4, and 28.3 m for *Farrea 2015*, *Peloponnesus*, and *Sponge Ridge West,* respectively (Figure 2-4 A-C). However, sponge areas may be spatially dependent at smaller scales than our minimum ROV sampling distance of 25 m given range distances are 28-36 m. Nonetheless, semivariogram model parameters were used for kriging to spatially interpolate sponge cover between survey grid points to create a continuous surface. Sponge areas were also evaluated for anisotropy at 0, 45, 90, and 135° for all semivariograms and directional autocorrelation was found to be non-significant.

Maps created by kriging showed where dense aggregations of live and dead sponges were located in each field site. Sponge cover at *Farrea 2015* was patchily distributed across the survey area with few regions where live and dead sponge reached >40% (Figure 2-5, A). The areas between sponge patches were comprised of muddy clay-rich sediments and deeply buried portions of sponge with no exposed three-dimensional structure at the surface. In contrast, live and dead sponge densely covered between 40 to 100% of the area surveyed at *Peloponnesus* (Figure 2-5, B). At *Sponge Ridge West*, there were also few areas with buried sponge and mud patches with more areas of live and dead sponge cover found between 40 to 100% (Figure 2-5, C).

Sponge areas within the entire northern reef complex were found between 130-235 m depth. Populations of glass sponges were found at all three field sites on relatively flat bottom surface features with no distinct ridge forms or mounds. Although live sponges were found at slightly shallower depths at *Farrea 2015* (169.4 ± 1.8 m, mean ± SD) than at *Peloponnesus* (190.7 ± 1.7 m, mean ± SD) and *Sponge Ridge West* (178.4 ± 1.2 m, mean ± SD) (Table 2-5), densities of live glass sponges were not correlated with depth (Spearman rank correlation, p = 0.21). The sloped topography on which live sponge cover was found did not differ between sites (Table 2-5); however, a strong positive correlation was observed between slope angle and percent live sponge cover (Figure 2-6; Spearman rank correlation, p = 0.001). At all field sites as slope angles increased, a higher percentage of live sponge cover was observed.

2.3.3 Juvenile sponge recruitment

No juvenile sponges were found on live sponge and very few juveniles were found in areas with no sponge cover (i.e. buried portions of sponge and patches of mud). The density of juvenile sponge was higher on dead glass sponge skeletons (2.8 ± 0.3 juveniles m^{-2}, mean ± SE) than areas with no sponge cover (0.4 ± 0.1 juveniles m^{-2}, mean ± SE) (Figure 2-7 A; Mann-Whitney U-test, $p < 0.001$). Juveniles sponge densities also differed between field sites, with the highest density of juvenile sponges found at *Sponge Ridge West* (1.9 ± 0.2 juveniles m^{-2}, mean ±

SE) and lower juvenile sponge densities at *Farrea 2015* (0.9 ± 0.1 juveniles m^{-2}, mean ± SE) and *Peloponnesus* (0.7 ± 0.1 juveniles m^{-2}, mean ± SE) (Figure 2-7 B; Kruskall-Wallis, $H = 27.1$, $p < 0.001$).

2.3.4 Associated megafauna in the reefs

The northern reef supports numerous megafauna associates (Figure 2-8) with representatives from 6 phyla and 13 classes (Table 2-6). The most abundant taxon in the reefs was Arthropoda, comprising 76% of all organisms identified. Squat lobsters *Munida quadraspina* and spot prawns *Pandalus platyceros* were the most common arthropods with densities up to 9.7 individuals m^{-2} and 27.3 individuals m^{-2}, respectively. The most common fish among glass sponges were rockfish *Sebastes* spp. (up to 2.1 individuals m^{-2}) and flatfishes (up to 0.9 individuals m^{-2}). Other taxa found in the reefs in notably high abundances included seastars (Class Asteroidea), snails and clams (Phylum Mollusca), and other non-reef forming sponges (Phylum Porifera).

Diversity of fauna did not differ between fields sites or between areas where sponge reef was present (live and dead sponges) and absent (buried sponge and patches of mud) (Figure 2-9). However, at all field sites total megafauna densities were significantly greater in the presence of reef sponges than in the absence of sponges (Figure 2-10; Mann-Whitney U-test, $p < 0.0001$). NMDS ordination analyses showed there was a significant correlation between reef (total live and dead sponge) substrate on megafauna associates at *Farrea 2015* and *Peloponnesus*, but not at *Sponge Ridge West* (Figure 2-11, A-C). These differences in associations were driven mostly by squat lobsters *M. quadraspina*, seastars, and rockfish, which were taxa strongly associated with areas of high live and dead sponge cover. In contrast, spot prawns *P. platyceros*, flatfish, and molluscs were more abundant in the presence of low live and dead sponge cover and large patches of mud.

2.3.5 Habitat complexity

Optical intensity was a purely visual approach for measuring sponge habitat complexity in the reefs (Figure 2-12 A, B). A positive relationships was found between normalized optical intensity measures and amount of live sponge cover observed in ROV images (Figure 2-13 A, $r^2 = 0.27$, $p < 0.001$). The relationship between normalized optical intensity measures and the total number of animals counted in an image were also positive (Figure 2-13 B, $r^2 = 0.09$, $p < 0.001$). ROV images with greater areas without sponge cover were negatively related with normalized optical intensity measures (Figure 2-13 C, $r^2 = 0.21$, $p < 0.001$).

2.3.6 Farrea occa densities and oscula sizes

A strong positive relationship was found between the number of oscula counted in ROV images and the area of live sponge cover (pixel units) (Figure 2-14, A; $r^2 = 0.76$, $p < 0.001$). This relationship was used to estimate the number of *F. occa* oscula at each field site. The density of *F. occa* oscula within continuous patches of live sponge was significantly greater at *Farrea 2015* (455.3 oscula m^{-2}) and *Peloponnesus* (481.9 oscula m^{-2}), but low at *Sponge Ridge West* (262.6 oscula m^{-2}) (Figure 2-14 B; Kruskall-Wallis, $H = 31.6$, $p < 0.001$). Despite there being fewer *F. occa* oscula at *Sponge Ridge West*, the size of oscula at this site (6.3 ± 0.2 cm^2, mean ± SE) were slightly larger than at *Farrea 2015* (5.5 ± 0.2 cm^2, mean ± SE) and *Peloponnesus* (5.7 ± 0.1 cm^2, mean ± SE) (Kruskall-Wallis, $H = 11.7$, $p = 0.003$). The average diameter of *F. occa* oscula among all field sites averaged 2.4 cm. Proportion of live sponge cover comprised of *F. occa* differed significantly among field sites, with high proportions of *F. occa* found at *Peloponnesus* (89.1%) and *Farrea 2015* (60.5%), and low proportions of *F. occa* found at *Sponge Ridge West* (25.2%) (Figure 2-14 C; Kruskall-Wallis, $H = 31.5$, $p < 0.001$). While live *F. occa* was a dominant species in the reefs at *Peloponnesus* and *Farrea 2015*, the other reef-forming species *H. calyx* and *A. vastus* predominated at *Sponge Ridge West*.

2.4 Discussions

This study is the first to document the spatial pattern and faunal associations of glass sponges in the Hecate Strait northern reef. Reef polygons mapped in past studies by multibeam bathymetry were resolved at finer spatial scales using ROV imagery and distinct patterns in the distribution of live and dead sponge cover were found at each sampling site. Results also revealed the relationships between glass sponges and associated megafauna in the reefs, whereby associations occurred at a taxon-specific level. Oscula densities were quantified for understanding *F. occa* abundance and can be used in future measurements of water and nutrient cycling in the Hecate Strait northern reef. Possible factors are discussed below that elucidate the patterns of sponge distributions and animal interactions in glass sponge habitat.

2.4.1 Approaches for measuring sponge cover

Current techniques for measuring sponge cover in ROV images vary among university researchers and government scientists, but there have been no conclusive tests evaluating the accuracy of these methods. In past studies in the SoG reefs, the manual method was used for delineating sponge cover in ROV images (Chu and Leys 2010); however this approach can be tedious and inefficient when hundreds of images require processing. Since this work, DFO government scientists have returned to the SoG for reef status assessments and the 'grid' method was applied to imagery collected by ROV (Dunham et al. In Press). While the 'grid' method can markedly reduce time spent on image processing, operator decisions are still required to determine what substrate type is observed in each grid cell. In this study, an automated auto-thresolding method was trialed for measuring live and dead sponge cover in ROV images. Results of this work demonstrate that live and dead sponge cover can be accurately measured using either of the manual, 'grid', or auto-thresholding methods. The Hecate Strait and QCS reefs were recently designated as a MPA and there will be future efforts in monitoring changes in the reef, which may involve repeat visits with ROV surveying. Auto-thresholding has now been shown to be a standard yet efficient approach for measuring sponge cover in ROV imagery that researchers can confidently apply to monitor changes in sponge abundance.

2.4.2 Differences in sponge cover

ROV imagery revealed differences in glass sponge abundance in different sectors of the Hecate Strait northern reef. Total reef cover (live and dead sponge) was high at *Peloponnesus* (46.2%) and *Sponge Ridge West* (45.9%), and lowest at *Farrea 2015* (15.9%). At all reefs the proportion of bare substrate was exceedingly high (over 50%) out of the total area surveyed by ROV. This data is consistent with past studies that examined sponge cover at Galiano, Howe, and Fraser reefs in the SoG (Chu and Leys 2010). However, Chu and Leys (2010) observed substantially lower amounts of live and dead sponge cover (11 to 26%) in the SoG reefs compared to the Hecate Strait reefs. This difference likely reflects the oceanographic conditions specific to each location.

A unique set of conditions is required for glass sponge reef formation including bathymetry at 20-260 m depth, temperatures ranging between 9-10^{o}C, high dissolved silicate concentrations, and low sedimentation rates (Leys et al. 2004). Although reef formation is dependent on the burial of glass sponges by sediments, excessively high sedimentation rates are detrimental to sponge health because the feeding apparatus of the sponge can become clogged by sediments. The Fraser River supplies the largest source of sediment to the greater SoG region, which is the third largest river discharge from North America to the Pacific (Johannessen et al. 2003). Sediment traps measured sedimentation accumulation rates of 97 mm year^{-1} at Galiano reef and 137 mm year^{-1} at Fraser reef (Kahn et al., 2016). In contrast, sedimentation rates near the Hecate Strait northern reef are estimated to be much lower at 0.68 mm year^{-1} (S. Johannessen, Fisheries and Oceans Canada, pers. comm.), with bottom tidal currents reaching up to ~35 cm s^{-1} that would eliminate any sediment that may accumulate in the reefs and neighbouring areas (Whitney et al. 2005). Therefore, total reef cover might be lower in the SoG reefs than the Hecate Strait northern reef due to higher sediment loading, which would smother glass sponges and fully bury large portions of reef. Furthermore, assessments of the status of glass sponge reefs in the SoG revealed over half of the reef areas surveyed were mechanically damaged by bottom trawling (Cook et al. 2008). The Hecate Strait northern reef is known to have experienced less trawling activity than other reefs in the Hecate Strait and QCS (Jamieson and Chew 2002), but comparisons in bottom fishing activities between the Hecate Strait and SoG have not been made. Exploring whether substantial anthropogenic impacts within the vicinity of the SoG reefs account for lower sponge abundance is a topic for future study.

Percent live sponge cover was highest at *Sponge Ridge West* (12.4%), located in the SW sector of the northern reef, and lower at *Peloponnesus* (8.4%) and *Farrea 2015* (6.9%), located in the SE sector. Morphology of the reefs and bottom current hydrodynamics may be an important control on live sponge cover that would account for the distribution pattern of live sponges observed in this study. Reef shapes are highly variable depending on their location within the northern reef complex, with elongate ridge forms (biostromes) found in the SW sector and coalescing mounds (bioherms) in the SE sector (Conway et al. 2005). This variability in reef forms is thought to develop in response to current velocities interacting with local seabed types (Conway et al. 2005). The Hecate Strait northern reef occurs along the upper canyon north of the Moresby Trough where near-bottom currents flow in a NW direction along the axis of the canyon (Whitney et al. 2005). Biostromal reefs at *Sponge Ridge West* are oriented in a NW-SE pattern and limited to elongate glaciomarine sediments (Conway et al. 2005). Bottom tidal currents might be enhanced as they are channeled along these ridges in a northern direction, increasing ambient flow rates, which are beneficial for the sponges as nutrients are replenished to local waters, sponge wastes are removed, and suspension feeding becomes heightened (Leys et al. 2011). The advantageous effects of increased current velocities have been observed in similar suspension-feeding communities such as coral reefs (Sebens 1984, Fabricius et al. 1995). Contrary to *Sponge Ridge West,* the reefs at *Peloponnesus* and *Farrea 2015* possibly experience suboptimal hydrodynamics given these reefs are mound-like in form and can reach tall heights that create obstructions that deflect tidal currents (Conway et al. 2005). Therefore, the lower percentage of live sponge cover at these sites might reflect slower tidal regimes in these areas.

These findings suggest that glass sponges inhabit a specific ecological niche where a balance exists between low sedimentation and high flow rates. High enough rates of sedimentation are required to form the reefs, but not too high that the entire sponge becomes buried. The abiotic pressures understood here to mediate sponge growth can be applied in environmental niche modelling for predicting glass sponge distributions that might aid in sponge reef conservation planning.

2.4.3 Multibeam polygons assessment

Reef areas were mapped into polygons based on multibeam acoustics (courtesy of K.W. Conway, NRCan), and were ground-truthed in this study by ROV to determine the amount of sponge reef present within and outside these polygons. ROV images containing a high percent of live and dead sponge cover were strongly correlated with survey grid points found within multibeam polygons. These results suggest reef extents were adequately delimited from past mapping efforts. Although most of the region beyond the multibeam polygons was comprised of bare substrate (90.3%), there was a small amount of live and dead sponge (~10%) cover discovered outside the polygons. This may indicate shifting spatial patterns in sponges to other regions in the reef. Despite being sessile and slow-growing, sponge communities are dynamic systems that have been demonstrated to respond to oceanographic climate shifts and inter-annual changes in food supply (Dayton 1989, Kahn et al. 2012). In the SoG reefs, Kahn et al., (2016) observed the appearance and growth of new sponges concomitantly with the death of sponges, indicating sponge populations are in a constant process of renewal and replacement. However, glass sponge growth rates are slow (1 to 3 cm year^{-1}) (Kahn et al. 2016) and thus it is expected expansion of the reef in the Hecate Strait would occur at gradual rates possibly too slow to measure in one year. As the northern reef undergoes short and long-term fluctuations in distribution, polygon delimitations based on multibeam mapping may become out-dated in upcoming years. Therefore, my data provides baseline information on the spatial pattern of sponges in the Hecate Strait that can assist in monitoring future changes in reef distribution.

2.4.4 Spatial structure and reef distributions

Grid sampling at 25 m resolution using a ROV showed sponges in the Hecate Strait northern reef were spatially structured in 'patchy' distributions. Based on semivariogram analyses, spatial autocorrelation occurred at distances of 30.0, 36.4, and 28.3 m for *Farrea 2015*, *Peloponnesus*, and *Sponge Ridge West,* respectively. This patchy pattern in sponge distributions matches existing literature on the spatial structure of sponges in the SoG reefs. However, spatial dependence in the SoG reefs occurred at larger distances (42 to 72 m) (Chu and Leys 2010). Chu and Leys (2010) commented that discontinuity in sponge patches observed in the SoG reefs was the consequence of larval dispersion patterns and new sponge recruitment, and it may be presumed the same is true for glass sponges in the Hecate Strait and QCS reefs. Larval selectivity during settlement has implications for determining the distribution of many sponges (Uriz et al. 1998, Maldonado 2006, Whalan et al. 2008). Differences in spatial structuring between the reefs might reflect variability in larval behaviours among the reef-forming sponge species. The Hecate Strait and QCS reefs are composed mainly of *F. occa*, whereas reefs in the SoG are formed only by *A. vastus* and *H. calyx.* While nothing is known about the dispersal potential for larvae of *F. occa* and *H. calyx*, the larvae and/or broadcast sperm of *A. vastus* were found to disperse extensively throughout the SoG region (Brown et al. 2017). Hence, reef patches in the SoG may be spatially structured at larger distances if the aptitude for larval dispersal in *A. vastus* is much greater than *F. occa* larvae. Other studies have shown dispersal of sponge larvae can be restricted to short larval stages coupled with poor motility, causing next generations of sponges to be locally retained (Uriz et al. 1998). Small-scale spatial structuring in the Hecate Strait northern reef may be partially explained if *F. occa* larvae have poor swimming abilities and a short pre-settlement stage. Asexual reproduction through budding has also been postulated to explain patchy distributions of glass sponge populations in Antarctica (e.g. from *Rossella racovitzae*, Dayton (1979)). Budding would maintain local retention of juvenile recruits, forming spatially dependent patches of sponges observed in my surveys. However, the reproductive modes of reef-forming glass sponges remains poorly understood and should be interpreted with caution.

Sponges were on average found at deeper depth ranges (170-190 m) in the Hecate Strait northern reef than the SoG reefs (80-160 m). Chu and Leys (2010) found a lack of correlation with slope and sponge cover, but in contrast this study found a strong correlation between slope and live sponges. The SoG reefs are located on different bathymetric features (ridges and hummocks) than the Hecate Strait northern reefs, which are located on relatively level surfaces. Reefs in the SoG were found near the crest of their respective underlying features (Chu and Leys 2010) and it was suggested their locations were due to accelerated flow patterns resulting from water flowing over seafloor ‘bumps’. As water flows over a ridge, fluid is forced to converge and accelerate on the leeward side (Dewey et al. 2005) where many glass sponges were found in Fraser Ridge reef (Chu and Leys 2010). Live sponges were found on both sides of the ridge at Galiano reef where flow was thought to run parallel to the crest, generating localized small-scale upwellings. Given ridge and hummock-like features are not found in the Hecate Strait northern reef, other ecological processes are suggested to be involved in influencing reef distributions in this area. Increased slope topography was an important abiotic predictor of where live sponges were observed in the northern reef and reasons behind this relationship may be related to reaching suitable heights above the seafloor for acquiring exposure to increased water flows. The race to reach elevated portions of substratum is common among organisms seeking to benefit from higher flow rates. Anemones, crinoids, and ophiuroids were most often found at the very top of stalks of the glass sponge *Hylonema* (Beaulieu 2001). Higher growth rates were also observed in the sponges *Amphimedon compressa* and *Iotrochota birotulata* when associated specifically to the upper-level of octocoral skeletons (McLean and Lasker 2013). For reef-forming glass sponges, *A. vastus* has been found to benefit from current-induced flow that allow the sponge to passively feed on ultraplankton (<10 µm) without the energetic expenditure (at least 28% of respiration) used for pumping (Leys et al. 2011). Amplification of flow resulting in sloped topography can thus explain the increased abundance of live sponges observed in these locations.

2.4.5 *Juvenile sponge recruitment and reef growth*

Juvenile sponge densities were more than 5 times higher on dead sponge cover (average 2.8 ind. m^{-2}) than on areas with no sponge cover (average 0.3 ind. m^{-2}). This finding agrees with past studies that also found higher juvenile sponge densities near adult sponges and dead sponge skeleton (Kahn et al. 2015). Considering settlement of reef-forming sponge larvae is contingent on the availability of hard substrata, the three-dimensional framework of dead sponge skeleton likely provides good substrate and growing conditions for juvenile sponges. Flattening of the seafloor has been shown to occur over time with bottom trawling activities, whereby sediments are displaced and removed from fishing grounds as heavy nets and gear are dragged along the seafloor (Puig et al. 2012). Given benthic habitat in the Hecate Strait northern reef is dominated by soft bottom sediments, removal of dead sponge skeleton by trawling would reduce optimal attachment sites for larval settlement and have severe implications on juvenile sponge recruitment.

The density of juvenile sponges was observed to be higher at *Sponge Ridge West* than at *Farrea 2015* and *Peloponnesus*. The presence of many small sponges at *Sponge Ridge West* gives insight into reproduction and recruitment at this location. Juvenile sponges are estimated to grow 1-3 cm $year^{-1}$ (Kahn et al. 2016), and with this growth rate, juveniles observed in the reef (< 5 cm) likely settled within the past year. A recent reproductive event may have occurred at *Sponge Ridge West*, but since little is known about reproduction in glass sponges, it is difficult to determine what conditions would induce a reproductive period. Juvenile sponges are also thought to replace sponges that have died, and thus high juvenile sponge densities may indicate reef expansion and regeneration. However, for juvenile sponge populations to reach great densities, reef environments must be stable and undisturbed by human activities. Kahn et al. (2015) carried out large-scale disturbance experiments in the SoG reefs by crushing reef sites, and recovery of reef structures did not occur after 3 years with no new juvenile sponges seen anywhere on damaged reef skeletons. Given glass sponges are exceptionally slow-growing and long-lived, recovery is expected to take hundreds of years and conservation managers should be wary of interpreting juvenile sponge growth as a sign of reef recovery.

2.4.6 *Reef-associated megafauna*

Megafauna associates representing 6 phyla and 13 classes were observed in the Hecate Strait northern reef. This data is comparable with other published studies documenting animal associations in the SoG reefs (Cook et al. 2008, Chu and Leys 2010, Dunham et al. 2015). While benthic habitats are often featureless and dominated by soft bottom sediments, these findings show the importance of reef-forming glass sponges in deep ocean environments for building habitat that increases the density of commercially-important fish and crustaceans. Glass sponge canals and oscula act as condominiums for animal inhabitants. I observed squat lobsters *M. quadraspinia*, lithode crabs, brittles stars, and rockfish *Sebastes* spp. hiding within the oscula of live and dead sponges, perhaps as a means for evading predation and escaping strong currents. This study likely underestimated animal abundances given associations between microfauna < 2 cm (e.g. polychaete worms, bryozoans, diatoms, and foraminifera) and sponges could not be observed in ROV images; however, a diversity of micro-organisms is expected to be found upon closer inspection of glass sponge canals and surfaces. Unique intimate relationships have been documented where microorganisms embed themselves directly within glass sponge tissue. The Mediterranean cave hexactinellid *Oopsacus minuta* is pervaded with rod-shaped bacteria in its aquiferous system, but it is uncertain what benefits may be exchanged in this association (Vacelet et al. 1994). Diatoms adherent to the internal skeleton of the Antarctic glass sponge *Rossella racovtizae* Topsent 1901 are thought to benefit from light transfer emitted from the siliceous spicules (Cattaneo-Vietti et al. 1996). It is not known if reef-forming glass sponges in the Hecate Strait and QCS exhibit similar small-scale symbioses, but future ultrastructure examinations may reveal further diversity in these sponge ‘hotels’.

Species diversity of megafauna did not differ among field sites nor between areas in the presence and absence of sponge reef (live and dead sponges). This observation was driven by taxon-specific associations with glass sponges, in which some but not all taxa increased in abundance when glass sponges were present. Rockfish *Sebastes* spp., echinoderms, squat lobsters *M. quadraspina*, and other non-reef forming sponges were more associated with high to medium glass sponge cover. In contrast, spot prawns *P. platyceros*, molluscs, cnidarians, and flatfish were found where glass sponge cover was low and in patches of mud. These taxon-specific interactions in the reefs may indicate competitive exclusion between organisms vying for habitat or food resources in a space-limited environment. Chu and Leys (2010) also observed the majority of molluscs in mud patches between areas of glass sponges. This distribution in softbodied invertebrates was suggested to reflect behaviours for avoiding sharp hexactin spicules of *A. vastus* and *H. calyx* that can potentially pierce their soft tissue on contact. The dorid nudibranch *Peltodoris lentiginosa* was one exception to this, and was found directly on *A. vastus* and *H. calyx* (L. Law pers. obs.), which is consistent with observations made by Chu and Leys (2010). Glass sponge spicules have been found in the gut content of *P. lentiginosa*, suggesting this species is a regular predator on glass sponges (Chu and Leys 2012). Brittle stars *Ophiura* spp. and the asteroid *Mediaster* sp. were the most abundant echinoderms found directly on glass sponges. The sea stars *Pteraster tesselatus* and *Henricia* sp. have been documented in high abundances in other glass sponge populations in the NE Pacific (Leys et al. 2007). The glass sponge *Rhapdocalyptus dawsoni* is known to be actively preyed upon by *P. tesselatus*, but it is unknown if the *Mediaster* sp. feeds on glass sponges in the northern reef.

Taxon-specific associations with glass sponges were found at *Farrea 2015* and *Peloponnesus*, but this was not observed at *Sponge Ridge West.* This difference may reflect habitat specialization dependent on the community assemblage of reef-forming glass sponges. The species *F. occa* was the dominant reef-forming sponge at *Peloponnesus* and *Farrea 2015*, with a distinct growth pattern bush-like in form with many hundreds of oscula (average 2.4 cm in diameter). The sponges *A. vastus* and *H. calyx* were dominant at *Sponge Ridge West* and these species have variable oscula sizes (up to 15 cm in diameter, L. Law pers. obs.) with mitten-like or finger-like projections. Sponge associates are likely size-limited by these growth patterns and perhaps show host specificity to a reef-forming species.

2.4.7 Optical intensity and habitat complexity

Optical intensity analysis was found to be a simple technique for predicting the amount of live sponge cover and animal abundances in ROV images. These observations match findings of Shumway et al. (2007), where optical intensity values were found to corresponded well with rugosity (surface topography) measures in video-based imagery collected in Lake Tanganyika, Tanzania. Particularly for coral reef communities, rugosity has been a common metric applied to monitor structural changes in the reefs resulting in coral death, bioerosion, and reef flattening events (Komyakova et al. 2013, Burns et al. 2015, Newman et al. 2015). The chain/tape ratio has been a traditional approach for measuring rugosity, which requires hands-on operations of chains that often tangle easily and comes into contact with bottom substrates (Risk 1972). In recent years, a surge of off-bottom and remotely operated techniques have been developed to measure reef-scale rugosity, but these methods remain too time consuming for routine application (Du Preez and Tunnicliffe 2012) and/or require the use of divers (Dustan et al. 2013). Optical intensity offers a remotely sensed and an automated approach for assaying habitat complexity in sponge reef habitats. Although our findings show a weak but significant positive relationship between normalized optical intensity values and live sponge cover, this technique provides a methodological baseline that can be fine-tuned for monitoring changes in glass sponge reefs that are surveyed using any remote technology. In many other marine communities, a positive relationship has been found between rugosity and abundance of associated fauna, which is consistent with our findings (Du Preez and Tunnicliffe 2012, Dustan et al. 2013, Komyakova et al. 2013, Burns et al. 2015). This positive relationship opens up avenues for future research, including the investigation of small-scale rugosity within the internal sponge framework and its influences on the richness of sponge-associated fauna. Understanding the relationship between reef complexity and diversity also has implications for determining how sponge reefs will respond to mechanical damage by bottom trawling, which is expected to severely reduce benthic seascape complexity and ultimately threaten marine biodiversity (Puig et al. 2012).

2.4.8 Oscula densities and benthic-pelagic coupling estimates

The quantification of sponge oscula revealed varying amounts of *F. occa* among different sectors of the Hecate Strait northern reef. Two reef subtypes were found, with field sites *Peloponnesus* and *Farrea 2015*, in the SE sector dominated by *F. occa*, while *Sponge Ridge West* in the SW sector was dominated by *H. calyx* and *A. vastus*. The species *H. calyx* and *A. vastus* are the main reef-builders in the SoG reefs, while the species *F. occa* is unique to the Hecate Strait and QCS. Glass sponges in the SoG are speculated to be adapted to unusual sedimentation conditions by developing a narrower osculum that can reduce the amount of sediment accumulation in the sponge cavity (Conway et al. 2004, Cook et al. 2008). This hypothesis has been contradicted in the SoG reefs by Chu and Leys (2010) who observed smaller oscula in an area with relatively low sedimentation rates and larger oscula in an area with comparably high sedimentation rates. Therefore, it is unlikely differences in reef subtypes in the northern reef are influenced by sediment accumulation. However, given sedimentation rates are much lower in the Hecate Strait and QCS than the SoG, oscula sizes for *H. calyx* and *A. vastus* could be compared between these reef locations to further test the 'narrow osculum' hypothesis. Slight differences observed in the area of *F. occa* oscula at each sampling site suggests differences in reef subtypes more likely reflect local hydrodynamic patterns. Sponges are known to show plasticity in the size and position of their oscula as an adaptive response to current flow direction and velocities (Bidder 1923, Warburton 1960, Palumbi 1986). Local flow regimes at each sampling site could be measured in future studies to substantiate whether current velocities are correlated to the variability in *F. occa* oscula sizes and reef subtypes.

The size and density of *F. occa* oscula were quantified here to be combined with known *F. occa* pumping and feeding rates for estimating the volume of water the entire northern reef can process. Although this was beyond the scope of this study, qualitative *in situ* observations of *F. occa* pumping were recorded during the 2017 Hecate Strait reefs research cruise. Green fluorescein dye was released next to *F. occa* sponges to verify if they were pumping water, but uptake of dye was infrequently observed (L. Law pers. obs.). This may imply *F. occa* is a more passive suspension-feeder than other glass sponges such as *A. vastus* that has an active pumping rate of 2-3 cm s^{-1} (Leys et al., 2011). The Galiano reef in the SoG, composed predominantly of *A. vastus*, was estimated to process water at 83 000 l s^{-1} (Chu and Leys 2010). Estimates of water processing for the Hecate Strait northern reef will be more challenging given this reef is comprised of multiple glass sponge species. The proportion of reef subtypes within the Hecate Strait and QCS reefs require future consideration when estimating the effects of all four major reef complexes in benthic-pelagic coupling.

2.5 Conclusions

A ROV was used to sample the Hecate Strait northern reef at small spatial scales to gain insight into the patterns of live and dead sponge growth and megafauna associations. The distribution of live and dead sponges differed among field sites in the northern reef, which likely reflects variability in sedimentation rates, hydrodynamics, and juvenile sponge recruitment. Reef habitat complexity and the presence of sponges substantially increased megafauna densities, but megafauna associations within the reef varied depending on the taxa. The amount of water and ultraplankton the entire northern reef complex may process can be estimated from our quantification of sponge abundances and oscula measures. Given this study focused on only one of the four massive reef complexes in the Hecate Strait and QCS, future studies in this region should involve larger surveys that cover other reef complexes. Future MPA monitoring efforts will greatly benefit from the results of this work, which provided baseline empirical data on the status of sponges in the Hecate Strait northern reef.

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Table 2-1. Estimates of sponge cover at field sites *Farrea 2015*, *Peloponnesus*, and *Sponge Ridge West*. Areas of sponge reef indicated as 'bare' consisted of buried sponge or patches of mud. The proportion of area covered by live and dead sponges and bare substrate relative to the total sponge areas surveyed is shown in parentheses. Proportion of total reef includes both live and dead sponges.

Site	**Total area surveyed (m^2)**	**Area of sponge reef (m^2)**			Proportion Total Reef (%)
		Live	**Dead**	**Bare**	
Farrea 2015	1297.7	89.2 (6.9%)	117.0 (9.0%)	1091.5 (84.1%)	15.9
Peloponnesus	348.9	29.5 (8.4%)	131.9 (37.8%)	187.6 (53.8%)	46.2
Sponge Ridge West	730.7	90.5 (12.4%)	244.8 (33.5%)	395.4 (54.1%)	45.9

Table 2-2. Estimates of sponge cover at each field site (*Farrea 2015*, *Peloponnesus*, and *Sponge Ridge West*) for the areas surveyed inside and outside multibeam predicted polygons. Polygons represent predicted reef areas based on swath multibeam bathymetric surveys completed by the Geological Survey of Canada and obtained courtesy of K.W. Conway (NRCan). Areas of sponge reef indicated as 'bare' consisted of buried sponge or patches of mud. Survey grid points not located outside the polygons are denoted by dashed lines where no sponge quantities were measured.

Site	Sponge areas inside polygons (m^2)				Sponge areas outside polygons (m^2)			
	Live	**Dead**	**Bare**	**Total Area Surveyed**	**Live**	**Dead**	**Bare**	**Total Area Surveyed**
Farrea 2015	56.5 (8.7%)	86.6 (13.3%)	506.0 (78.0%)	649.1	32.7 (5.0%)	30.4 (4.7%)	585.5 (90.3%)	648.6
Peloponnesus	29.5 (8.4%)	131.9 (37.8%)	187.6 (53.8%)	348.9	---	---	---	---
Sponge Ridge West	90.5 (12.4%)	244.8 (33.5%)	395.4 (54.1%)	730.7	---	---	---	---

Table 2-3. Estimates of sponge cover for the entire northern reef complex. Areas based on the proportions of live sponge, dead sponge, and bare substrate measured from field sites *Farrea 2015*, *Peloponnesus*, and *Sponge Ridge West*. Areas of sponge reef indicated as ‘bare’ consisted of buried sponge or patches of mud.

Site	**Total area (km^2)**	**Area of sponge reef (km^2)**			**Proportion Total Reef (%)**
		Live	**Dead**	**Bare**	
Northern Reef	118.5	12.1 (10.2%)	31.8 (26.8%)	74.7 (63.0%)	37.0

Table 2-4. Spherical semivariogram statistics for all sampling sites based on UTM coordinates and total percent live and dead sponge cover. The nugget (C_0) is the variation found at finer scales than the field sampling has captured. The range (A_0) shows the distance over which samples are spatially autocorrelated. The variance explained by the semivariogram model (C) divided by the sill or total variance ($C_0 + C$), yields $C/(C_0 + C)$, which is the proportion of sample variance explained by spatial structure. The RRS is the residual sum of squares indicating how well the data fit a semivariogram model.

Site	**Points**	**Semivariogram parameters**				
		Nugget (C_0)	**Range (A_0)**	**Sill ($C_0 + C$)**	**$C/(C_0 + C)$**	**RRS**
Farrea 2015	169	0.008	30.00	0.554	0.985	1.22 E-3
Peloponnesus	50	0.042	36.40	0.801	0.947	1.32 E-1
Sponge Ridge West	100	0.014	28.30	0.482	0.970	4.56 E-3

Table 2-5. Distribution of live sponges at field sites *Farrea 2015*, *Peloponnesus*, and *Sponge Ridge West* with depth and slope characteristics. Depth (m) and slope (degrees) values are shown as a mean ± standard deviation and range.

	Depth		**Slope**	
Site	**Mean**	**Range**	**Mean**	**Range**
Farrea 2015	169.4 ± 1.8	164 – 174	4.1 ± 2.5	0 – 11
Peloponnesus	190.7 ± 1.7	187 – 195	3.7 ± 2.2	0 – 10
Sponge Ridge West	178.4 ± 1.2	175 – 185	1.9 ± 1.1	0 – 4

Table 2-6. Total counts of animals living on live sponge, dead sponge, and bare substrate observed in ROV images collected in 2015 and 2017 in the northern reef complex. Identifications were made to lowest taxonomic level possible and only include animals >2 cm. n/a: not available

Phylum **Class**	**Taxon**	**Common name**	**Live**	**Dead**	**Bare**
Porifera					
Demospongiae	**Desmacella* sp.	Demosponges	n/a	n/a	n/a
	Poecillastra sp.			180	37
Hexactinellida	*Rhabdocalyptus dawsoni/Staurocalyptus* sp./*Acanthascus* sp.	Boot sponges		334	58
	Unidentified species	Glass sponges	2	258	83
Echinodermata					
Asteroidea	*Ceramaster* sp.	Cookie star		10	26
	Culcita sp.	Cushion star	1	1	1
	Henricia sp.	Blood star			13
	Mediaster sp.	Vermillion star	16	73	46
	Orthasterias sp.	Rainbow star		1	

	Pteraster tesselatus	Slime star		3	
	Unidentified species	Sea stars	2	9	12
Echinoidea	Unidentified species	Sea urchins			1
Holothuroidea	*Parastichopus leukothele*	Whitespotted sea cucumber			7
	Parastichopus californicus	Giant red sea cucumber			1
	Synallactes challenger	Papillose sea cucumber		2	
Ophiuroidea	*Ophiura* sp.	Brittle stars	55	23	4
Arthropoda					
Malacostraca	Superfamily: Paguroidea	Hermit crab			1
	Acantholithodes hispidus	Spiny lithode crab	3		
	Chlorilia longipes	Longhorn decorator crab	3		
	Munida quadraspina	Squat lobster	1017	1042	565
	Pandalus platyceros	Spot prawn	11	366	3881
Pycnogonida	Order: Pantopoda	Sea spiders	4		
Mollusca					
Bivalvia	Order: Veneroida	Clams		50	315
Cephalopoda	*Enteroctopus dofleini*	Giant Pacific octopus		1	

	Rossia pacifica	Pacific bobtail squid			2
Gastropoda	Family: Columbellidae	Dovesnails			48
	Calliostoma sp.	Topsnails			124
	Fusitriton oregonensis	Oregon hairy triton			6
	Peltodoris lentiginosa	Dorid nudibranch		6	1
Cnidaria					
Anthozoa	Order: Actinaria	Sea anemones			3
Chordata (Fish)					
Osteichthyes	Family: Cottoidea	Sculpins		3	5
	Family: Pleuronectidae	Flatfishes			42
	Family: Stichaeidae	Pricklebacks			1
	Gadus chalcogrammus	Walleye pollock			2
	Sebastes flavidus	Yellowtail rockfish		1	6
	Sebastes diploproa	Splitnose rockfish			2
	Sebastes spp.	Rockfish	31	127	88
	Unidentified species	Fish		5	13
Chondrichthyes	*Hydrolagus colliei*	Spotted ratfish			3

Raja rhina	Longnose skate	2

*NOTE: *Desmacella* sp. were encrusting sponges growing on live and dead hexactinellid reef-forming species (e.g. *Farrea occa*, *Heterochone calyx*, and *Aphrocallistes vastus*) and was recorded as area m^2.

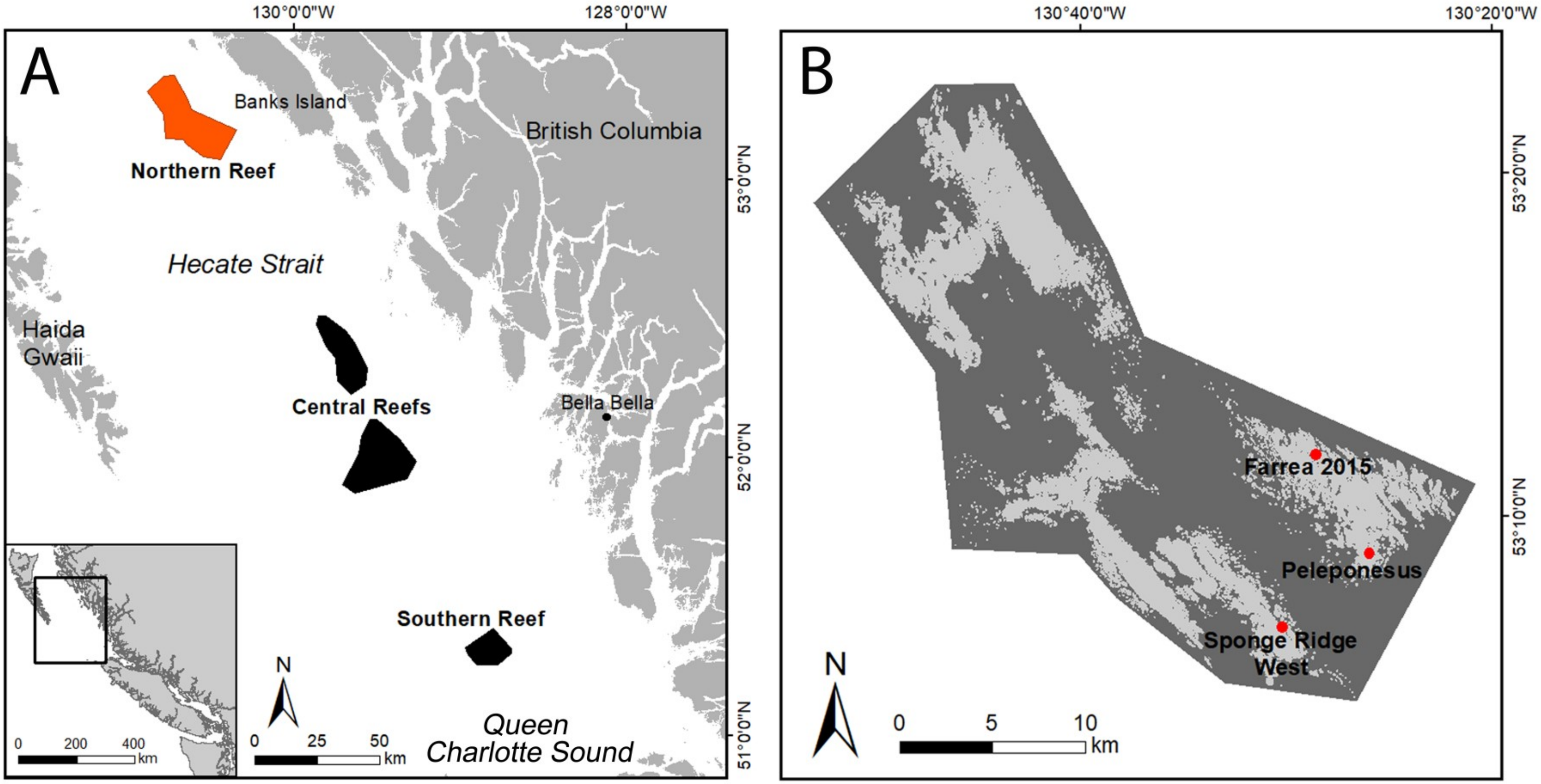


Figure 2-1. Glass sponge reef complexes in the Hecate Strait and Queen Charlotte Sound (QCS). (A) Reefs of the Hecate Strait and QCS are comprised of the northern, central, and southern reef complexes. The northern reef complex (orange) was the primary study location of this thesis. (B) A map of the northern reef complex showing the locations of three field sampling sites *Farrea 2015*, *Peloponnesus*, and *Sponge Ridge West*. Light grey regions indicate areas predicted to be reef based on multibeam mapping.

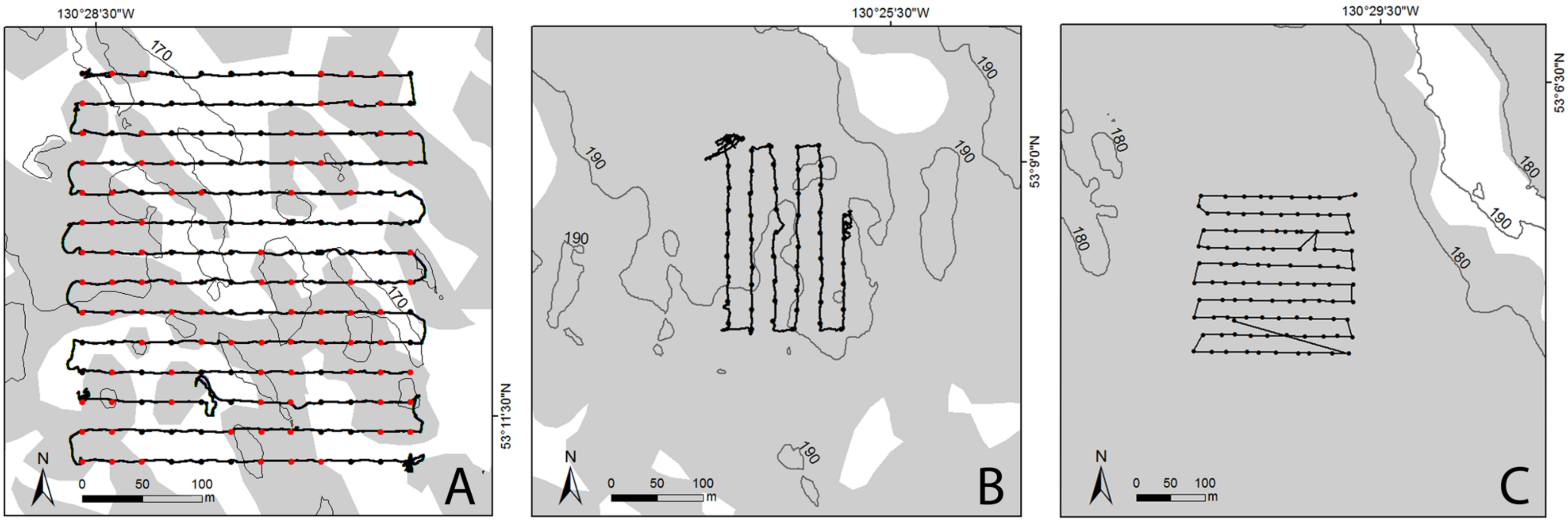


Figure 2-2. ROPOS surveying tracks conducted in October 2015 and May 2017 at field stations. (A) *Farrea 2015* (*n* = 169), (B) *Peloponnesus* (*n* = 50), and (C) *Sponge Ridge West* (*n* = 100). A 25 m stratified grid of points was overlaid on areas predicted to be reef (grey polygons) from multibeam mapping (Conway et al., 2005). Survey points outside (black dots) and inside (red dots) multibeam mapped polygons are shown at field site *Farrea 2015*.

Figure 2-3. Statistical comparisons between the manual, grid, and auto-thresholding approaches for estimating sponge cover in ROV images. (A) Average estimates of bare substrate (Wilcoxon signed-rank, $p = 0.08$), dead sponge (Wilcoxon signed-rank, $p = 0.42$), and live sponge (Paired t-test, $p = 0.10$) cover (m^2) compared between the manual and grid methods. Symbol * above columns indicates no significant difference between the pairs. (B) Average estimates of percent live sponge cover between the manual and auto-thresholding methods. Different letters above columns indicate a significant difference (Wilcoxon signed-rank, $p = 0.002$). Error bars are ± SE.

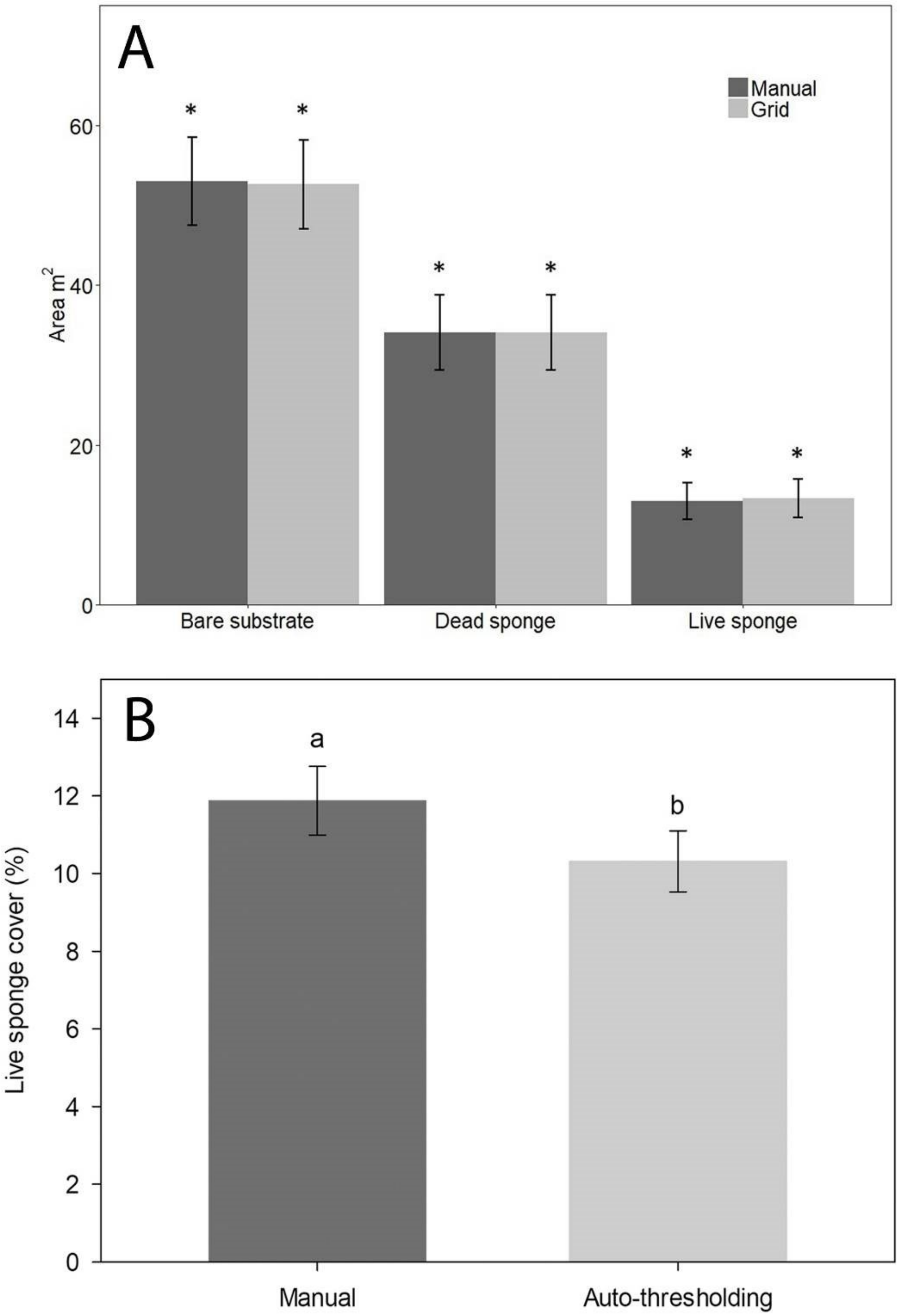

A
Manual
Grid
*
*
*
*
*
*
60
40
20
0
Area m²
Bare substrate
Dead sponge
Live sponge
B
a
b
14
12
10
8
6
4
2
0
Live sponge cover (%)
Manual
Auto-thresholding

Figure 2-4. Semivariograms showing spatial structure of sponges at sampling sites. (A) *Farrea 2015*, (B) *Peloponnesus*, and (C) *Sponge Ridge West*. Spatial autocorrelation occurred at each reef up to the range (A_0) and is signified by the sill (plateau) of each semivariogram. Dots represent lag distance intervals.

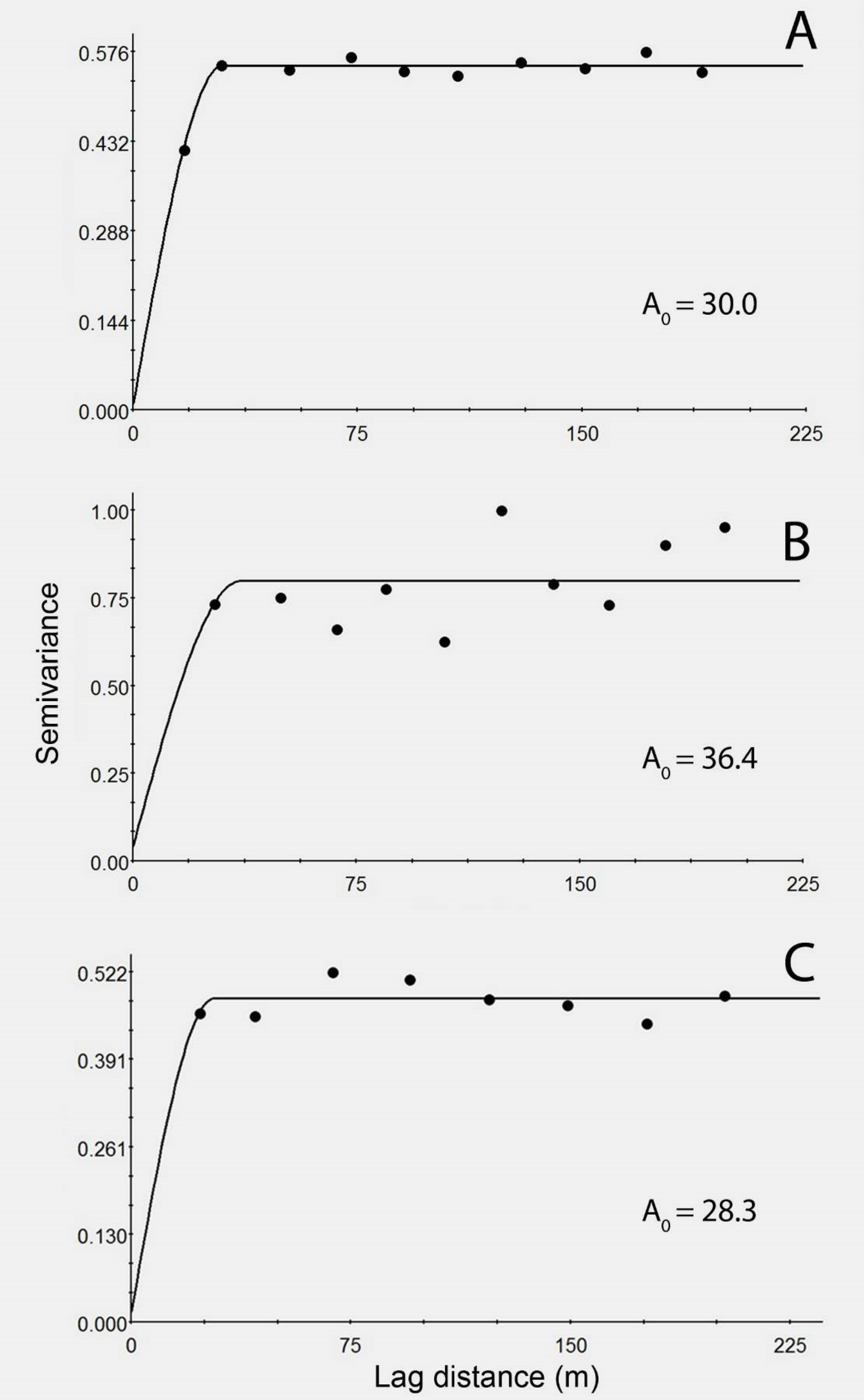
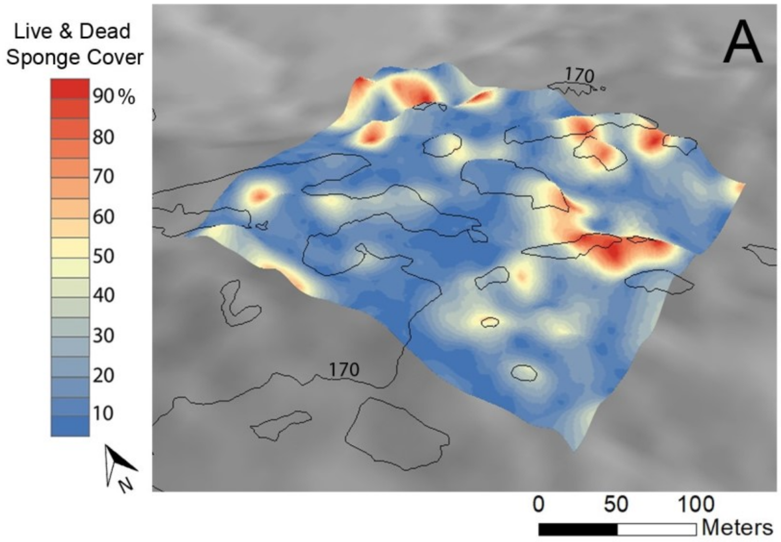
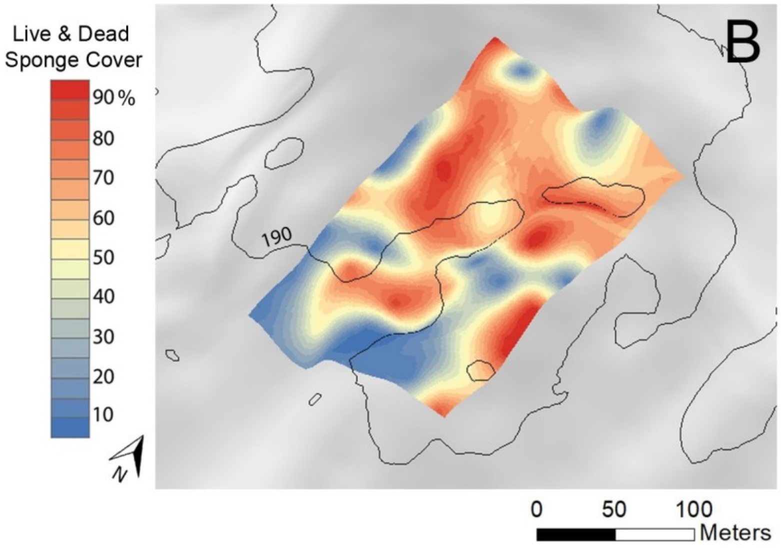
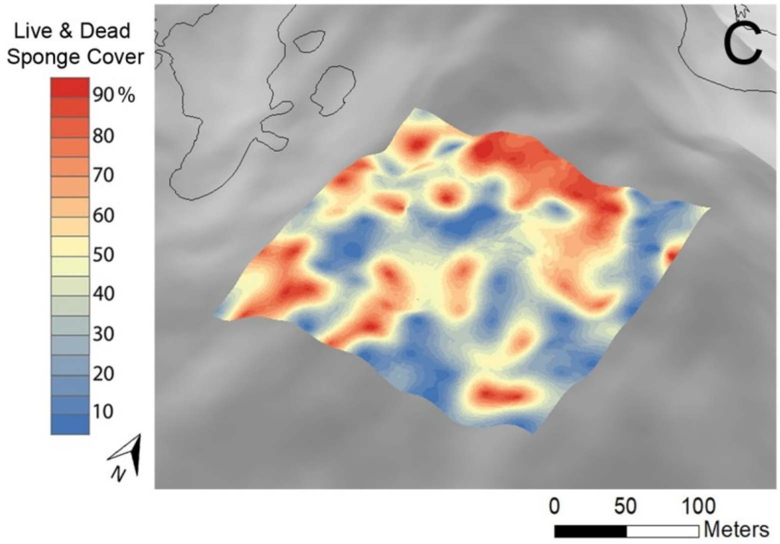

A
0.576
0.432
0.288
0.144
0.000
0
75
150
225
$A_0 = 30.0$
B
1.00
0.75
0.50
0.25
0.00
0
75
150
225
$A_0 = 36.4$
Semivariance
C
0.522
0.391
0.261
0.130
0.000
0
75
150
225
$A_0 = 28.3$
Lag distance (m)

Figure 2-5. Distribution of live and dead sponge cover at each sampling site. (A) *Farrea 2015*, (B) *Peloponnesus*, and (C) *Sponge Ridge West.* Kriging was performed to interpolate sponge areas using the semivariogram parameters in Table 2-4.


Live & Dead
Sponge Cover
90 %
80
70
60
50
40
30
20
10
N
A
170
170
0
50
100
Meters


Live & Dead
Sponge Cover
90 %
80
70
60
50
40
30
20
10
N
B
190
0
50
100
Meters


Live & Dead
Sponge Cover
90 %
80
70
60
50
40
30
20
10
N
C
0
50
100
Meters

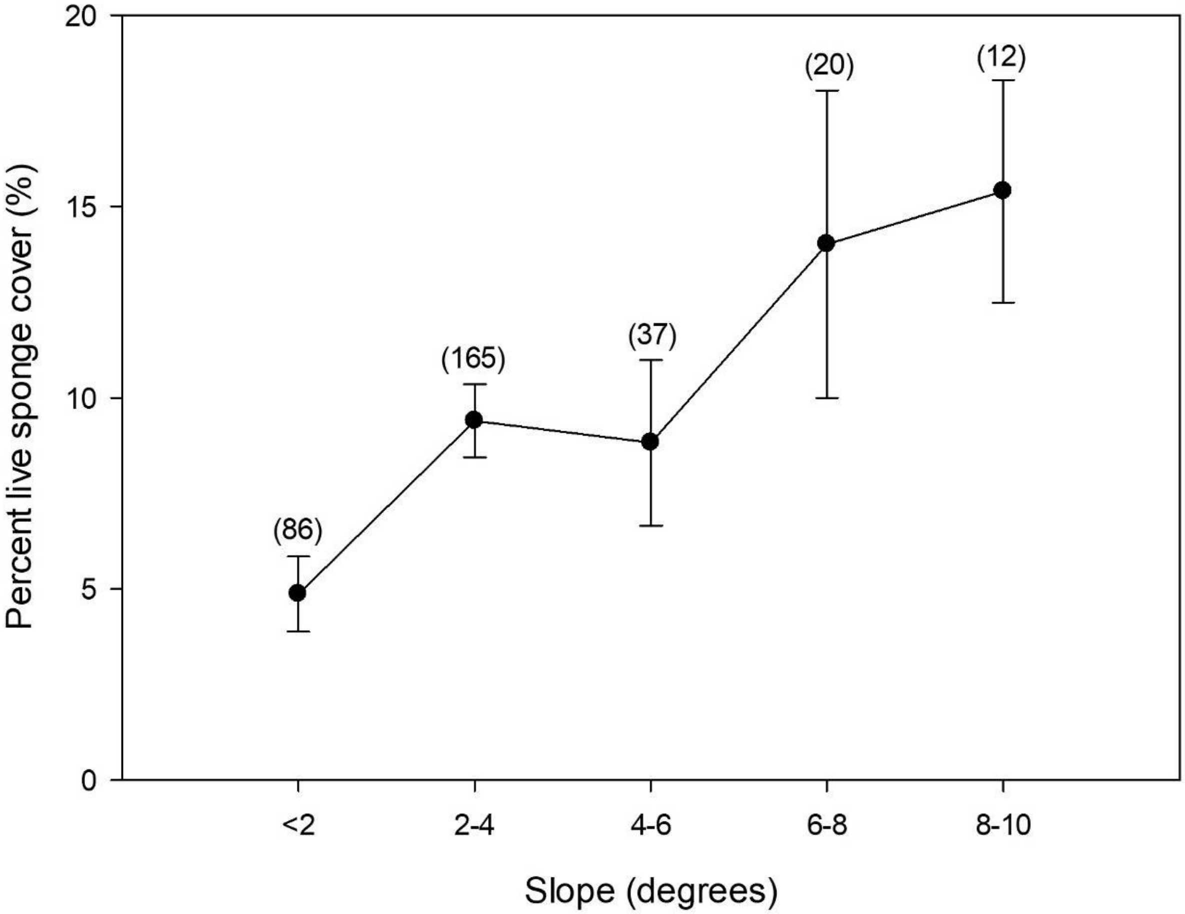


Figure 2-6. Relationship between percent live sponge cover and slope angles (incline in degrees). Sample sizes are shown in parentheses. Error bars are ± SE.

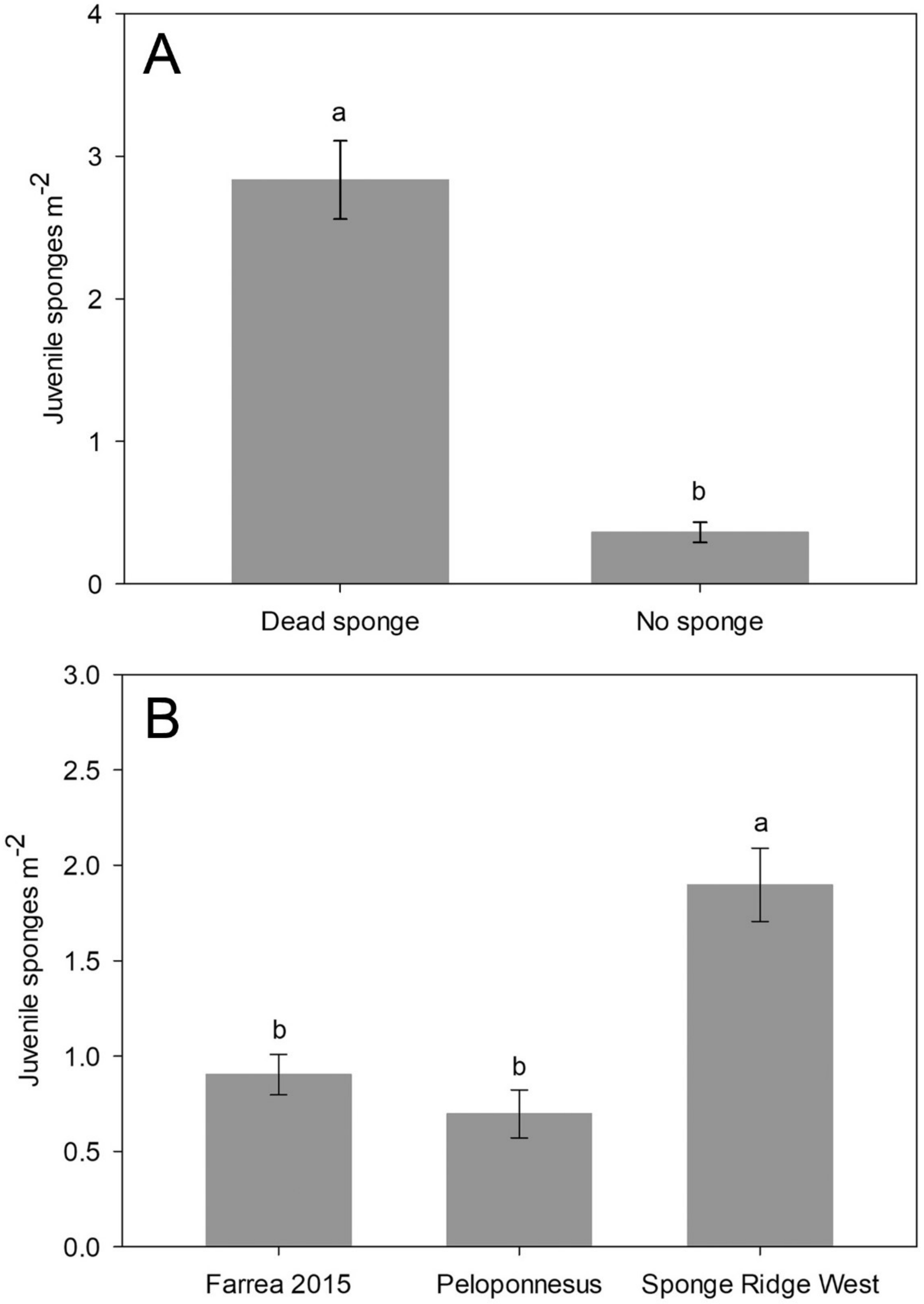


Figure 2-7. Comparison of juvenile sponge densities between cover types and field sites. (A) Density of juvenile sponges on dead sponge cover and areas with no sponge (i.e. buried portions or patches of mud). (B) Density of juvenile sponges found at each field site. Error bars are ± SE. Different letters above columns indicate statistical significant difference from others ($p < 0.001$ in all cases).

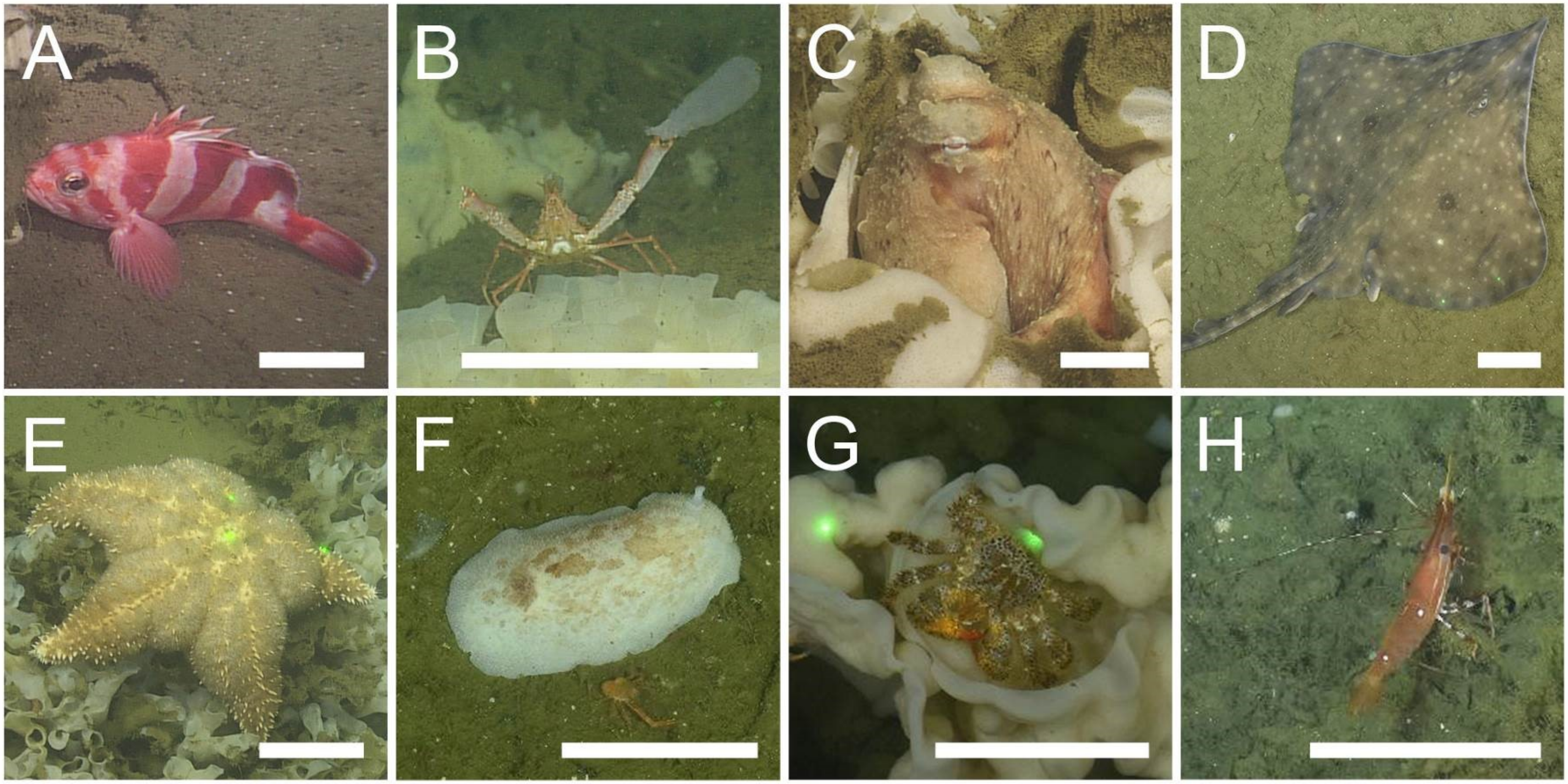


Figure 2-8. Examples of biodiversity in the Hecate Strait northern reef. (A) Rockfish, *Sebastes* sp.; (B) Squat lobster, *Munida quadraspina*; (C) Octopus, Class Cephalopoda; (D) Longnose skate, *Raja rhina*; (E) Sea star, Class Asteroidea; (F) Dorid nudibranch, *Peltodoris lentiginosa*; (G) Spiny lithode crab, *Acantholithodes hispidus*; (H) Spot prawn, *Pandalus playceros*. All scale bars 10 cm.

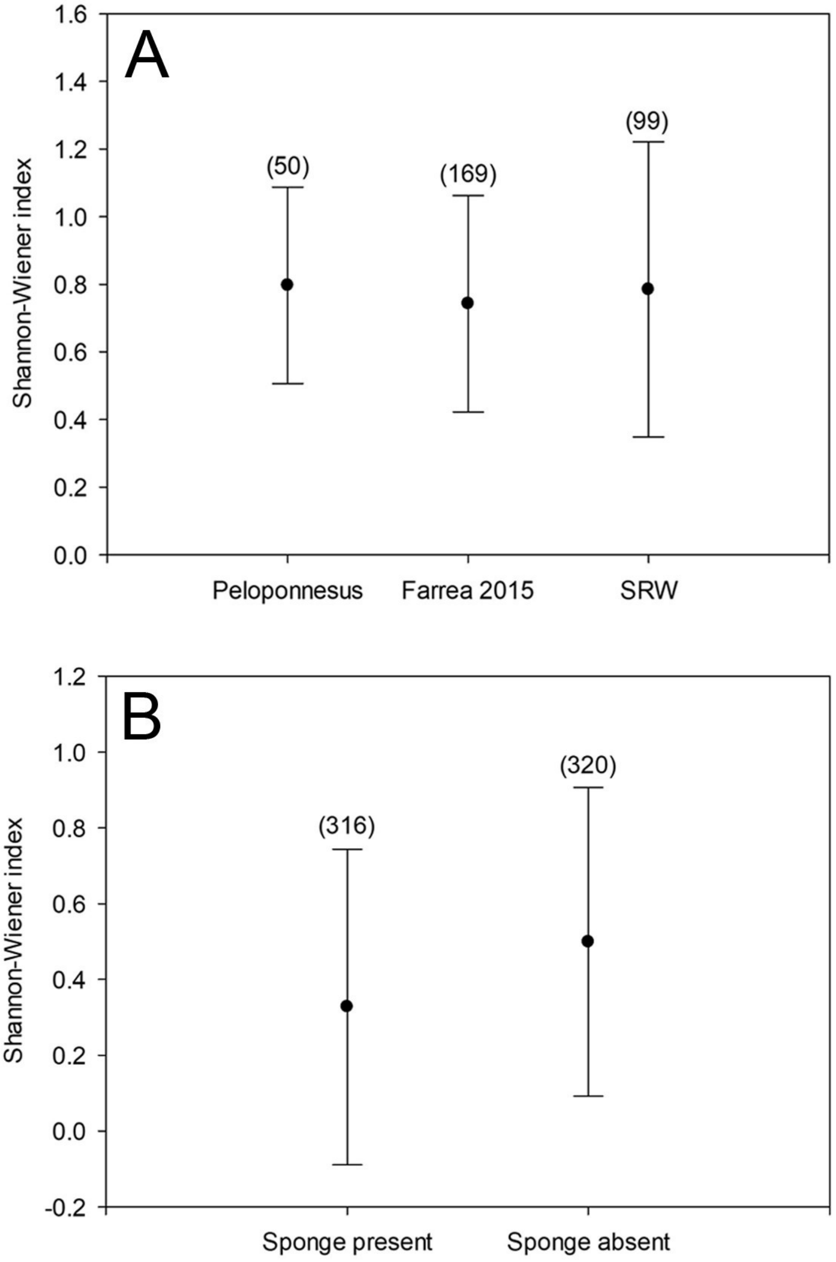


Figure 2-9. Comparison of Shannon-Wiener diversity indices. (A) Species diversity among field sites *Peloponnesus*, *Farrea 2015*, and *Sponge Ridge West* (SRW). (B) Species diversity in the presence and absence of reef sponges (live and dead glass sponges). Sample sizes are shown in parentheses. Error bars are ± SD.

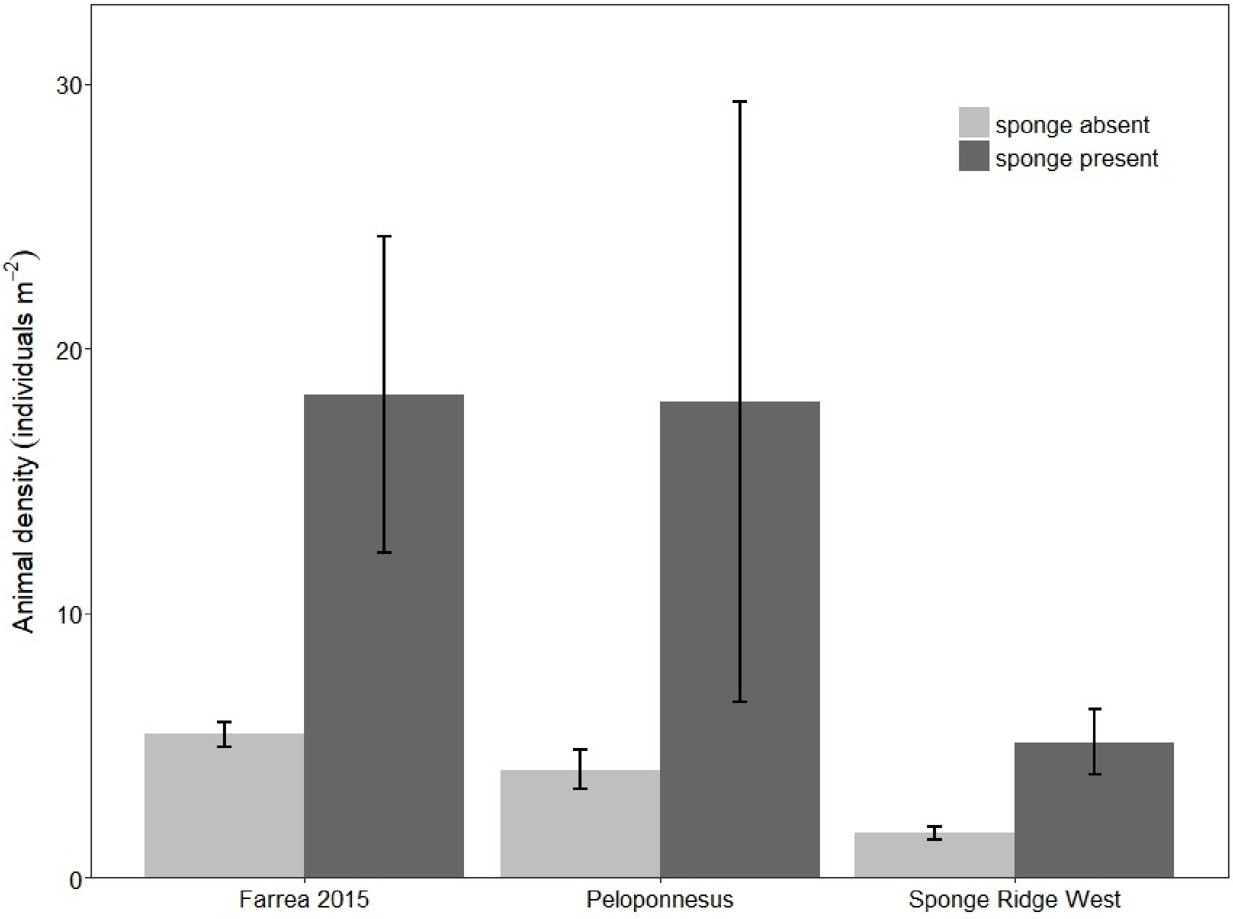
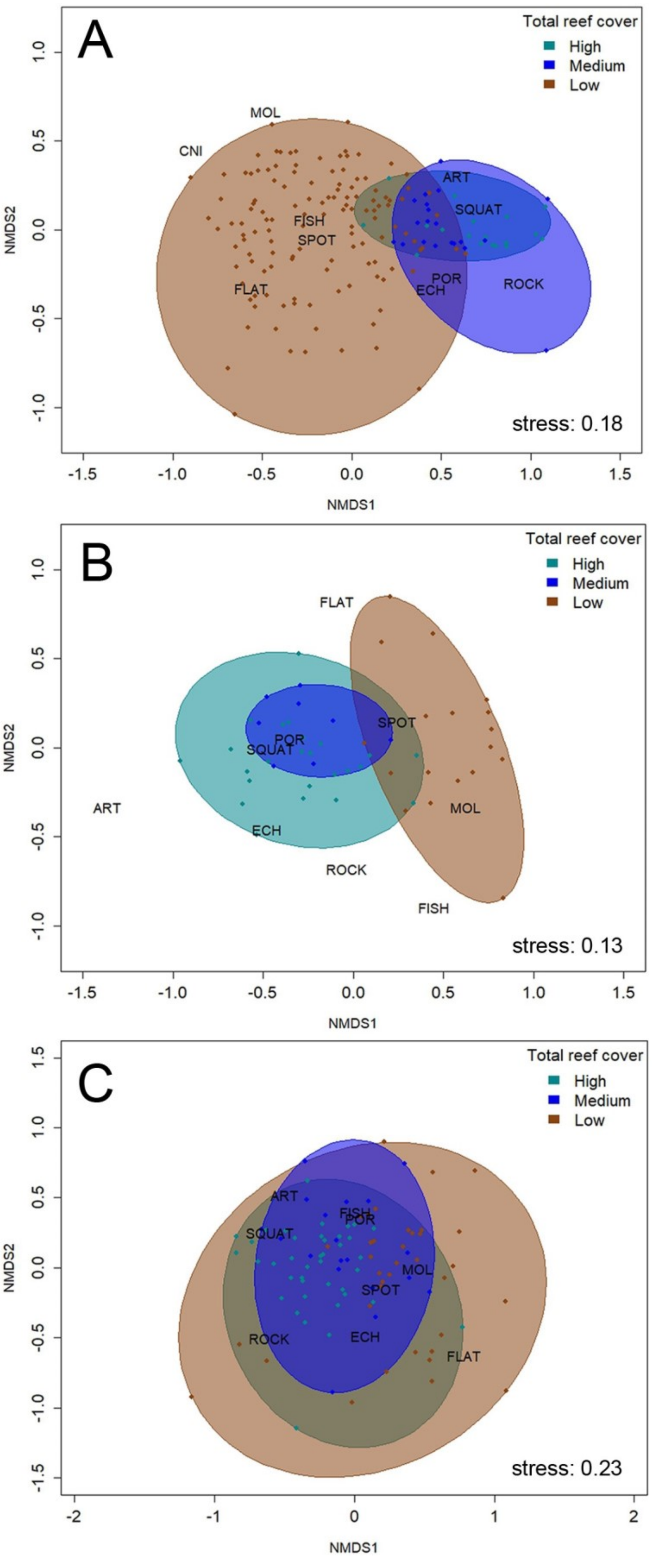


Figure 2-10. Comparison of total megafauna density at each field site in the absence and presence of live and dead glass sponges. Error bars are ± SE. All comparisons between sponge presence and sponge absence were significantly different (Mann-Whitney U-test, $p < 0.0001$ in all cases).

Figure 2-11. Non-metric multidimensional scaling plots. Ordination of species community composition in areas with high (turquoise), medium (blue), and low (brown) amounts of live and dead sponges (total reef). Similarities (Bray-Curtis) are shown for field sites (A) *Farrea 2015*, (B) *Peloponnesus*, and (C) *Sponge Ridge West*. Animals counts were grouped by phylum or by species common name. ART: Arthropoda; CNI: Cnidaria, ECH: Echinodermata; MOL: Mollusca; POR: Porifera; SPOT: Spot prawns, *Pandalus platyceros*; SQUAT: Squat lobster, *Munida quadrasipina*; FLAT: Flatfishes, Family Pleuronectidae; ROCK: Rockfish, *Sebastes* spp.; and FISH: All other fish except rockfish and flatfish. *Note Cnidaria were not observed at *Peloponnesus* and *Sponge Ridge West*.


A
Total reef cover
High
Medium
Low
MOL
CNI
ART
SQUAT
FISH
SPOT
FLAT
POR
ECH
ROCK
stress: 0.18
NMDS1
NMDS2
B
Total reef cover
High
Medium
Low
FLAT
SPOT
POR
SQUAT
ART
MOL
ECH
ROCK
FISH
stress: 0.13
NMDS1
NMDS2
C
Total reef cover
High
Medium
Low
ART
FISH
POR
SQUAT
MOL
SPOT
ROCK
ECH
FLAT
stress: 0.23
NMDS1
NMDS2

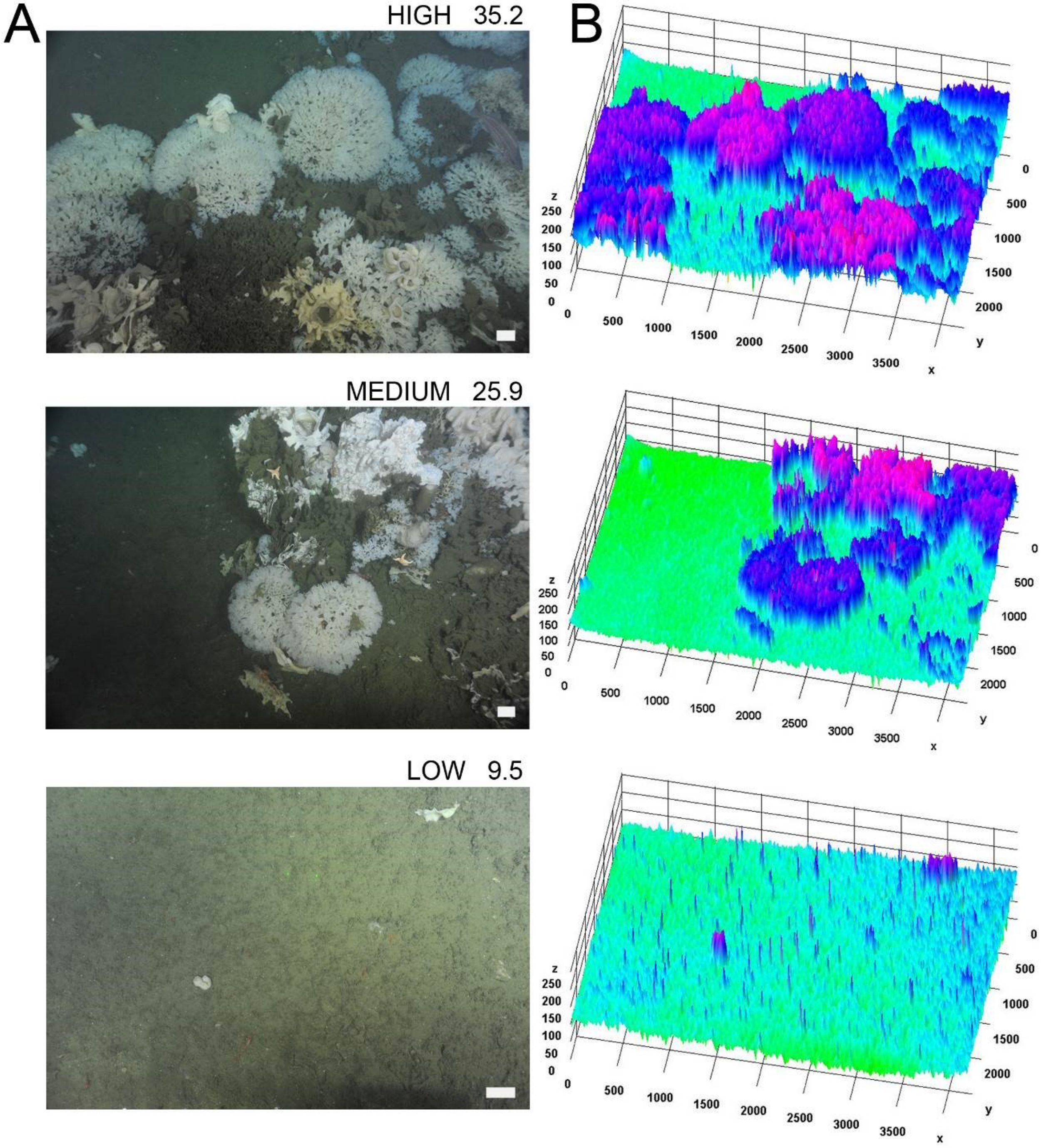


Figure 2-12. Demonstration of how optical intensity (spectra) of ROV images is measured in ImageJ v. 1.3.3.67. (A) ROV images showing examples of high, medium, and low live and dead sponge cover. The numbers at the top indicate the standard deviation (SD) of optical variance in the image. (B) Corresponding 3D histogram surface plots showing the spectral variation in the images.

Figure 2-13. Biotic parameters as a function of normalized optical intensity measures. Positive relationships were found between (A) live sponge cover and (B) abundance of animals with optical intensity values. A negative relationship was observed in the absence of sponge cover (C) and optical intensity values. All regressions are significant ($p < 0.001$).

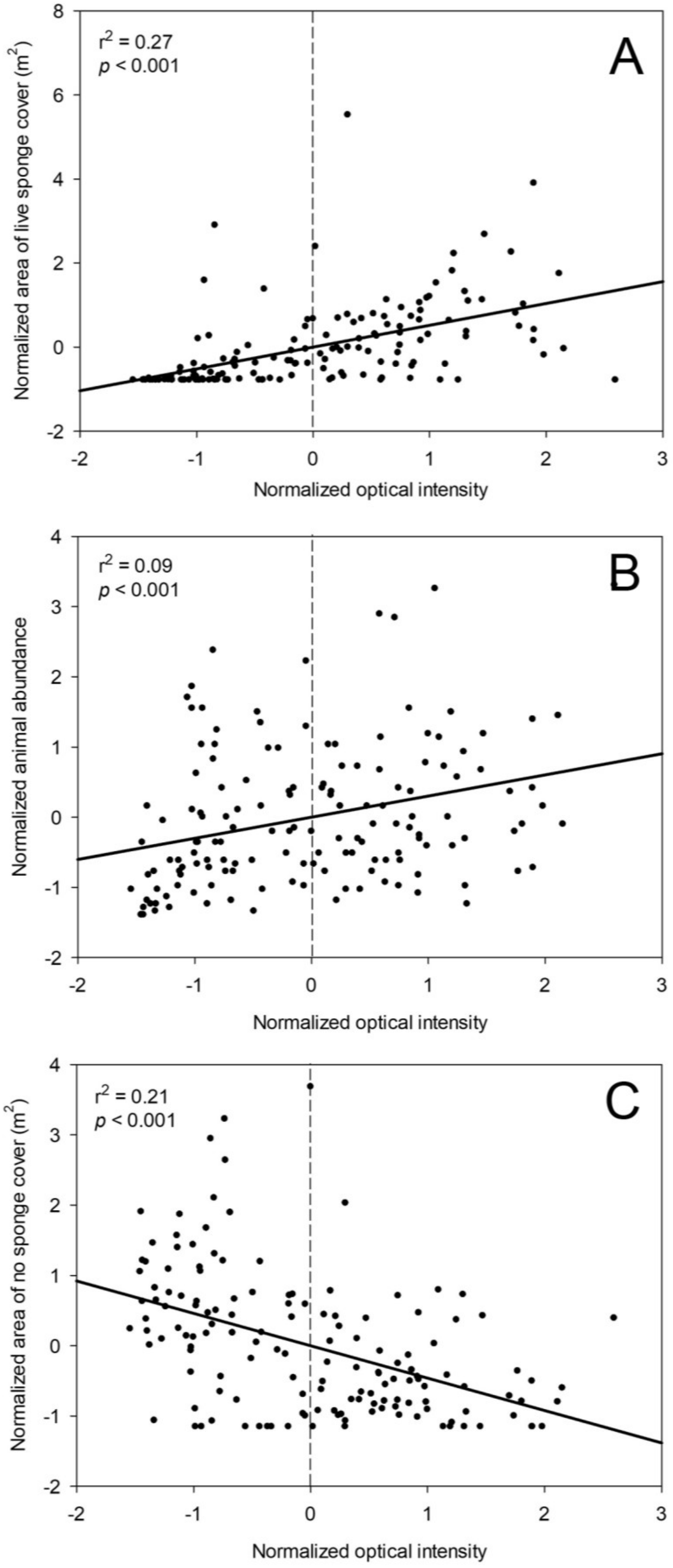
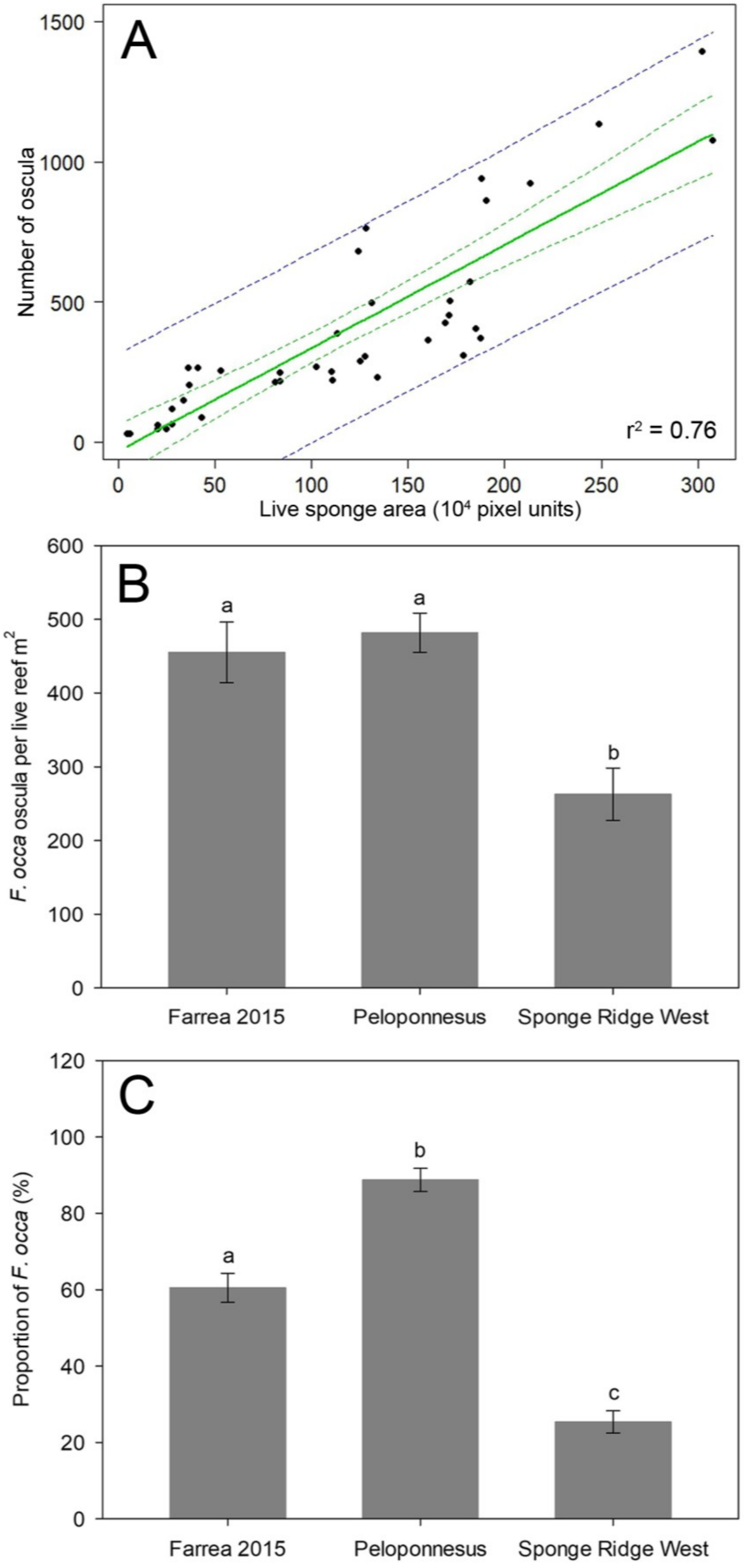

A
$r^2 = 0.27$
$p < 0.001$
Normalized area of live sponge cover (m^2)
8
6
4
2
0
-2
-2
-1
0
1
2
3
Normalized optical intensity
B
$r^2 = 0.09$
$p < 0.001$
Normalized animal abundance
4
3
2
1
0
-1
-2
-2
-1
0
1
2
3
Normalized optical intensity
C
$r^2 = 0.21$
$p < 0.001$
Normalized area of no sponge cover (m^2)
4
3
2
1
0
-1
-2
-2
-1
0
1
2
3
Normalized optical intensity

Figure 2-14. Linear regression model used to estimate the density of *F. occa* oscula and the comparisons of abundance and *F. occa* oscula densities between field sites. (A) Simple linear regression showing a strong positive relationship between *F. occa* oscula counts and areas of live sponge (in pixel units) ($p < 0.001$). (B) The proportion of live cover that is comprised of *F. occa* represented as a percentage. (C) *F. occa* oscula densities estimated from the linear regression model and standardized for a continuous area of live sponges (m^2). Error bars are ± SE. Different letters above columns indicates statistical significant difference from others (Kruskall-Wallis, $p < 0.001$ in all cases).


A
Number of oscula
1500
1000
500
0
r² = 0.76
0
50
100
150
200
250
300
Live sponge area (10⁴ pixel units)
B
F. occa oscula per live reef m²
600
500
400
300
200
100
0
a
a
b
Farrea 2015
Peloponnesus
Sponge Ridge West
C
Proportion of F. occa (%)
120
100
80
60
40
20
0
a
b
c
Farrea 2015
Peloponnesus
Sponge Ridge West

Chapter 3

Sponge-sponge associations and the discovery of a new cryptic species of *Desmacella* Schmidt, 1870 (Porifera, Order Desmacellida) in the Hecate Strait glass sponge reefs

3.1 Introduction

Sponges of the class Hexactinellida form unusual reef systems that cover hundreds of kilometers of seafloor on the western Canadian continental shelf (Conway et al. 1991, Conway 1999, Conway et al. 2005). Like large trees in a rainforest, the sponges in the reef generate three-dimensional habitats known to increase local micro- and megafauna abundance (Chu and Leys 2010, Du Preez and Tunnicliffe 2011). Sponge structures, which form tubes and stalks, add heterogeneous microhabitats that provide increased niches for a diversity of marine life (Buhl-Mortensen et al. 2010, Beazley et al. 2013). Spot prawns (*Pandalus platyceros*), squat lobsters (*Mundia quadraspina*), Pacific halibut (*Hippoglossus stenolepsis*), and multiple rockfish species (*Sebastes* spp.) are among the most ubiquitous motile megafauna found in glass sponge reefs (Cook et al. 2008, Chu and Leys 2010); however, until now, sponge-sponge associations in glass sponge habitats have been largely overlooked.

Populations of glass sponges exist in shallow-waters (<500 m) around the world in oceans in Antarctica, fjords in New Zealand, and submarine caves in the Mediterranean, but the Canadian north Pacific hosts the most extensive accumulations of glass sponges known on Earth (Barthel and Gutt 1992, Vacelet et al. 1994, Vacelet and Boury-Esnault 1996, Hogg et al. 2010). In the late 1980s the Geological Survey of Canada (GSC) discovered four massive reef complexes at 150-250 m depth north of Vancouver Island in the Hecate Strait and Queen Charlotte Sound (QCS) (Conway et al. 1991, Conway 1999). Further surveying of Pacific coast waters led to the discovery of several smaller reef complexes in the Strait of Georgia (SoG) at 90-200 m depth (Conway et al. 1991, Conway 1999, Conway et al. 2005). These reefs are modern analogues of extinct glass sponge reefs that were once prevalent during the Jurassic in the Tethys Sea, a region that now forms much of Europe (Leinfelder et al. 1994, Krautter et al. 2001).

Three glass sponge species *Aphrocallistes vastus, Heterochone calyx,* and *Farrea occa* make up the reef structure in the Hecate Strait and QCS (Krautter et al. 2001, Conway et al. 2005). These species differ from other glass sponges in having a fused skeleton of silica spicules termed dictyonine, whereas lyssacine glass sponges have a loose skeletal framework (Leys et al. 2007). The fused skeleton of dictyonine sponges remains relatively intact after the death of the sponge and provides the mainframe for the construction of the reefs as clay-rich sediments bury them with time (Conway et al. 1991, Conway et al. 2005, Kahn et al. 2016). The reef framework develops as dictyonine sponge (e.g. *A. vastus*, *H.calyx*, and *F.occa*) larvae settle on previous generations of dead sponges cemented together by sediment (Conway et al. 2005, Krautter et al. 2006). Reefs may eventually rise to heights of 21 m above the seafloor and provide vertical structure for a variety of motile and sessile organisms that use the reefs as refuge from predation and nursery grounds for juvenile and larval recruitment (Conway 1999, Conway et al. 2005, Cook et al. 2008, Du Preez and Tunnicliffe 2011).

Sponges from the class Demospongiae and lyssacine sponges are among the most conspicuous sessile megafauna living on the Pacific coast reefs (Lehnert et al. 2005, Cook et al. 2008). One of the more evident sponge-sponge associations observed in the reefs is the colonization of dead glass sponge skeleton by non-reef forming lyssacine species, such as *Rhabdocalyptus dawsoni* and *Staurocalyptus dowlingi* (Leys et al. 2007). Non-reef forming sponges have also been documented to grow directly on live reef-forming dictyonine species (Lehnert et al. 2005), but it remains unclear whether this association is mutually beneficial for both participating sponges or that this overgrowth is indicative of competitive dominance for growing space. Few published studies have documented the occurrence and abundance of non-reef forming sponges in the Pacific coast reefs (Cook et al. 2008, Chu and Leys 2010), yet their presence in glass sponge habitats has important implications for sponge reef development and ecology.

Today, the species *Desmacella austini* Lehnert, Conway, Barrie, & Krautter, 2005 is one of the few non-reef forming sponges that has been examined in some detail. *D. austini* is an abundant demosponge that grows directly on main reef-forming dictyonine species. The first samples of *D. austini* were collected in the SoG reefs and this species was described as an encrusting sponge with two colour morphotypes – yellow and blue (Lehnert et al. 2005). The yellow form was predominantly found covering live *H. calyx*, while the blue form was often observed growing on dead *H. calyx* (Lehnert et al. 2005). The yellow and blue morphotypes of *D. austini* are currently the only confirmed colours for the genus *Desmacella* Schmidt, 1870 in the SoG reefs, however a third white coloured morphotype of a possible *Desmacella* sp. has been speculated to exist. During the 2015 scientific research cruise in the Hecate Strait northern reef complex, video footage was captured by remote operated vehicle (ROV), which revealed the presence of an encrusting sponge with three colour morphotypes (yellow, white, and blue) growing on live and dead *H. calyx* and *A. vastus*. These colour morphotypes are postulated to be *Desmacella* spp., but whether these colour forms represent different species has remained in question until now.

Damage to reef areas heavily fished by bottom trawlers has been documented by sidescan sonar and video surveys (Conway 1999). In recognition of their susceptibility to mechanical damage, Fisheries and Oceans Canada designated the Hecate Strait and QCS reefs a marine protected area (MPA) in February 2017 (Fisheries and Oceans Canada 2017). It has since become of greater concern to better understand the relationships between sessile epibenthic fauna and glass sponges for ensuring these reefs are appropriately protected. The aim of this study was to document and describe non-reef forming sponge associates in the reef and to determine if multiple species of *Desmacella* occur in the northern reef of the Hecate Strait, British Columbia. Results of this work provide baseline empirical data about the abundance of non-reef forming sponges and also documents the distribution of *Desmacella* spp. in the reefs.

3.2 Materials and Methods

3.2.1 Study Location

The Hecate Strait and QCS reefs spread across over 700 km^2 of seafloor (Conway et al. 2005) and are comprised of four separate reef complexes located off the west coast of Banks Island to the northern tip of Vancouver Island (Figure 3-1 A). Reefs in the Hecate Strait and QCS are separated into the northern, central, and southern reefs based on their geographic location along the west coast of British Columbia, Canada. The most heavily trawled regions in the Hecate Strait and QCS are documented near the central and southern reefs (Jamieson and Chew 2002). Given the extent of trawling activity, the northern reef complex was specifically chosen for ROV surveying and sponge sampling.

3.2.2 ROV survey and image analysis

Field work was carried out in October 2015 and May 2017 aboard the Canadian Coast Guard Ship (CCGS) *John P. Tully* at three field sites called here *Farrea 2015* (53°11′34.3″N, 130°28′22.2″W, mean depth 170 m), *Peloponnesus* (53°8′57.4″N, 130°25′36.4″W, mean depth 191 m), and *Sponge Ridge West* (53°11′6.20.3″N, 130°29′36.1″W, mean depth 178 m) (Figure 3-1 B). Field sites were mapped extensively using the Canadian ROV ROPOS (ropos.com) along a grid of stratified georeferenced points separated 25 m apart. Non-overlapping photos were captured one to two meters above the seafloor from birds-eye view with a 12.4 megapixel digital still camera (DSC, Nikon D7000) mounted on a pan and tilt function on ROPOS. Lasers 10 cm apart on the camera provided a scale in the images.

The number of non-reef forming sponges (excluding *Desmacella* spp.) living in the reefs were counted in all 2015 and 2017 ROV images. The type of substrate (e.g. live, dead, or buried portions of sponges) that each sponge was growing on was recorded. Sponge identifications were not feasible from ROV images alone without the collection of specimens, therefore where reliable species identification could not be made, the unknown sponge was designated a number and referred to as ‘unidentified sponge’ coded as UI. In some cases, an unknown sponge was given a descriptive name based on distinct visual characteristics it possessed when observed in ROV images. Lyssacine sponges in the reefs often share morphological similarities that cannot be distinguished in ROV images. Given extensive sampling could not be performed to differentiate between lyssacine species, they were referred to simply as ‘lyssacine sponges’ in image analysis. Data on non-reef forming sponges were assessed for normality using a Shapiro-Wilk’s test, which indicated data were non-normally distributed. To determine how dictyonine reef structure influences non-reef forming sponge growth, the density of non-reef forming sponges was calculated from the total photo area for each survey grid point and compared among live and dead dictyonine sponge and no sponge cover using a Kruskal-Wallis test (STATISTICA 13.3).

To determine the amount of *Desmacella* spp. cover in the reefs, areas of the yellow, white, and blue colour morphotypes were delineated in ROV images using an image analysis tool in Adobe Photoshop CS5. These areas were first measured in pixel units in ImageJ v. 1.3.3.67 and then converted into area per meter-square using the 10 cm laser dots for scale.

Percent cover of total live and dead reef-forming dictyonine sponges and bare substrate (i.e. buried sponge or patches of mud) were also measured from each image. These data were used to determine the relative abundance of *Desmacella* spp. on live and dead sponge cover. Spatial distributions of *Desmacella* spp. were mapped and analyzed using ArcGIS v. 10.0 (ESRI, Redlands, CA, USA), and compared to the distribution of live and dead dictyonine sponge cover interpolated by kriging (see Chapter 2). A Spearman Rank correlation was performed to determine how live and dead dictyonine sponge growth influences the percent cover of *Desmacella* spp. in the reefs (STATISTICA 13.3).

3.2.3 Spicule preparations

Specimens (yellow, $n = 6$; white, $n = 6$; blue, $n = 5$) of *Desmacella* spp. and other non-reef forming sponges ($n = 8$) were collected opportunistically during ROV dives at each field site. Samples were either suction-sampled into a suction jar or grab-sampled and placed into a collection box with a sealed lid using ROPOS. Samples were stored in 95% ethanol on board the ship and transported to the University of Alberta for processing. Portions of samples were dissolved in bleach overnight, rinsed four times with distilled water and twice with 95% ethanol to isolate spicules. Spicule suspensions were pipetted onto glass slides and dried before mounting in DPX with a coverslip. Spicules were imaged using a Zeiss Axioskop2 compound microscope with a QIcam camera using Northern Eclipse. Spicule dimensions were measured using ImageJ and dimensions were compared with data for other species of *Desmacella* catalogued in the *World Porifera Database* (www.marinespecies.org).

3.2.4 Scanning electron microscopy preparations

Sponge spicules were studied using scanning electron microscopy (SEM). Pieces of sponge tissue 1 x 0.5 cm were dissolved in bleach overnight to isolate spicules. Spicules were rinsed four times in distilled water and twice with 95% ethanol. Circular coverslips were mounted onto aluminum SEM stubs using double-sided adhesive tabs. Ethanol-spicule suspensions were dropped onto the coverslips and left to dry for 3-5 hours. The stubs were sputter coated with gold using the Nanotek SEMprep 2 sputter coater and imaged using a Zeiss Sigma 300 VP-FESEM. SEM images were processed in Corel PaintShop Pro X3 to adjust brightness and contrast using the histogram adjustment tool, and the sharpness was adjusted using the high pass sharpen tool.

3.2.5 DNA sequencing and phylogenetic analysis

Sponge tissue approximately 1 cm^2 in size was cut from all *Desmacella* spp. samples (*n* = 17) and processed using the DNeasy Blood and Tissue Kit (Qiagen, Germany) according to the manufacturer instructions. DNA concentrations (ng/µL) were evaluated using a Nanodrop 1000 spectrophotometer before PCR amplification. Extracted DNA samples were sent to the Molecular Biology Service Unit (MBSU) at the University of Alberta for PCR amplification. PCR amplification of the standard barcoding region, located at the 5' end of the mitochondrial cytochrome C oxidase subunit I gene, was performed by S. Dang (MBSU) using degenerate primers dgLCO1490: 5'- GGT CAA CAA ATC ATA AAG AYA TYG G - 3', and dgHCO2198: 5'- TAA ACT TCA GGG TGA CCA AAR AAY CA - 3' modified from Meyer et al., (2005). Primer dgLCO1490 was 5' tailed with M13F sequence 5'- GTA AAA CGA CGG CCA GTG-3' and dgHCO2198 was 5' tailed with M13R sequence 5'-GGA AAC AGC TAT GAC CAT G-3'. PCR amplifications were performed in an Eppendorf Mastercycler EP in 50 µL reactions containing 1X PCR buffer, 2.5 mM $MgCl_2$, 0.2 mM of each dNTP, 0.5 µM of each primer, 0.3 U of Invitrogen Platinum Taq polymerase and 4 µL of template genomic DNA. A standard three-step PCR program was used with an initial denaturation at 95°C for 2 minutes followed by 40 cycles of 95°C for 30 seconds, 50°C for 30 seconds and 72°C for 1 minute, and the reaction was completed with a final extension for 10 minutes at 72°C. The resulting PCR products were visualized via 1% agarose gel electrophoresis and a ≈750 bp band was excised. DNA was recovered from the agarose band using the Qiagen Qiaquick gel extraction column following the manufacturer protocol. Sequencing was completed with 7 µL of purified PCR product using the BigDye 3.1 kit (Applied Biosystems) and sequencing reactions were analyzed on an ABI 3730DNA Analyzer. DNA sequences were examined, manually edited for errors by C. Davis (MBSU), and aligned using the SeqMan Pro application of the lasergene suite (DNA star). Phylogenetic trees were constructed in MEGA7.0 using the maximum likelihood method based on the Jukes-Cantor model. Statistical support of the branches was generated with 500 bootstrap pseudoreplicates.

3.3 Results

3.3.1 Non-reef forming sponge composition

Overall there were 9 different unidentified (UI) non-reef forming sponges observed in the reefs (Figure 3-2). The abundance of non-reef forming sponges was standardized to individuals per-meter square of the total area surveyed at each field site (Table 3-1). Of the 9 UI sponges, 4 were present at *Peloponnesus*, 5 at *Sponge Ridge West*, and all 9 were present at *Farrea 2015.* Lyssacine sponges were dominant at sites *Farrea 2015* (0.16 ind/m^2) and *Peloponnesus* (0.25 ind/m^2), accounting for 57% and 93% of the total non-reef forming sponge cover, respectively. The abundance of lyssacine sponges (0.15 ind/m^2) was much lower at *Sponge Ridge West* (30%) compared to the other field sites, with the UI 4 'plate sponge' (0.28 ind/m^2) contributing to 57% of the non-reef forming sponge cover instead. Many unidentified non-reef forming sponges had low abundances in the reefs, however there were a few sponges that were noticeable exceptions. The UI 2 sponge (0.03 ind/m^2) and UI 9 'finger sponge' (0.04 ind/m^2) were found in high abundance at site *Farrea 2015* accounting for 15% and 10% of the non-reef forming sponge growth, respectively. The 'finger sponge' was observed visually in ROV images to grow in close association with live and dead *F.occa*. Total non-reef forming sponge density was highest on the structures of dead dictyonine sponge skeletons with almost no non-reef forming sponges found growing on live dictyonine sponges and bare substrate (Kruskal-Wallis test, $H = 207.48$, $p < 0.001$) (Figure 3-3).

3.3.2 Description of Desmacella *colour morphotypes*

Three colour morphotypes of *Desmacella* spp. were observed as thinly encrusting sponges growing on live and dead dictyonine reef-forming species. Sponges with *Desmacella* growth displayed necrosis and were easily identified by having a 'dirty' appearance and wrinkled and/or broken edges at the lip of the osculum (Figure 3-4 A-C). The yellow morphotype appeared as off-white and was often associated with live and dead *H. calyx*, but examples of this species growing on live and dead *A. vastus* were also observed (Figure 3-4 A). The white morphotype was bone-white in colour, often speckled with mud, and frequently found growing in association with both living and dead *H. calyx* and *A. vastus* (Figure 3-4 C, D). The blue morphotype did not show associations with any dictyonine reef-forming species and was commonly found growing in patches of mud or at the base of dead reef skeleton (Figure 3-4 B).

3.3.3 Desmacella *abundance and spatial distribution*

The yellow morphotype comprised 10.7% of the live sponge cover at site *Farrea 2015* and 7.2% at *Sponge Ridge West*, but presence of this colour form was nearly undetected at *Peloponnesus* (0.3%) (Table 3-2). Coverage of the white morphotype in the reefs was also high at *Farrea 2015* forming 6.4% of the live sponge cover, however this morphotype was found in substantially lower amounts at *Peloponnesus* (2.4%) and *Sponge Ridge West* (2.9%). The proportion of live sponge cover comprised of the blue morphotype made up only a fraction of total *Desmacella* spp. present in the reefs, with less than 1% of this morphotype observed at each field site. The percent cover of all three *Desmacella* spp. morphotypes was greatest in areas where percent live and dead dictyonine sponge cover was high (Figure 3-5 A-C) and cover of these demosponges was strongly correlated with the presence of live and dead dictyonine sponges (Spearman rank correlation, $\rho = 0.702$, $p < 0.0001$).

3.3.4 Spicule and ultrastructure morphology

Spicule types and morphologies for samples of all three colour morphotypes are summarized in Table 3-3. Samples of the yellow morphotype were light grey to off-white in preservative with a hispid surface and non-apparent oscules. Spicules found in the yellow samples matched spicule types described in *D. austini* (Lehnert et al., 2005). Megascleres of long, thin tylostyles were found with one end pointed and an elliptical tyle (a globular swelling) situated at their base. Tylostyles ranged from 166-548 µm long (mean = 312.2 µm, SD = 87.4; n = 180) and 5-10 µm wide (mean = 7.2 µm; SD = 1.0; n = 180) (Figure 3-6 A, B). Tylostyles were smooth at the surface and straight to curved in form. Microscleres of sigmas in three size classes were present and consistent with past descriptions for *D. austini*. The chord length of large sigmas I ranged from 50-80 µm (mean = 60.8 µm; SD = 5.2; n = 180); medium sigmas II, 24-49 µm (mean = 36.6 µm; SD = 6.0; n = 180); and small sigmas III, 13-23 µm (mean = 18.6 µm; SD = 2.3; n = 180) (Figure 3-6 C-E). Microspines were present at the terminal ends for all size classes of sigmas (Figure 3-6 F-H).

Specimens of the white morphotype differed from the yellow morphotypes and contained slight, but distinct differences in spicules that suggest this is a new cryptic *Desmacella* species for the reefs, named here as *Desmacella* sp. nov.. The ectosome consisted of dense tylostyle spicule bundles found in tight clusters with points facing outwards to form bouquets. Tylostyles in white specimens were on average slightly smaller than tylostyles in the yellow morphotype, ranging from 185-478 µm long (mean = 289.6 µm; SD = 66.1; *n* = 180) and 5-10 µm wide (mean = 6.7 µm; SD = 0.9; *n* = 180). Tylostyles were also long and thin, smooth at the surface, with one end pointed and an elliptical tyle at their base (Figure 3-7 A, B). The characteristic that separates samples of the white morphotype from the yellow was the presence of two size classes of sigmas rather than three. The chord length of large sigmas I ranged from 22-58 µm (mean = 30.3 µm; SD = 5.7; *n* = 180) and small sigmas II, 8-20 µm (mean = 16.3 µm; SD = 2.2; *n* = 180) (Figure 3-7 C, D). All size classes of sigmas exhibited terminal ends with microspines (Figure 3-7 E, F).

Samples of the blue morphotype were revealed to be of two separate species. These species were not distinguishable in ROV images simply by shape and colour, but required the analysis of spicule types and morphologies to expose their identities. Two of the five blue samples, named *R1989_0111* and *R1989_0112*, had megascleres of tylostyles with the exact same form as in the white morphotype described above. These tylostyles ranged from 220-528 µm long (mean = 310.5 µm; SD = 76.8; *n* = 60) and 5-10 µm wide (mean = 7.1 µm; SD = 0.9; *n* = 60). There were also two size classes of sigmas observed in these blue samples, with large sigmas I ranging in chord length from 24-40 µm (mean = 30.9 µm; SD = 3.6; *n* = 60) and small sigmas II, 8-20 µm (mean = 17.6 µm; SD = 2.1; *n* = 60). The other three blue samples, named *R1995_0243, R1995_0251,* and *R1995_0255*, contained megascleres of long, thin styles with one end pointed and the other end blunt ranging from 160-578 µm long (mean = 389.3 µm; SD = 56.6; *n* = 90) and 4-9 µm wide (mean = 7.1 µm; SD = 0.8; *n* = 90) (Figure 3-8 A, B). Microscleres of oxeas pointed at both ends were also found and ranged from 88-312 µm long (mean = 169.9 µm; SD = 47.5; *n* = 90) and 3-7 µm wide (mean = 4.9 µm; SD = 0.9; *n* = 90) (Figure 3-8 C, D). Spicule types dominated by styles and oxeas are rare in the genus *Desmacella* and suggests these three blue specimens are of a separate genus.

3.3.5 DNA sequencing

DNA sequences were successfully obtained for all the yellow and white morphotypes, while only three samples of the blue morphotype were effectively sequenced. Almost all colour morphotypes were confidently distinguished from each other using COI sequences and spicule morphometric measurements. Phylogenetic analysis grouped the yellow and white colour morphotypes into two separate groups (Figure 3-9). All samples of the yellow morphotype (*n* = 6) were grouped together with high support (100% bootstrap) and did not mix with any white or blue specimens. Molecular analyses were paired with spicule measurements and the identity of the yellow morphotype matched closely to *D. austini* as described by Lehnert et al. (2005). Phylogenetic analysis also grouped all samples of the white morphotype (*n* = 6) together with high support (100% bootstrap). Spicule measurements were paired with COI sequences for the white samples, which strongly suggest this to be *Desmacella* sp. nov. in the reefs. However, one blue morphotype (*n* = 1) with the sample name *R1989_0111* was grouped within the white samples, and contained spicule types and morphology that agreed with *Desmacella* sp. nov., but not with *D. austini*. The other two samples of the blue morphotype (*n* = 2), named *R1995_0243* and *R1995_0255*, grouped together with high support (100% bootstrap) in a separate genus from the yellow and white morphotypes. These blue samples contained spicules of styles and oxeas that are typically not found in *Desmacella* specimens.

3.4 Discussion

Glass sponges are ecosystem engineers (Jones et al. 1994), forming three-dimensional habitat for numerous motile and sessile megafauna (Cook et al. 2008, Chu and Leys 2010). Among sessile marine animals, sponges are unique in that they host a variety of associations (Wulff 2006, Leys et al. 2007). In the Pacific coast reefs, most studies have examined the association between glass sponge structures and motile organisms such as fish and crustaceans (Cook 2005, Cook et al. 2008, Chu and Leys 2010, Du Preez and Tunnicliffe 2011); however, the relationship between reef-forming glass sponges and other sponge associates has often been overlooked. This work highlights the importance of glass sponge habitat for non-reef forming sponges and reveals for the first time the existence of cryptic sponge diversity in the Canadian north Pacific glass sponge reefs.

3.4.1 Reef as important substrate for sponge associates

One of the more intriguing associations of glass sponges are those that occur with other sponge species. Numerous non-reef forming sponges were found in close association with dead dictyonine sponge cover, but not with live dictyonine sponges and areas with no sponge. Past studies have shown the spicule remains of dead hexactinellid sponges can host higher levels of sponge-sponge associations than surrounding environments (Barthel and Gutt 1992). In the Weddell Sea, Antarctica, large mats comprised mainly of hexactinellid spicules contained much higher diversities of sponge associates than on neighbouring muddy substrate (Barthel and Gutt 1992). This clear positive relationship between non-reef forming sponge associates and dead hexactinellid sponges was also observed in the Hecate Strait northern reef.

Sponge associates are likely to recruit on dead dictyonine sponges than on mud substrate given niche spaces are elevated by the three-dimensional multistoried structures created by dead sponge skeletons (Kahn et al. 2016). The siliceous skeletal framework left behind by dead dictyonine sponges serves an ecological role comparable to that of nursery logs in an old growth forest. Nurse logs in temperate forest ecosystems are especially important for the recruitment of seedlings, which in turn initiates forest regeneration and succession (Sanchez et al. 2009). Likewise, this study shows dead dictyonine sponge skeleton provides significant recruitment sites for pioneering sponge associates. Although there are no studies that have examined community succession in glass sponge reefs, there are examples where coral reef systems, undergoing stress by global warming and ocean acidification, have shifted to sponge-dominated communities (Bell et al. 2013). It is plausible higher densities of non-reef forming sponge associates observed in glass sponge reefs are symptomatic of a successional transition brought on by disturbance regimes, but such interpretations should be made with caution since no studies have assessed sponge succession in glass sponge habitats.

At first glance, dead glass sponge may seem less functionally important than living sponge in a reef. However, the spicule remains of dead dictyonine sponges also provides good attachment points for juvenile dictyonine sponge recruits. Density of juvenile sponges in the SoG reefs have been observed to be higher near adult sponges and dead dictyonine skeletons than in patches of mud (Kahn et al. 2016). The presence of many small sponges on dead skeleton may indicate reproductive success and recruitment, which in turn can be translated as a healthy functioning reef ecosystem (Kahn et al. 2016). The number of colonized non-reef forming sponges on dead sponge skeleton may be interpreted in a similar manner, and perhaps can serve as a management tool for monitoring reef health in the Hecate Strait and QCS sponge reefs (Wulff 2001, Bell 2007). Our results suggest dead reef-forming sponge skeleton is as equally important as live dictyonine sponges for providing biogenic structures for non-reef forming sponge recruitment, and should not be overlooked in future conservation planning.

3.4.2 Desmacella *cover and distribution*

Various colour morphotypes of *Desmacella* spp. were observed encrusting on live and dead *H. calyx* and *A. vastus*. Where *Desmacella* sp. growth was present, symptoms of necrosis were observed in the reef-forming dictyonine sponges with a noticeable interface and distinct colour change between the sponge types. It has been proposed *D. austini* competes for and/or limits the availability of growing space for the main-reef forming dictyonine species (Lehnert et al. 2005). Since dictyonine sponge larvae require hard substrata for settlement (Kahn et al. 2016), and considering that dead and live sponges are the most accessible hard substratum within a sponge reef, this competition could severely limit reef growth and recruitment. Particularly in perturbed ecosystems, successful space-occupiers with a disproportionate capacity for rapid colonization and high growth rates can out-compete other benthic organisms (González-Rivero et al. 2011). Many reef areas in the Hecate Strait and QCB have been damaged due to bottom trawling (Conway 1999, Jamieson and Chew 2002, Cook et al. 2008) and where *Desmacella* spp. growth is prevalent, the ability of juvenile dictyonine sponges to re-colonize damaged reef areas may be hindered.

Space as a limiting resource is common among sessile benthic organisms, however collaboration among sponge species for substratum is known to exist. A large body of evidence has been gathered indicating sponges may receive considerable benefits from the colonization of predator deterring encrusting sponges (Pawlik et al. 1995, Wilcox et al. 2002, Wulff 2008). Numerous predators consume sponges including seastars (Dayton et al. 1974), nudibranchs (Chu and Leys 2012), and a variety of fish (L. Law pers. obs.). In the Florida Keys seagrass meadows, Wilcox et al. (2002) studied the overgrowth of *Geodia* (0.075-0.91 individuals per m^2) by a sponge in the genus *Haliclona*, which is a genus thought to be chemically defended with toxic metabolites. Wulff (2008) also documented collaborative sponge associations in Belize, where seastar predation on *Lissodendoryx colombiensis* was significantly reduced for individuals overgrown with unpalatable seagrass sponges. The propensity for reef-forming dictyonine sponges to engage in similar beneficial interactions with *Desmacella* spp. is unknown, and whether a species of *Desmacella* has chemical deterring compounds is a compelling topic for future assessment.

Overgrowth and many other forms of intimate sponge-sponge associations have been reported from around the world (Rützler 1970, Wilcox et al. 2002). One seemingly facultative and symbiotic sponge association was described in the Adriatic Sea and Florida Keys (Rützler 1970, Wilcox et al. 2002), where several sponges were shown to cope elegantly with being fully overgrown in a relationship referred to as epizoism. Growth of *Desmacella* spp. on the exterior of live and dead dictyonine sponges is a type of sponge epizoism observed in the Pacific coast sponge reefs. The most fascinating feature of such sponge-sponge symbioses is the ability of the internal sponge to maintain its feeding despite being fully covered by an external sponge. Most sponges feed by pumping large volumes of water through their body wall and any impediment to water flow would presumably impact sponge health negatively (Reiswig 1971, Leys et al. 2007). However, in the Florida Keys, microscopic sections of the interface between two adhering sponges in an epizoic relationship revealed the presence of a small interstitial space, which might permit high enough rates of water flow for the internal sponge to continue feeding (Wilcox et al. 2002). It is still unclear whether growth of *Desmacella* spp. in the reefs is a symbiotic or parasitic association, but further ultrastructure examinations between reef-forming dictyonine sponges and *Desmacella* spp. may unveil a unique adaptation for overgrowth. Future studies should also evaluate what exactly is being derived from the association between *Desmacella* spp. and reef-forming dictyonine sponges and if trauma to the covered sponge is incurred.

3.4.3 Cryptic species diversity

For the first time in this study, morphological observations (sponge external colour and spicule types) were combined with molecular-data to give strong support for cryptic speciation in the genus *Desmacella*. Molecular data corresponded with spicule measurements to suggest *D. austini* and *Desmacella* sp. nov. were the yellow and white morphotypes in the reefs, respectively. Tylostyles in both species resembled each other in size and form, and did not serve as a diagnostic tool for separating the species. The only characteristic different between the species was that three size classes of sigmas (sigmas I, sigmas II, and sigmas III) occurred in *D.*

austini, whereas *Desmacella* sp. nov. only contained two (sigmas I and sigmas II). All size classes of sigmas in both species had microspined ends, however these microspines were overlooked in past descriptions for *D. austini* (Lehnert et al. 2005). When comparing *Desmacella* sp. nov. to other known species of the genus (Table 3-4), there are several species of *Desmacella* also with two size categories of sigmas. These species are generally found in shallow (<150 m) waters in the tropics, and thus conspecifity is unlikely from a biogeographical standpoint. The only other deep-water *Desmacella* sp. comprised of two sigma size categories is *Desmacella vicina* Schmidt, 1870, but in comparison to *Desmacella* sp. nov., this species is found in substantially deeper waters (472 m) with tylostyles much longer and wider (600 x 12 μm).

One sample of the blue morphotype had spicules and DNA sequences that agreed more closely to *Desmacella* sp. nov. than with *D. austini*. This sample may have been biologically contaminated by the white encrusting sponge growing with it that was unnoticed during sampling. All other blue samples contained spicules of styles and oxeas and were grouped apart in phylogenetic analysis from *Desmacella* sp. nov. and *D. austini* into a genus currently unidentified. BLAST searches in GenBank returned sequences that grouped these blue samples most closely with sponges in the family Suberitidae, however gene similarities were low at 94%. The blue morphotype may be a successional species growing on *Desmacella* sp., however the only evidence of succession described by Lehnert et al. (2005) was by the species *Topsentia disparilis* (Lambe 1893). It is unlikely blue samples are representative of *T. disparilis* given this species is only comprised of oxeas, whereas blue samples in this study contained oxeas and styles.

Various theories have been generated to explain why cryptic species are observed in an ecosystem. One theory suggests cryptic speciation is an evolutionary adaptation for species occurring in severe environmental extremes, such as deep-sea environments (Bickford et al. 2007). ‘Extremophiles’ are expected to converge in physical characteristics given there are limited number of ways an organism can adapt to harsh conditions. Although glass sponge reefs occur in deeper waters, they are not considered ‘extreme’ habitats; however, reefs are limited to specific environmental conditions including low sedimentation rates, high silica concentrations, low light levels, and water temperatures ranging between 9 to 10°C (Leys et al. 2004). These conditions may limit variations in morphology for *Desmacella* spp., and perhaps growth of

Desmacella spp. with high specificity to dictyonine sponges also limits morphological changes among the genus.

3.4.4 Implications for conservation

Efforts to conserve glass sponge reefs off the coast of Canada should take our findings into account that non-reef forming sponges and cryptic diversity is greater than previously known. There are several reasons that underscore the importance of recognizing non-reef forming sponge and cryptic diversity in glass sponge reefs, but one of the more important reasons is for conservation management. The effective protection and monitoring of biologically important species for sponge reef conservation hinges on the ability to identify species, particularly when cryptic organisms exist. Loss of habitat in both terrestrial and marine settings is one of the greatest threats to global biodiversity, and deciding on what habitats should be prioritized for conservation often requires an understanding of species richness and endemism. This study gives first insights on the distribution pattern of non-reef forming and cryptic sponges in the Pacific coast reefs, which might warrant certain sponge areas for greater conservation concern.

3.5 Conclusions

Glass sponge reefs are an important source of biogenic structure in deep water habitats for supporting a wide range of motile and sessile benthic megafauna. In particular, dead dictyonine sponge structures provide hard substrata for the recruitment of numerous non-reef forming sponges. Among the sessile benthic fauna living on the reefs are encrusting sponges in the genus *Desmacella*. Three colour morphotypes of *Desmacella* spp. (yellow, white, and blue) were observed in the reefs and were identified to be different species. Taxonomic criterion and molecular analysis suggest *D. austini* as the yellow morphotype and *Desmacella* sp. nov. as the white morphotype; however, the identity of the blue morphotype remains unknown. Growth and distribution of *Desmacella* spp. in the reefs was more prevalent that previously recognized in past studies. The diversity of non-reef forming sponge associates hosted by dictyonine sponges has also been overlooked in past scientific explorations of the Canadian Pacific glass sponge reefs. Therefore, special attention should be given to *Desmacella* spp. and non-reef forming sponges in future conservation planning for sponge reef MPAs in Canada.

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Table 3-1. Densities of non-reef forming sponges. Values standardized to individuals per meter-square based on the total area surveyed at each field site: *Farrea 2015*, *Peloponnesus*, and *Sponge Ridge West*. The percentage of each non-reef forming sponge out of the total area surveyed is shown in parentheses.

Unidentified Sponge No.	**Density individual/m^2**		
	Farrea 2015	**Peloponnesus**	**Sponge Ridge West**
Lyssacine sponges	1.6 x 10^{-1} (57%)	2.5 x 10^{-1} (93%)	1.5 x 10^{-1} (30%)
UI 1	1.5 x 10^{-3} (<1%)	2.8 x 10^{-3} (1%)	---
UI 2	2.8 x 10^{-2} (10%)	5.7 x 10^{-3} (2%)	1.9 x 10^{-2} (4%)
UI 3	2.5 x 10^{-2} (9%)	2.8 x 10^{-3} (1%)	3.0 x 10^{-2} (6%)
UI 4	8.5 x 10^{-3} (3%)	---	2.8 x 10^{-1} (57%)
UI 5	7.7 x 10^{-4} (<0.5%)	---	1.2 x 10^{-2} (2%)
UI 6	2.3 x 10^{-3} (<1%)	---	2.7 x 10^{-3} (1%)
UI 7	7.7 x 10^{-4} (<0.5%)	---	---
UI 8	1.2 x 10^{-2} (4%)	---	---
UI 9	4.4 x 10^{-2} (15%)	5.7 x 10^{-3} (2%)	---

Table 3-2. Estimates of cover for *Desmacella* sp. colour morphotypes in the Hecate Strait northern reef complex. Percentages in parentheses represent the proportion of area at each site covered by white, yellow, and blue morphotypes relative to the total live cover of dictyonine reef-forming sponges. Dictyonine sponges include the species *Heterochone calyx*, *Aphrocallistes vastus*, and *Farrea occa*.

Reef	**Live sponge cover (m^2)**	**Area of *Desmacella* (m^2)**			**Total proportion of *Desmacella* (%)**
		White	**Yellow**	**Blue**	
Farrea 2015	89.2	5.7 (6.4%)	9.5 (10.7%)	0.5 (0.6%)	17.7
Peloponnesus	29.5	0.7 (2.4%)	0.1 (0.3%)	3.0×10^{-3} (0.01%)	2.7
Sponge Ridge West	90.5	2.6 (2.9%)	6.5 (7.2%)	0.1 (0.1%)	10.2

Table 3-3 Data comparing the spicules types and sizes between samples of *Desmacella* spp. colour morphotypes. Values are in micrometres (µm), expressed as follows: min-max or min-***mean***-max. All values for sigma types represent chord lengths.

Colour	**Tylostyles I**		**Other spicules**		**Sigmas I**	**Sigmas II**	**Sigmas III**
	Length	**Width**	**Length**	**Width**			
D. austini[1]	170-495	6-10	none	none	55-65	26-42	15-20
Yellow (*n* = 6)	166-***312.2***-548	5-***7.2***-10	none	none	50-***60.8***-80	24-***36.6***-49	13-***18.6***-23
White (*n* = 6)	185-***289.6***-478	5-***6.7***-10	none	none	22-***30.3***-58	8-***16.3***-20	none
Blue type 1 (*n* = 2)	220-***310.5***-528	5-***7.1***-10	none	none	24-***30.9***-40	8-***17.6***-20	none
Blue type 2 (*n* = 3)	none	none	styles: 160-***389.3***-578; oxeas: 88-***169.9***-312	4-***7.1***-9; 3-***4.9***-7	none	none	none

(1) Lehnert et al. (2005)

Table 3-4 Data comparing the spicule morphology and geographical distribution for all living species of *Desmacella* Schmidt, 1870. Values are in micrometres (µm), expressed as follows: minimum-maximum or minimum-***mean***-maximum; length/width. Sources are footnoted after the table from where data was retrieved.

Species	**Region Found / Depth (m)**	**Tylostyles I**	**Tylotyles II**	**Sigmas I**	**Sigmas II**	**Sigmas III**	**Other spicules**
Desmacella **sp. nov.**	Northeastern Pacific Ocean / 150-250	185-**289.6**-478 / 5-**6.7**-10	none	22-***30.2***-58	8-***16.3***-20	none	none
D. alba (Wilson, 1904)[1]	Galapagos, Kerguelen, Philippines / 195-320	216-1275 / 6.5-36	none	18.7-137 x 2-6.4	none	none	rhaphides 20-30, sometimes missing
D. ambigua Berquist and Fromont, 1988[1]	New Zealand / intertidal	390-530 / 10-13	280-360x7.5-10	none	none	none	rhaphides, 113-145; tylostyles, 160-250 / 5-9
D. annexa Schmidt, 1870[1,2]	Florida / 350-357	present, size not given	none	14-over 100	none	none	thin oxeas, size not given
D. annexa sensu (Van Soest & Stentoft, 1988)[2]	Barbados / 100	280-700 / 2.5-8	none	28-42	11-15	none	53-115 / 0.5-2 (toxiform)
D. annexa (Calvanti et al., 2015)[2]	Brazil / 153	286-**392.5**-521 / 3-**8.1**-14	none	19-**29.8**-38	9-**11.6**-14	none	54-**76.7**-90 (toxiform)
D. arenifibrosa Hentschel, 1911[1]	Australia / 14-18	160-344 / 3-6, styles and subtylostyles	none	none	none	none	rhaphides, 304-342; toxa, 21-26
D. austini Lehnert, Conway, Barrie & Krautter, 2005[1]	Northeastern Pacific Ocean / 160-205	170-495 / 6-10		55-65	26-42	15-20	
D. campechiana (Topsent, 1889) as *Tylodesma*[1]	North Atlantic Ocean (?) / Not recorded	up to 1000 / 8	up to 200x8	55	25	7.5	none
D. corrugata (Bowerbank, 1866)[1,2]	Azores, Celtic Seas, UK, North Atlantic / Not recorded	present, size not given	none	present, size not given	none	none	none

D. democratica (Sollas, 1902)[1]	Malaysia / Not recorded	180-560 / 2.5-6	none	10-80 × 3	none	none	none
D. dendyi DeLaubenfels, 1936[1]	New Zealand / Not recorded	140-630 / 6-12	none	10-44	none	none	none
D. digitata (Lévi, 1960)[1,2]	Senegal / 25-30	180–270 x 1–2	none	22-26	14-18	none	none
D. grimaldii (Topsent, 1890) [1,2]	Azores, UK / 927	390–1900 x 8–30	none	28-45	none	none	none
D. groenlandica Fristedt, 1887[1]	Greenland (east coast) / 238 m	1200	none	min 7.5	none	none	Rhaphides 250-275
D. informis (Stephens, 1916)[1,2]	Ireland, Azores / 457-1024	180–1300 x 8–27	none	26-45	none	none	none
D. infundibuliformis (Vosmaer, 1885)[2]	Arctic, Azores / 228.6	250-500	none	25	none	none	none
D. inornata (Bowerbank, 1866)[1,2]	Aegean Sea, Alboran Sea, Azores, Mediterranean, Shetlands, Norway / 100-270	190–1000 x 6–18	none	20–45	none	none	none
D. ithystela Hooper, 1984 [1]	Australia / 40	135-222 × 4-10	100-164x1-4	12-20 × 0.5-2	29-55 × 2.5-4	96-192 × 5-10	none
D. jania Verrill, 1907[1,2]	Bermudas, Caribbean Sea, Mexico / Not recorded	220–250, styles and tylostyles	none	37–40	none	none	none
D. lampra DeLaubenfels, 1954[1]	Marshall and Palau Islands / 4	250 × 2.5	none	30-33	13	none	none
D. meliorata Wiedenmayer, 1977[1,2]	Bahamas, Caribbean Sea / Not recorded	210–230 x 3.5–4.5	none	37x2 (rare)	none	none	none
D. microsigma (Lévi, 1964)[1]	Philippines / Not recorded	500-1000x15-25	none	11-15x2	none	none	none
D. microsigmata Cavalcanti, Santos, Pinheiro, 2015[2]	Northeastern Brazil / 157	177-**286.3**-425	none	12-**14.6**-19	none	none	none
D. microstrongyla (Hentschel, 1912)[1]	Arufura sea / Not recorded	style, 336-496 × 7-22	none	9-10	none	none	160-240, in trichodragmata; microxeas, 40-60;

							microstrongyles 12.5-14x4-6
D. peachi sensu Ferrer-Hernandez, 1914[1,2]	Spain, South European Atlantic Shelf / Not recorded	present, long and sinuous, size not given	none	none	none	none	present, thin and curved, size not given
D. polysigmata van Soest, 1984[1,2]	Belize, Caribbean Sea / 100	513-**575.4**-635x10-**15.2**-19, styles to strongyles	none	30-**37.3**-42	10-**11.6**-15	none	none
D. pumilio Schmidt, 1870[1,2]	Florida, Caribbean sea, greater Antilles, Gulf of Mexico / 98.7	320-1400 × 9-17	none	30-46	12-27	none	none
D. suberea (Schmidt, 1870) as *Desmacodes*[1]	Atlantic, Portugal / Not recorded	mainly oxeas and styles, tylostyles present, size not given	none	612.8	none	none	none
D. suberitoides (Burton, 1932) as *Sigmotylotella*[1,2]	Tristan da Cunha, South Atlantic / 80-140	1000 x 18 (choanosomal)	600 x 12 (ectosomal)	28	none	none	none
D. topsenti (Burton, 1930)[1,2]	Azores / 927	250–730 x 5–10	none	43	none	none	none
D. toxophora Lévi, 1993[1]	New Caledonia / 540-600	300-600 × 10-12	none	none	none	none	toxa, 90-140
D. tylostrongyla Li, 1986[3]	Hong Kong / Not recorded	199-286 x 4-6 (smooth subtylostyle)	185-210 x 5-7 (subtylostrongyles)	34-42 x 2-3	none	none	none
D. tylovariabilis Cavalcanti, Santos, Pinheiro, 2015[2]	Brazil / 1130	315–**616.0**–1050 x 6–**11.0**–16	none	25–**34.2**–48	none	none	none
D. vagabunda Schmidt, 1870[1,2]	California, Florida / 30-44 m, 179-265	600x15	none	14–over 100	none	none	none
D. vestibularis (Wilson, 1904)[1,2]	Galapagos, Pacific Antarctica, Namibia, Philippines / 16-97	240–630 x 8–16	none	12–36; after (Lévi, 1964) 30-65	none	none	none

D. vicina Schmidt, 1870[1,2]	Florida / 472	600 x 12	none	36	12	none	none

(1) Lehnert et al. (2005); (2) Cavalcanti et al. (2015); (3) Li (1986)

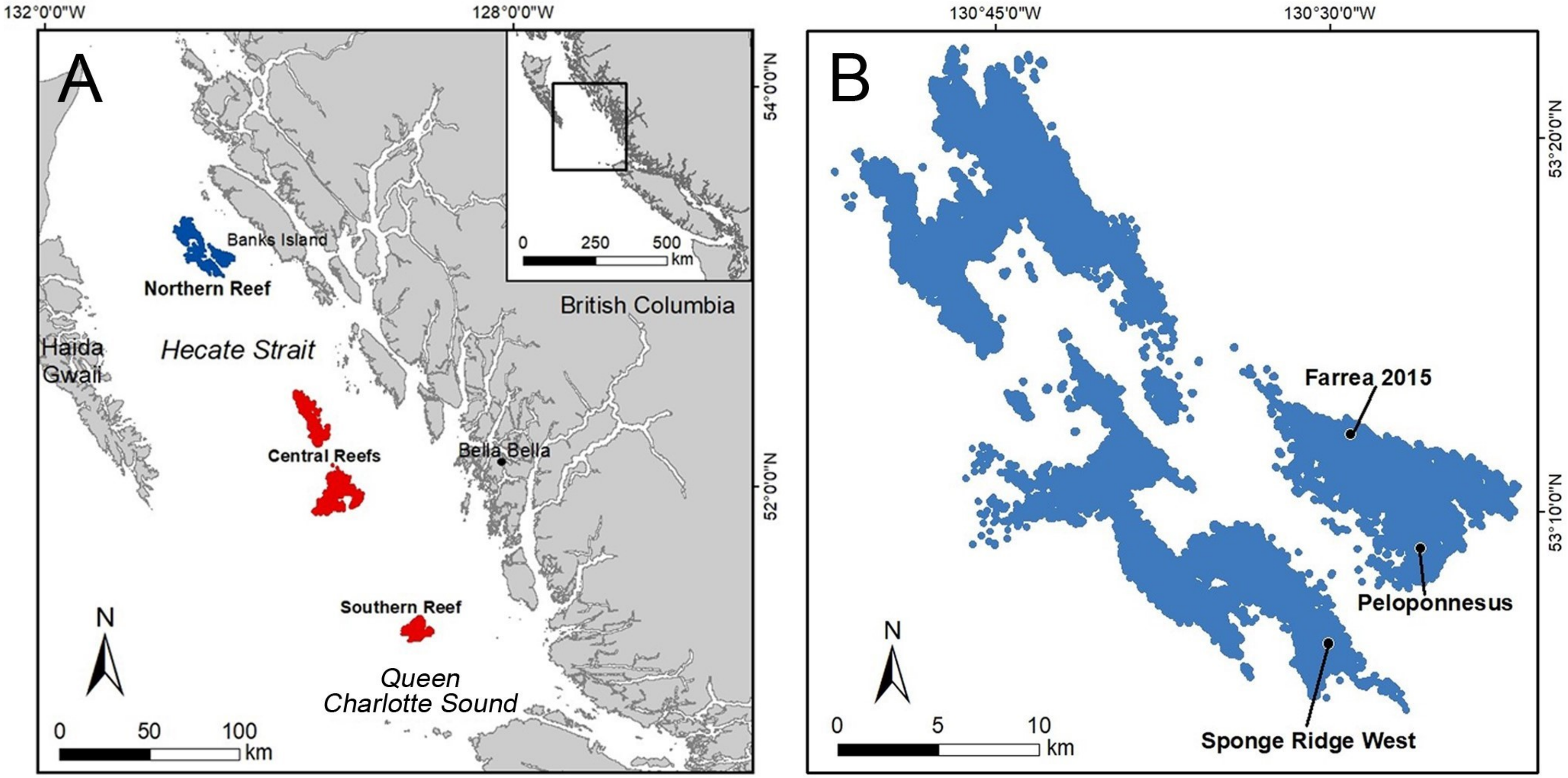


Figure 3-1. Locations of sponge reefs in the Hecate Strait and Queen Charlotte Sound (QCS). (A) The Hecate Strait and QCS reefs are comprised of four massive reef complexes named the northern, central, and southern reefs. All reefs lie on the continental shelf between Haida Gwaii and mainland British Columbia, Canada. Field sampling was conducted in the northern reef (blue). (B) Sampling locations in the northern reef complex at field sites *Farrea 2015*, *Peloponnesus*, and *Sponge Ridge West.* Distribution of sponge areas in the Hecate Strait and QCS are shown in blue and red (courtesy K.W. Conway, NRCan).

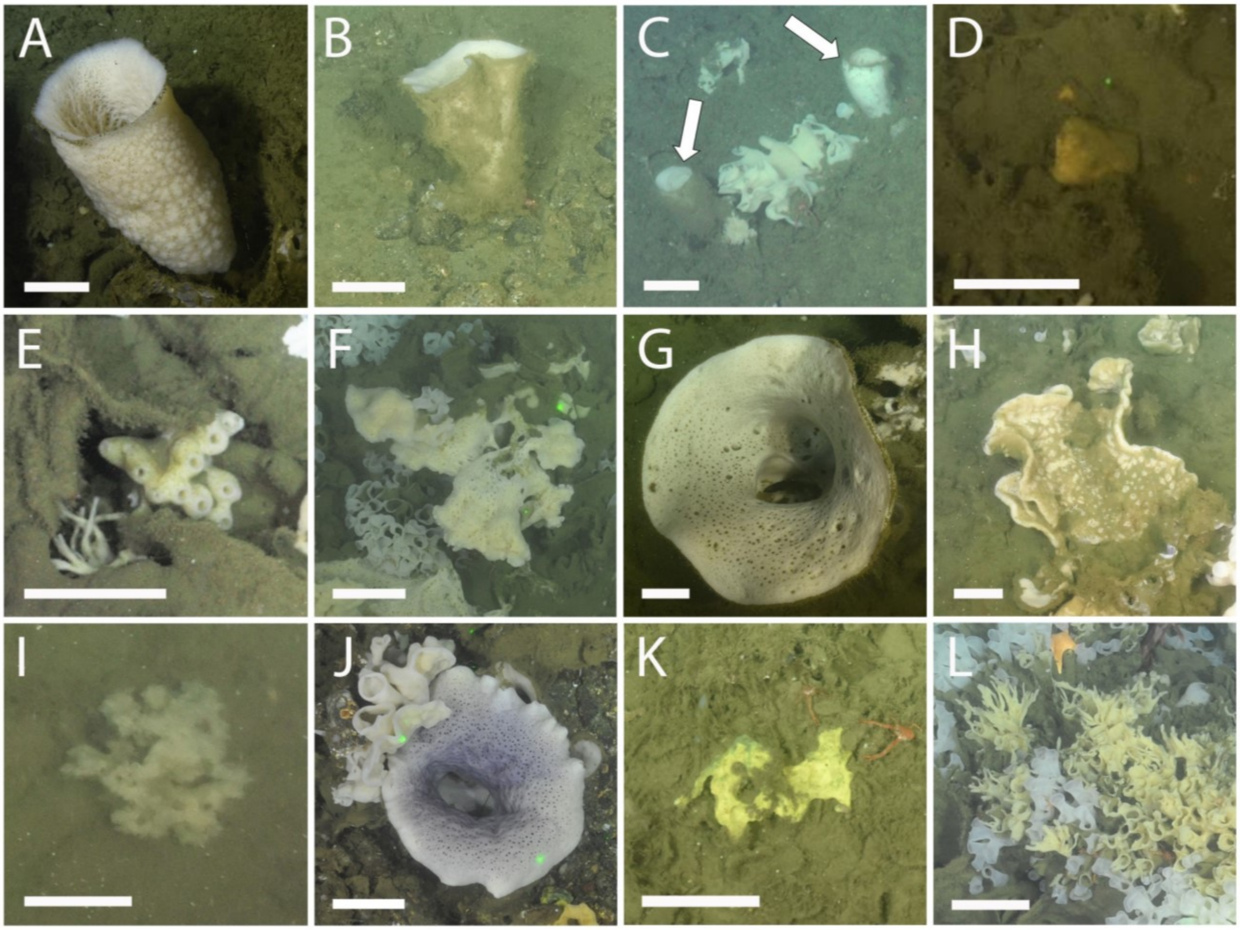


Figure 3-2. Non-reef forming sponge associations in the Hecate Strait northern reef complex. (A-C) Lyssacine sponges identified with samples collected using the remotely operated vehicle ROPOS. Arrows pointing to species *Rhapdocalyptus dawsoni* and *Staurocalyptus dowlingi* that cannot be distinguished from images alone. (D-L) Images of glass sponges that could not be identified from ROV samples and images. These sponges were given a number and referred to as 'unidentified sponge' coded as UI. Some sponges were also given a descriptive name based on their distinctive visual traits. (D) UI 1 'orange sponge' showing bright orange colouration and was often found growing in patches of mud; (E) UI 2; (F) UI 3; (G) UI 4 'plate sponge' showing plate-like morphology; (H) UI 5 'cheese sponge' showing cottage cheese-like appearance; (I) UI 6; (J) UI 7 'trumpet sponge' with vase-shaped morphology and purple colouration; (K) UI 8 'sunshine sponge' showing bright-yellow coloration and often growing in patches of mud; and (L) UI 9 'finger sponge' with finger-like projections that grows in close association with live and dead *F. occa.* Scale bars 10 cm.

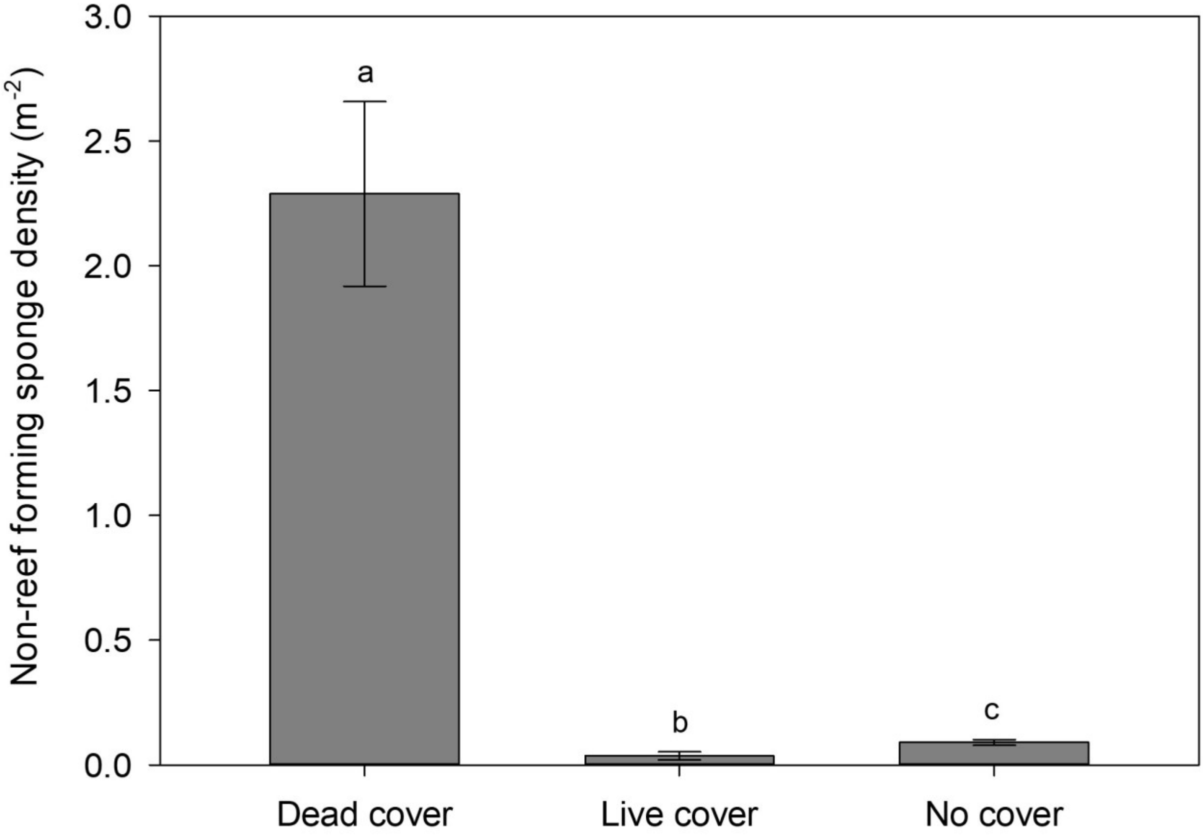


Figure 3-3. Comparison of non-reef forming sponge densities on different cover types. Counts of non-reef forming sponges were made from ROPOS 2015 and 2017 images. Cover types include live and dead reef-forming dictyonine species (*Heterochone calyx*, *Aphrocallistes vastus*, and *Farrea occa*) and no sponge cover (i.e. patches of mud and buried sponge). Error bars are ± SE. Different letters above columns indicate a significant difference form others ($p < 0.001$).

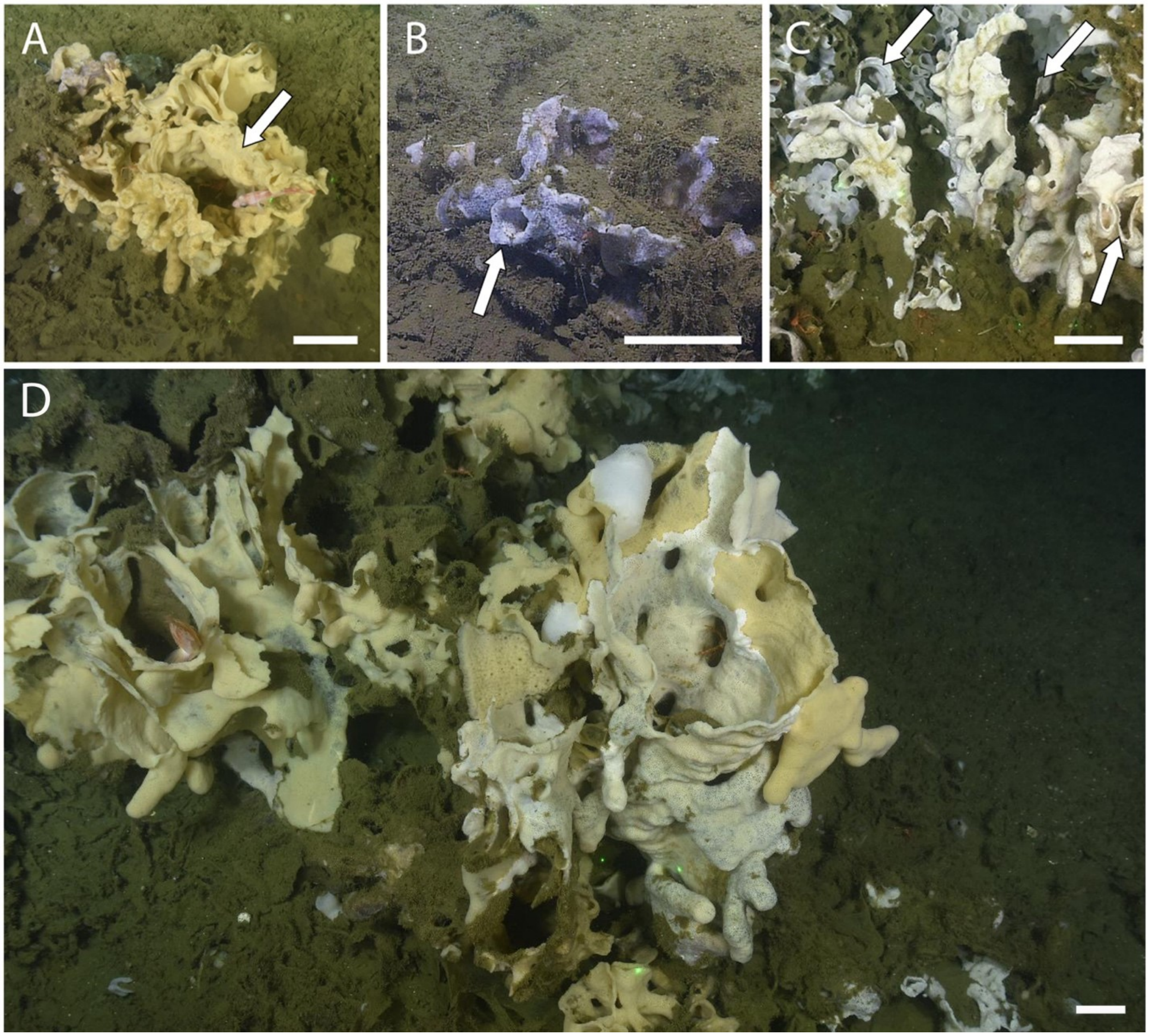
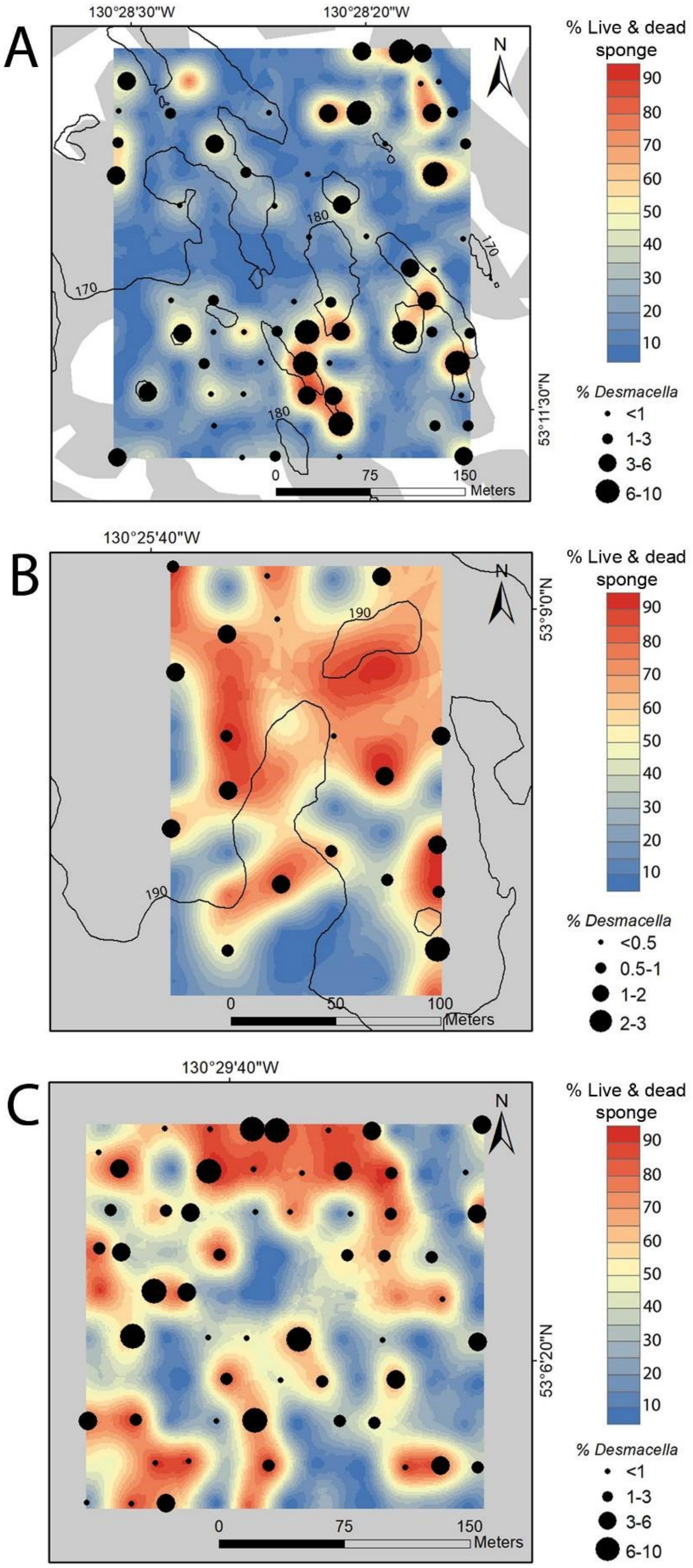


Figure 3-4. Colour morphotypes of *Desmacella* spp. observed on dictyonine reef-forming sponges. (A) Yellow morphotype, (B) blue morphotype, and (C) white morphotype. (D) Image showing the distinct interface between the white morphotype of a *Desmacella* sp. overgrowing live *A. vastus*. All arrows point at the osculum with characteristic 'wrinkling' and/or broken edges at the lip when *Desmacella* spp. growth is overtaking dictyonine sponges. Scale bars 10 cm.

Figure 3-5. Maps showing the percent cover of *Desmacella* spp. (yellow, white, and blue colour morphotypes combined) at each field site. Percent cover of *Desmacella* spp. is strongly correlated with the distribution of live and dead dictyonine reef-forming sponges ($p < 0.0001$) at field sites: (A) *Farrea 2015*, (B) *Peloponnesus*, and (C) *Sponge Ridge West*. Areas predicted to be reef based on multibeam mapping are shown in light-grey (courtesy K.W. Conway, NRCan).


A
130°28'30"W
130°28'20"W
53°11'30"N
N
170
180
170
180
170
0
75
150
Meters
% Live & dead sponge
90
80
70
60
50
40
30
20
10
% Desmacella
<1
1-3
3-6
6-10
B
130°25'40"W
53°9'0"N
N
190
190
0
50
100
Meters
% Live & dead sponge
90
80
70
60
50
40
30
20
10
% Desmacella
<0.5
0.5-1
1-2
2-3
C
130°29'40"W
53°6'20"N
N
0
75
150
Meters
% Live & dead sponge
90
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10
% Desmacella
<1
1-3
3-6
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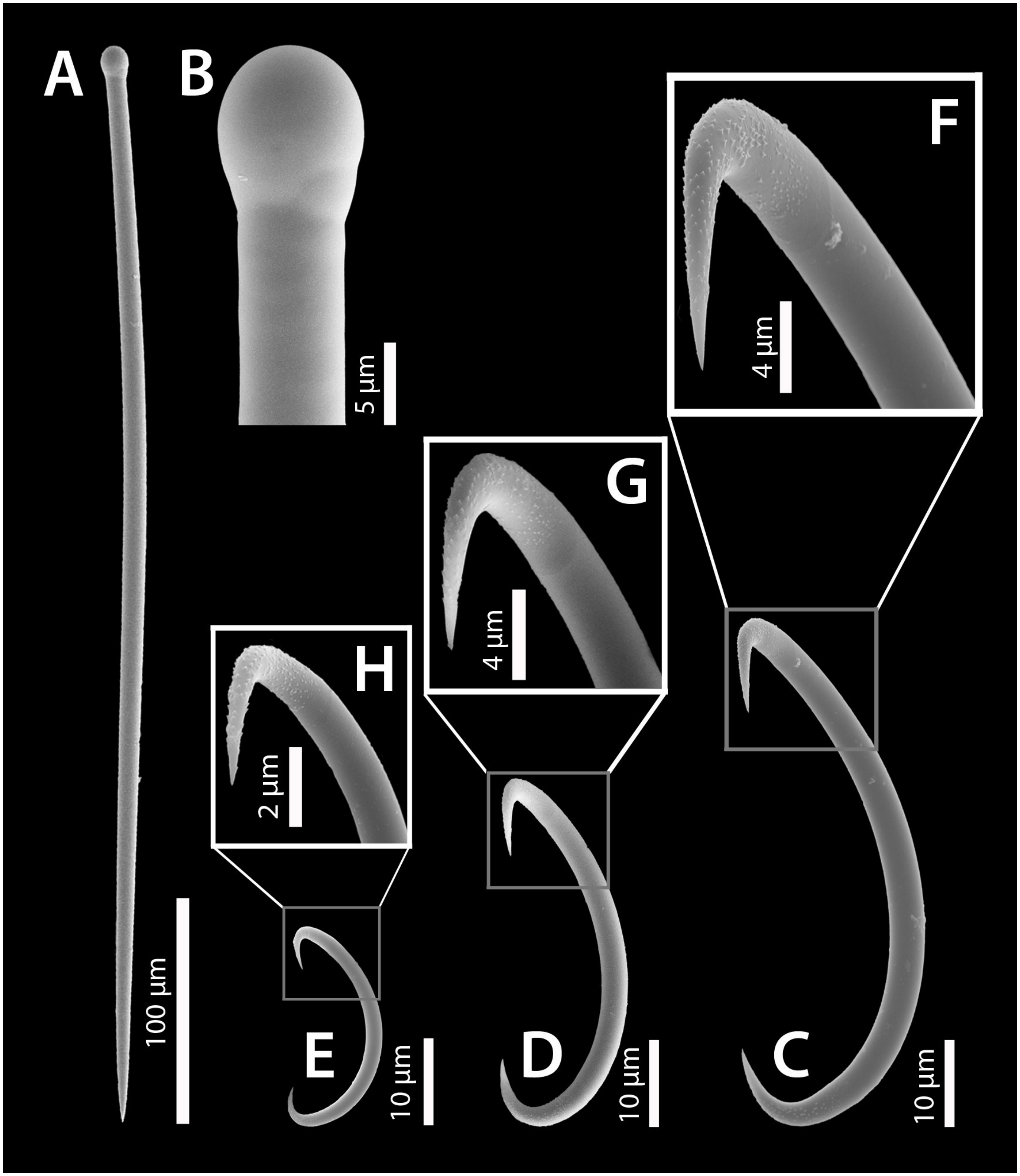

Figure 3-6. SEM images of spicule types in the yellow morphotype. (A) Full length tylostyle; (B) tylostyle base; (C) sigma I; (D) sigma II; (E) sigma III; (F) details of sigma I microspines; (G) details of sigma II microspines; (H) details of sigma III microspines.

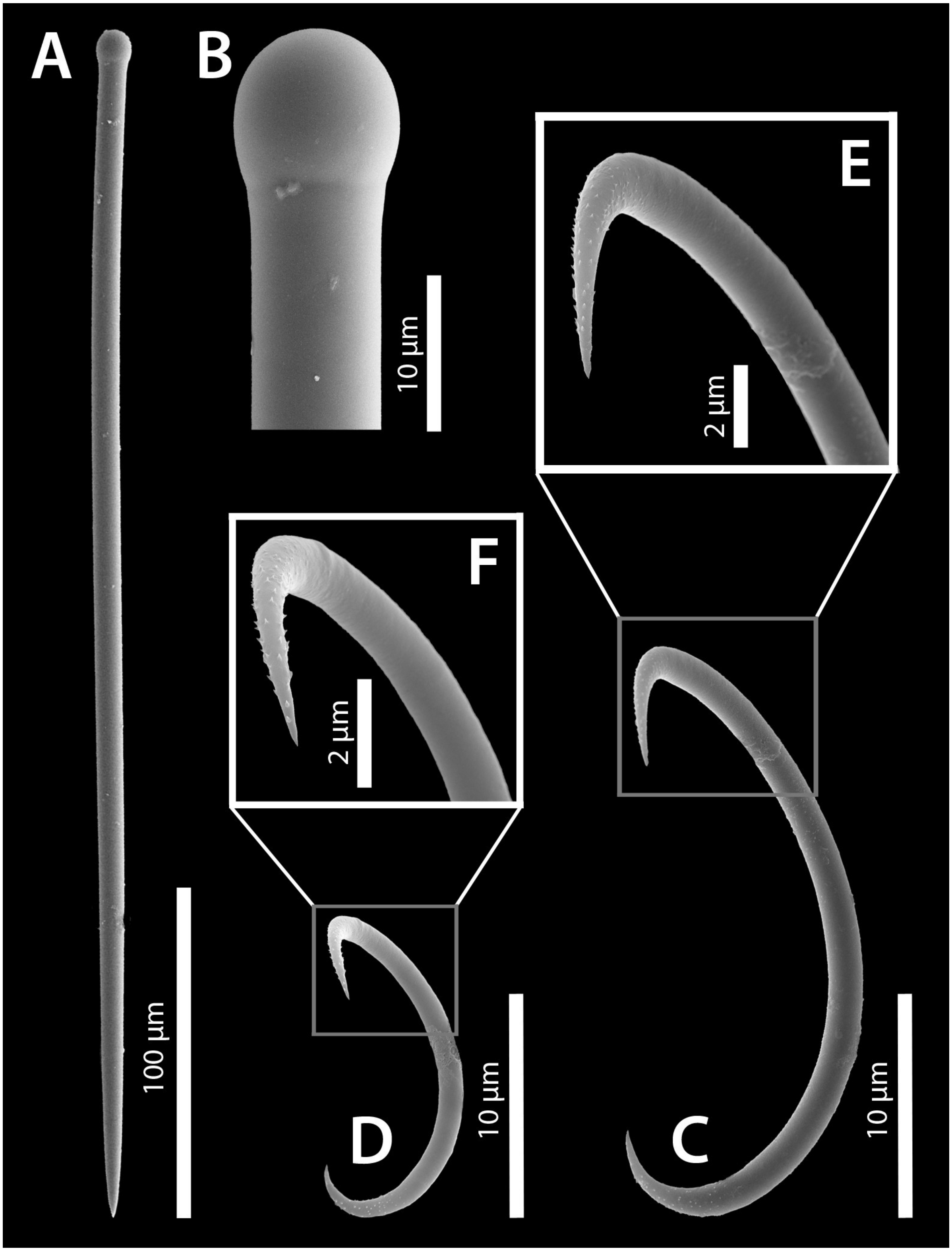

Figure 3-7. SEM images of spicule types in the white morphotype. (A) Full length tylostyle; (B) tylostyle base; (C) sigma I; (D) sigma II; (E) details of sigma I microspines; (F) details of sigma II microspines.

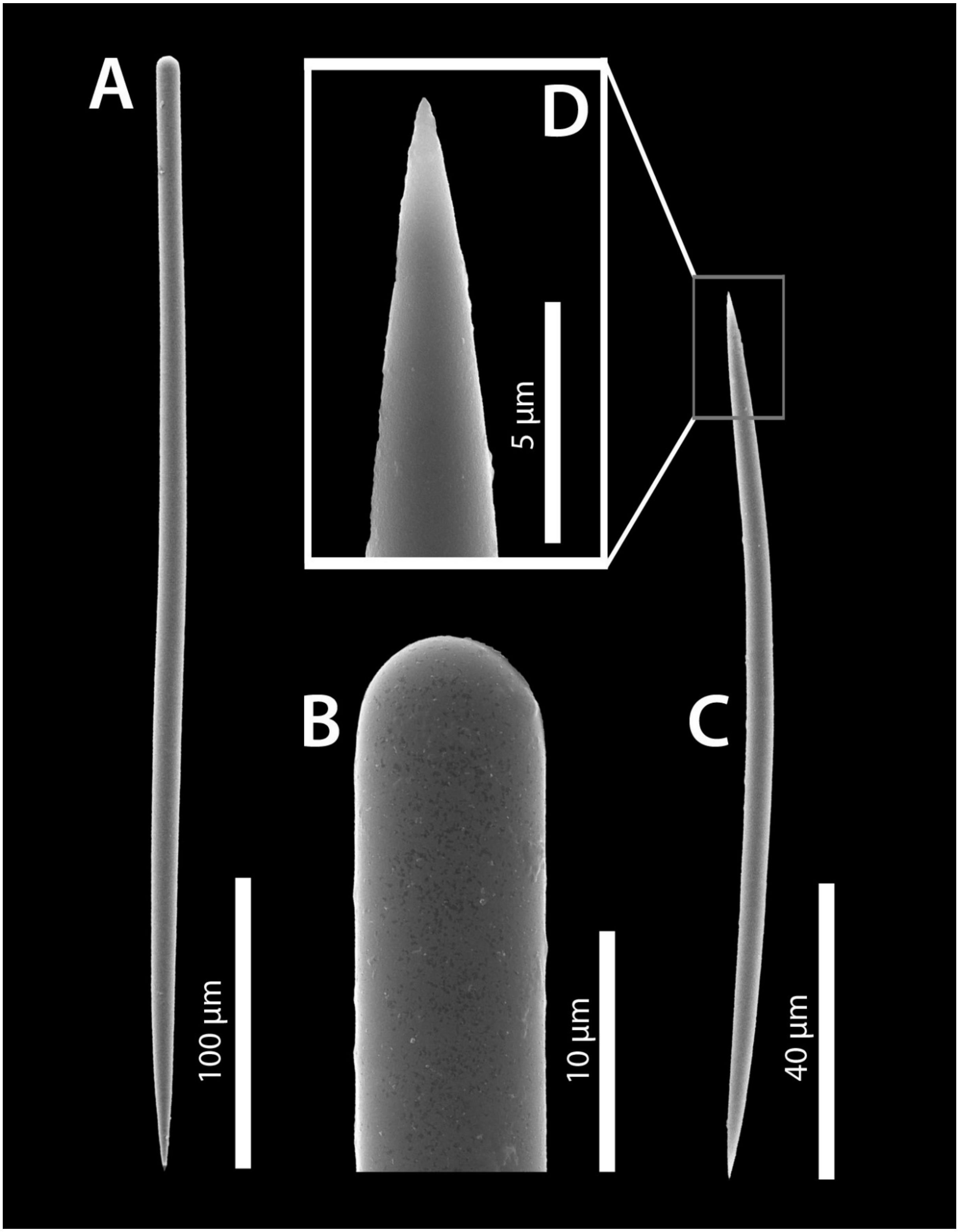

Figure 3-8. SEM images of spicule types in the blue morphotype. (A) Full length style; (B) style base; (C) oxea; (D) details of smooth oxea ends.

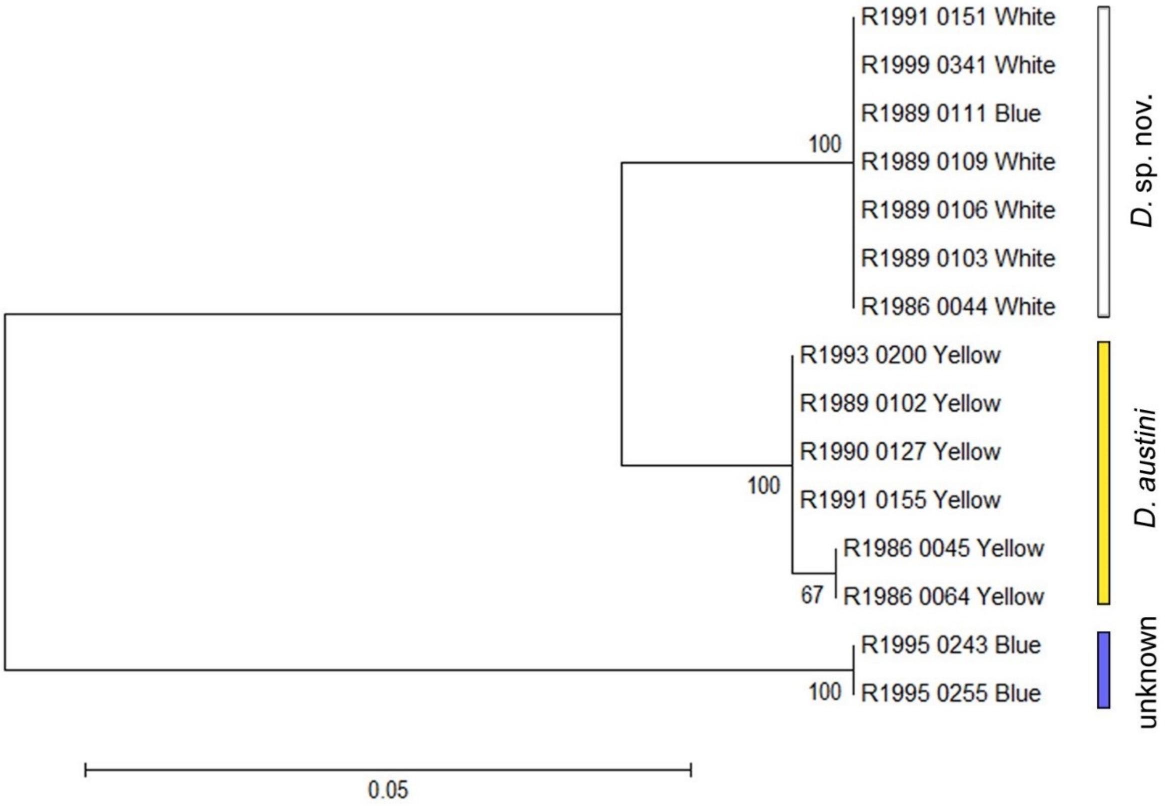

Figure 3-9. Phylogenetic analysis of sponge COI genes. Samples of the white ($n = 6$), yellow ($n = 6$), and blue ($n = 3$) colour morphotypes of *Desmacella* spp. were collected using ROPOS in the Hecate Strait northern reef complex. The maximum likelihood tree was based on the Jukes-Cantor model using MEGA v. 7.0. Values at each node indicate bootstrap support generated from 500 replicates.

Chapter 4

A general discussion

4.1 Overview

The Hecate Strait and QCS and were recently established as a MPA given their global rarity and biological importance (Fisheries and Oceans Canada 2017). MPAs are a widely accepted strategy for protecting marine health and biodiversity, however protected areas only achieve conservation targets if they are managed effectively (Agardy et al. 2003, Chape et al. 2005, Heck et al. 2012). Heck et al. (2012) studied the management of MPAs in British Columbia, Canada and found one of the main challenges in their effective management was an incomplete inventory of the marine communities existing within them. This issue has partly been galvanized under the international IUCN agreement to protect at least 10% of our oceans by 2020. Studies have shown that under this impending deadline there has been a rush by government authorities to implement MPAs, often without a firm scientific understanding about the systems being protected (Agardy et al. 2003). The Hecate Strait and QCS reefs represent an ecosystem that received federal MPA status despite there being scientific uncertainty. However, this decision was employed under the precautionary approach, which stipulates conservation actions shall not be postponed in the face of inadequate science, especially when human and environmental health is at serious risk (Agardy 1994, Santillo et al. 1998). While the establishment of glass sponge reefs as an MPA is a positive step towards reaching Canada's international marine conservation targets, how do we move ahead appropriately with managing and monitoring an MPA we know little about?

Research conducted in this thesis was aimed at expanding our scientific understanding of glass sponge reef ecology to better define these systems in need of protection. Chapter 2 examined the spatial distribution of sponges in relation to past multibeam mapping and topographic features, and in addition showed the importance of reef structure as habitat for numerous motile and sessile megafauna. Chapter 3 brought awareness to several non-reef forming sponge species living on dead dictyonine sponge skeleton, and provided a first description of a cryptic sponge species in the reefs for the genus *Desmacella*. Combining these findings, the most important contribution from this thesis was a baseline biological inventory of glass sponge communities in the Hecate Strait northern reef that can now be monitored and compared to in future studies. Here in Chapter 4, I raise new questions from my findings and describe avenues for future research on glass sponge distribution and community ecology.

4.2 Chapter Two: Reef status assessment

4.2.1 Distribution of reef-building glass sponges

Glass sponge reef complexes were initially mapped into polygons by the Geological survey of Canada using multibeam acoustics (Conway 1999, Conway et al. 2005). In Chapter Two, reef polygons in the Hecate Strait northern reef were resolved at finer spatial scales using ROV imagery to determine the amount of live, dead, and buried portions of sponges within a polygon. A sampling grid of points separated 25 m apart was used in this study to survey sponge areas, revealing sponge populations were patchily distributed in the northern reef. Reef patchiness is an important factor to consider in future routine MPA monitoring surveys, since sampling at large or small spatial scales may include or exclude entire sponge areas in a survey. Surveys of random fixed transects were recommended by the DFO for routine broad-scale monitoring (Dunham et al. In Press), but there is high likelihood some transects will miss certain cover types (e.g. live sponge and dead sponge) if reef patchiness occurs at large distances. Given spatial patchiness differed among sampling sites in the northern reef, variability in reef patchiness likely exists in other reef complexes in the Hecate Strait and QCS. Therefore, before a surveying approach can be determined for routine broad-scale MPA monitoring, I suggest additional ROV mapping is needed in the central and southern reef complexes to compile a more comprehensive understanding of sponge distributions in the Hecate Strait and QCS reefs.

4.2.2 Reef subtypes in the Hecate Strait northern reef

Two reef subtypes were observed within the Hecate Strait northern reef, with sites *Peloponnesus* and *Farrea 2015* dominated by *F. occa*, while site *Sponge Ridge West* was dominated by *H. calyx* and *A. vastus.* Chapter Two showed the area of *F. occa* oscula varied among sampling sites, suggesting hydrodynamic patterns may influence development of reef subtypes. Sponges in the Class Demospongiae exhibit considerable morphological plasticity in shape and oscula development in response to changes in water flow (Bidder 1923, Warburton

1960, Palumbi 1986). Thin and tall sponge morphologies are common in slow flow regimes and wide and short morphologies are often found in turbulent flow regimes (Kaandorp 1999, Bell and Barnes 2000). Chu and Leys (2010) observed a range of morphologies in *A. vastus* and *H. calyx*, and likewise *F. occa* has a growth form distinct from other reef-forming sponges (Law pers. obs.). Future studies may explore the link between flow and form in glass sponges, and if morphological differences are found between reef-forming sponge types, these results could be applied in future studies where growth forms are used to assess the state of the physical environment. For example, changes in sponge form have been used in bio-monitoring to predict disease recovery in coral reef sponges (Wulff 2006) and thus may potentially also be used to detect environmental fluctuations in the Hecate Strait and QCS reefs.

4.2.3 Reef-associated megafauna

Chapter Two revealed taxon-specific relationships in the reefs with potential predatory and mutualistic interactions between sponges and megafauna associates. Food web dynamics remain unclear in the reefs, but Chu (2010) suggested a conceptual food web for the SoG reefs with *P. lentiginosa* as the top carnivore feeding on glass sponges, and primary producers of heterotrophic bacteria and protists consumed by glass sponges. The DFO is currently in the process of understanding these relationships in more depth using stable isotope analysis. Whether food webs in the reefs are influenced by top-down or bottom-up forces is a fundamental research question in need of greater attention for determining how sponge reef ecosystems may respond to the removal of a species, climatic perturbations, and changes in food supply. Top-down controls by nudibranchs and asteroids have been documented in glass sponge populations in Antarctica, yet glass sponges seem to exhibit some resiliency to these predatory attacks (Dayton et al. 1974). I argue the conceptual food web created by Chu (2010) is far too simplistic to only have *P. lentiginosa* as the top predator, particularly when asteroids and fish species have been actively observed consuming glass sponges (Leys and Lauzon 1998, Leys et al. 2007). Moreover, certain sponge associations have likely been mistaken as competitive and parasitic when these relationships are symbiotic and commensal in nature, which has implications for building future food web models.

Chapter Two also highlighted habitat complexity as a fundamental property of sponge reefs that supports megafauna associates. Puig et al. (2012) showed bottom trawling on continental slopes causes seascape leveling that parallels agricultural ploughing on land. Quantification of sponge reef complexity (rugosity) should be of greater concern in coming years for monitoring changes in reef habitat, and rugosity metrics can in part act as a ‘litmus test’ for tracking reef health and abundance. Shumway et al. (2007) used optical intensity as a visual-based method for analyzing habitat complexities in video surveys. I applied the same methodology for the first time to ROV images and showed weak but positive relationships between normalized optical intensity values and live sponge cover and associated megafauna abundance. Accurate measurements of optical intensity and species abundance in ROV images was related to image quality. Murky and blurred ROV images altered spectral intensity values and made identification of associated megafauna sometimes impossible. The detection of certain taxa may also differ between sampling platforms (e.g. ROV still imagery versus video surveys). Many small sessile organisms are often detected more easily in still imagery than video, and future analyses may seek to compare these biases in sampling platforms in the Hecate Strait northern reef. Additionally, motile taxa can move quickly beyond the field of view (Law pers. obs.), resulting in these organisms to be underestimated and/or underrepresented in species counts. Hence, future monitoring programs in the Hecate Strait and QCS reefs should use standardized sampling protocols with compatible image resolutions for collecting comparable megafauna counts across space and time.

4.3 Chapter Three: Hidden biodiversity in the reefs

4.3.1 Non-reef forming sponges: space-competition or collaboration?

Chapter 3 highlighted several indirect and direct interactions between reef-forming dictyonine species and non-reef forming sponges. Non-reef forming sponges were found growing predominantly on dead dictyonine sponge skeleton. Whether these relationships are obligatory or facultative and mutualistic or parasitic remains to be studied, but more often than not published literature suggests competition occurs in the reefs between non-reef forming sponge associates and reef-forming dictyonine species (Lehnert et al. 2005, Chu and Leys 2010, Kahn et al. 2016). Although competition among sessile organisms often underlies many key theories aimed to explain patterns of species abundance in space-limited ecosystems, most community ecologists neglect that many sponge populations worldwide do not always default to competitive interactions (Rützler 1970, Wilcox et al. 2002, Wulff 2008). Given most non-reef forming sponges were found growing on dead sponge skeleton, this indirect interaction is most likely facultative and positive in nature. While epizoic overgrowth of *Desmacella* spp. on reef-forming dictyonine sponges appears obligatory, caution should be taken against readily assuming this as a sign of competitive elimination. If *Desmacella* spp. contain chemically defendant metabolites, its overgrowth on reef-forming hexactinellids may provide the reefs protection from predation. In return, *Desmacella* spp. may grow on reef structures to obtain access to higher water flows for enhancing their feeding and increasing growth rates. These questions clearly require further inquiry, but future exploration of these topics would give great insight into the benefits that can be conferred by both sponge types in direct reef interactions.

4.3.2 New sponge *species in the reefs*

I could not identify non-reef forming sponges to species using ROV images alone, but I began some taxonomic classification for non-reef forming sponges using spicule measurements as an aside to my work. Non-reef forming sponges were collected via ROV and prepared for spicule imaging using a Zeiss Axioskop2 compound microscope with a QIcam camera. Spicule images were examined, revealing many of the non-reef forming sponges were lyssacine sponges, which were comprised of hexactin spicules and a loose siliceous skeletal framework. Among the unidentified non-reef forming sponges, I was surprised to discover the UI 9 ‘finger’ sponge may be another potential *Desmacella* sp. that is currently unidentified for the reefs. Megascleres of tylostyles and microsleres of sigmas were observed in the ‘finger’ sponge, which are spicule types characteristic for the genus *Desmacella* (Figure A2-1). However, unique to this species was the presence of toxas that have not been found in either *D. austini* (yellow morphotype) or *Desmacella* sp. nov. (white morphotype). As performed in Chapter 3, future work into the ‘finger’ sponge should combine molecular analyses with spicule measurements to validate this as a new species, but initial examination of the spicule types in this sponge offers an exciting finding which alludes to a hidden biodiversity in the reefs remaining to be uncovered.

4.4 Conservation implications

4.4.1 Climate change concerns

The effects of climate change and ocean acidification on sponge reefs remains unknown and should receive greater attention in future studies. Temperatures may cause spicule dissolution in glass sponges, which was observed in the Antarctic glass sponge *Rosella racovitazae* when this sponge was experimentally placed in tropical waters (Bertolino et al. 2017). Over six months, the siliceous spicules of *R. racovitzae* exhibited a hollow axial canal. With rising global sea temperatures due to climate change, glass sponge reefs may become less resilient and more susceptible to damage if their siliceous spicule skeletons begin to dissolve.

Temperatures not only influence spicule dissolution rates, but also can control glass sponge pumping arrests (Leys and Meech 2006). Upon stimulation, sponges are unable to arrest their pumping above 12ºC and sponges stop pumping completely below 7ºC (Leys 2003). This narrow thermal range in which glass sponges can control pumping behaviour has implications for their feeding and energetics. If water temperatures were to rise, sponges may exhibit reduced abilities to control water pumping and thus experience greater susceptibility to clogging from sediments. Given reefs in the SoG are typically shallower (79 m at Howe reef, 90 m at Galiano reef) than the Hecate Strait and QCS reefs (150-250 m), they can be expected to face greater vulnerability to changes in sea surface temperatures. Interestingly, bottom water temperatures in the Hecate Strait northern reef are uncharacteristically low (ranging from 5.5-7.3ºC) compared to where many other sponge reefs are found (Whitney et al. 2005). This perhaps indicates the thermal range that sponge reefs can tolerate are much larger than currently expected, or glass sponges in the Hecate Strait have developed unique adaptations for persisting in colder waters.

4.4.2 Future monitoring challenges

The Hecate Strait and QCS reefs present future long-term MPA monitoring challenges given these reefs area location in remote waters beyond safe SCUBA diving limits. This study briefly examined automated methodologies that can be applied to ROV imagery for monitoring changes in sponge populations and habitat complexity. However, future studies should examine the application of alternative remotely operated methods that can be easily applied for ongoing monitoring in the reefs. In recent years, autonomous underwater vehicles (AUV) have become a widely available tool for use in conducting spatially repeatable monitoring surveys in other benthic habitats (Barrett et al. 2010, Smale et al. 2012). This technique can be used in future Hecate Strait and QCS reef MPA mapping surveys, and AUV imagery may be compared to reef distributions documented in this thesis to provide knowledge of whether sponge populations in the Hecate Strait northern reef are in growth or decline. Furthermore, assessment of sponge populations and associated megafauna using systematic automated procedures will greatly reduce visual census biases and procedural errors associated with sampler variabilities. Particularly in long-term monitoring programs, staff and annotator changes are common, and therefore development of an automated approach is essential for sound monitoring of changes in reef distributions and biodiversity.

4.4.3 Diagnostic indices for monitoring reef health

The DFO proposed a diagnostic decision tree for monitoring glass sponge reefs in the SoG and Howe Sound (Figure A2-2, Dunham et al. In Press). This diagnostic approach has been suggested for coral reef monitoring and follows a model similar to that of a medical exam, whereby the subject's (reef) history is 'clinically' reviewed and the current state of health in the subject is assessed to identify the cause of illness (Downs et al. 2005). This diagnostic decision tree can also be implemented for monitoring the Hecate Strait and QCS reefs. However, I suggest some additional indices that can be incorporated into the diagnostic tree for improving this monitoring approach.

Two indices are highlighted in the diagnostic tree that are important for monitoring sponge reef health: (1) decreasing trends in live reef-building glass sponges and (2) decreasing trends in indicator taxa associated with a healthy reef. In Chapter Two and Three, I showed the importance of dead reef-building sponge skeleton for juvenile and non-reef forming sponge recruitment. Currently, the recommended diagnostic tree only focuses on trends in live sponges, however this thesis highlights dead sponges may be an important indicator of reef health, equal to that of live sponges for diagnostic trend analysis. In coral reefs, changes in structural complexity (rugosity) has often been used as a predictor of ecosystem health (Graham and Nash 2013, Burns et al. 2015, Graham et al. 2015, Newman et al. 2015). A weak but significantly positive relationship between sponge reef rugosity and live sponge cover was shown in this study, suggesting that reef rugosity may be added as another 'branch' in the diagnostic tree for predicting changes in live and dead sponge abundance. This thesis also shows the associations of megafauna among different areas in the reefs, in which the abundance of squat lobsters *M. quadraspina* and rockfish *Sebastes* spp. were greater in the presence of high reef cover (live and dead sponges), while spot prawns and flatfish were often found in the presence of low reef cover and patches of mud. This knowledge of megafauna associations can now be used to aid in reef status diagnoses. For example, an increase in non-reef associated animals (e.g. spot prawns and flatfishes) would suggest the trajectory of the reefs towards a mud-dominated state. Finally, future studies may test the effectiveness of this diagnostic model by comparing new findings against baseline data presented in this thesis.

4.5 Concluding remarks

Glass sponge reefs have been an enigma for scientists since their first discovery in 1987 and our knowledge of sponge reef ecology continues to grow with every new research excursion to the reefs. This thesis presented first baseline data on status of sponge distributions and community assemblage of megafauna in the Hecate Strait northern reef, which is one of four major reef complexes designated as an MPA. I have provided empirical evidence that supports the importance of sponge reef habitat in benthic environments for increasing niche space for commercially importance species. I also give insight into the hidden biodiversity of the reefs not yet discovered. Glass sponge reefs remain threatened by multiple anthropogenic stressors and climate change, and so our continued understanding of glass sponge reef ecology should be prioritized for future scientific research.

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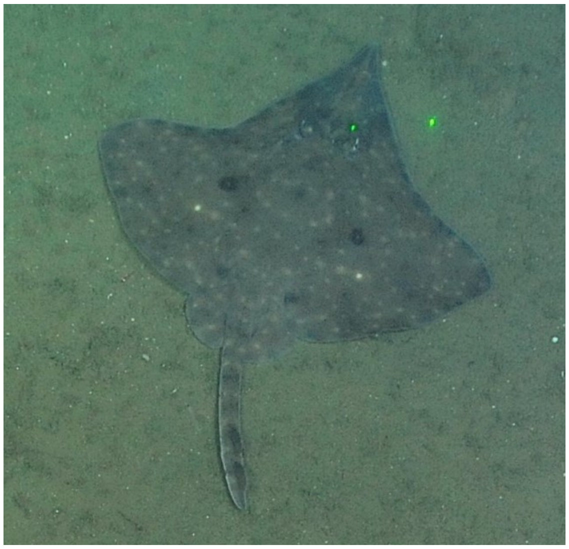
Appendix 1

Marine life field guide for the Hecate Strait northern reef

The following provides a field guide for all associated megafauna documented and observed in Chapter Two. ROV images are provided from which species identifications were made. This field guide can be cross referenced in future analyses of sponge reef biodiversity.

How to use this field guide



Longnose skate (1)

Raja rhina (2)

Location	Farrea 2015	(3)
Dive	R1894	(4)
Photo ID	00908	(5)
Depth	169 m	(6)
Confidence	● ● ●	(7)

Comments: Sometimes confused with *Raja binoculata* (Big skate). Big skate have large multi-ringed eye spots on each pectoral fin, whereas longnose skate have small eye spots. (8)

(1) Common name or common used taxonomic rank (if the common name is undetermined).

(2) Scientific name.

(3) Remotely operated vehicle (ROV) image location (see Figure 2-1).

(4) ROV dive identification number.

(5) ROV image sample number.

(6) Depth at which ROV image was taken.

(7) Rating scale indicating confidence in species identification. (● ● ● = Confident in species identification from ROV images, ○ ○ ○ = Cannot identify to species based on images alone)

(8) Comments about key features of the species, diagnostic traits, etc.

Cloud sponge

Aphrocallistes vastus

Location	Farrea 2015
Dive	R1991
Photo ID	01575
Depth	170 m
Confidence	● ● ●

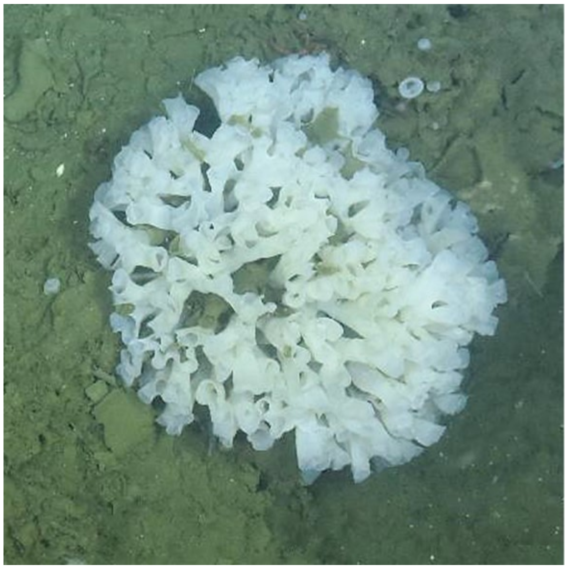
Comments: Has 'mitten-like' appendages. Can be confused with *Heterochone calyx* (Vase sponge).

Vase sponge

Heterochone calyx

Location	Farrea 2015
Dive	R1986
Photo ID	00395
Depth	172 m
Confidence	● ● ●

Comments: Has 'finger-like' appendages. Can be confused with *Aphrocallistes vastus* (Cloud sponge).

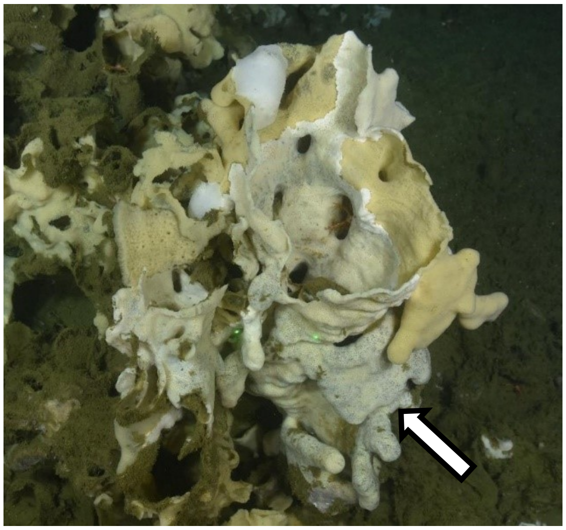


Bush sponge

Farrea occa

Location	Peloponnesus
Dive	R1895
Photo ID	01100
Depth	191 m
Confidence	● ● ●

Comments: Has a 'bush-like' growth form with many oscula.

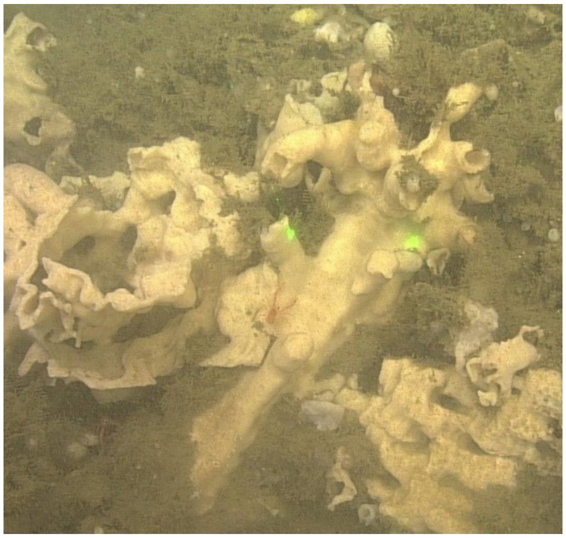


White *Desmacella*

Desmacella gwaiihaanii sp. nov.

Location	Farrea 2015
Dive	R1999
Photo ID	02917
Depth	169 m
Confidence	● ● ●

Comments: Bone-white in colour. Arrow pointing to *D. gwaiihaanii* sp. nov. (white encrusting sponge) growing over live *Aphrocallistes vastus.*

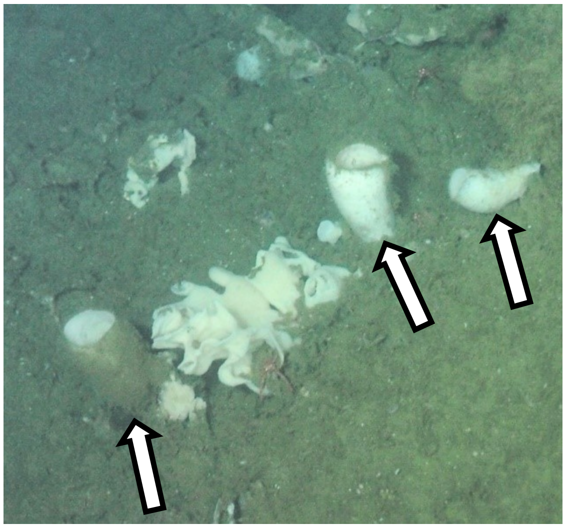


Yellow *Desmacella*

Desmacella austini

Location	Farrea 2015
Dive	R1986
Photo ID	00045
Depth	174 m
Confidence	● ● ●

Comments: Off-white to yellow in colour. Often found overgrowing live and dead *Heterochone calyx*.



Boot sponges (unidentified)

Location	Farrea 2015
Dive	R1897
Photo ID	01573
Depth	170 m
Confidence	○ ○ ○

Comments: Arrow pointing to boot sponges. Could be the species *Rhabdocalyptus dawsoni* or *Staurocalyptus dowlingi*.

Lyssacine (unidentified)

Location	Farrea 2015
Dive	R2000
Photo ID	03096
Depth	170 m
Confidence	○ ○ ○

Comments:

Lyssacine (unidentified)

Location	Farrea 2015
Dive	R1986
Photo ID	00062
Depth	172 m
Confidence	○ ○ ○

Comments

Sponge (unidentified)

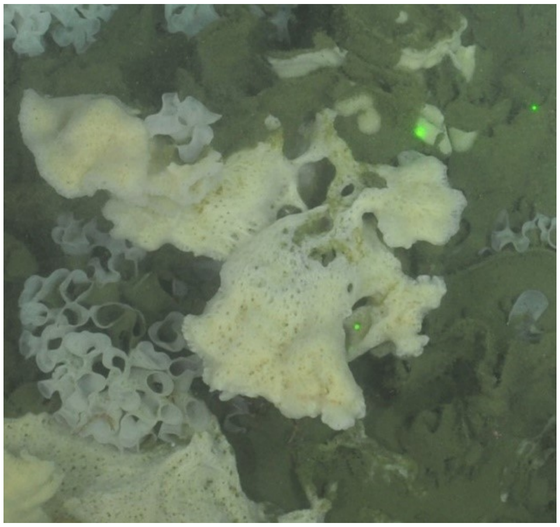
Location	Farrea 2015
Dive	R1894
Photo ID	00958
Depth	170 m
Confidence	○ ○ ○

Comments: Bright orange colour.

Sponge (unidentified)

Location	Farrea 2015
Dive	R1897
Photo ID	01661
Depth	169 m
Confidence	○○○

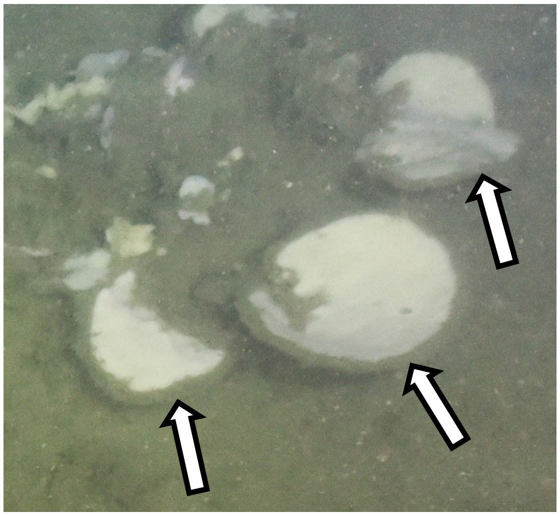
Comments



Sponge (unidentified)

Location	Farrea 2015
Dive	R1894
Photo ID	00851
Depth	172 m
Confidence	○○○

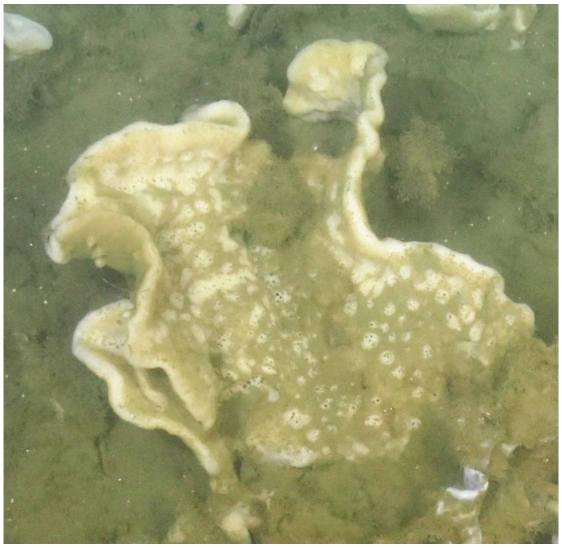
Comments



‘Plate’ sponge (unidentified)

Location	Farrea 2015
Dive	R1894
Photo ID	00958
Depth	170 m
Confidence	○○○

Comments: Has a ‘plate-like’ appearance.



‘Cheese’ sponge (unidentified)

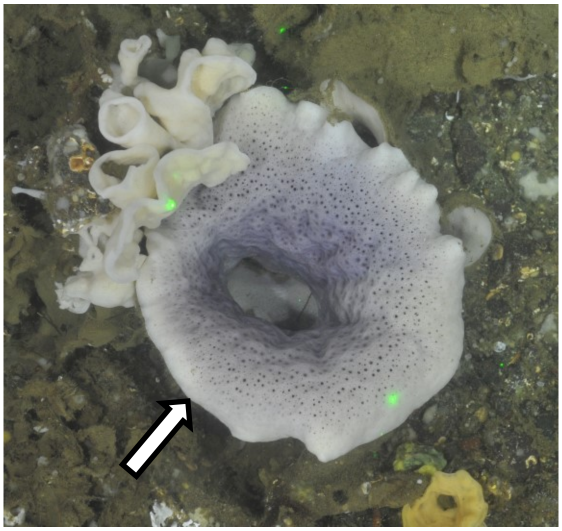
Location	Sponge Ridge West
Dive	R1989
Photo ID	00592
Depth	178 m
Confidence	○○○

Comments: Has a ‘cottage-cheese-like’ appearance.

Sponge (unidentified)

Location	Sponge Ridge West
Dive	R1989
Photo ID	00649
Depth	180 m
Confidence	○○○

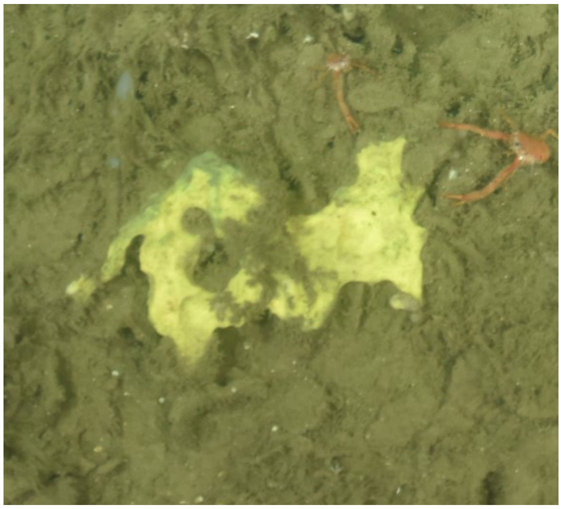
Comments



‘Trumpet’ sponge (unidentified)

Location	Farrea 2015
Dive	R1888
Photo ID	00372
Depth	172 m
Confidence	○○○

Comments: Arrow pointing to the ‘trumpet’ sponge. Purple colour and is shaped like a trumpet.



‘Sunshine’ sponge (unidentified)

Location	Farrea 2015
Dive	R1991
Photo ID	00889
Depth	169 m
Confidence	○ ○ ○

Comments: Bright yellow colour.

‘Finger’ sponge (unidentified)

Location	Farrea 2015
Dive	R1894
Photo ID	00866
Depth	168 m
Confidence	○ ○ ○

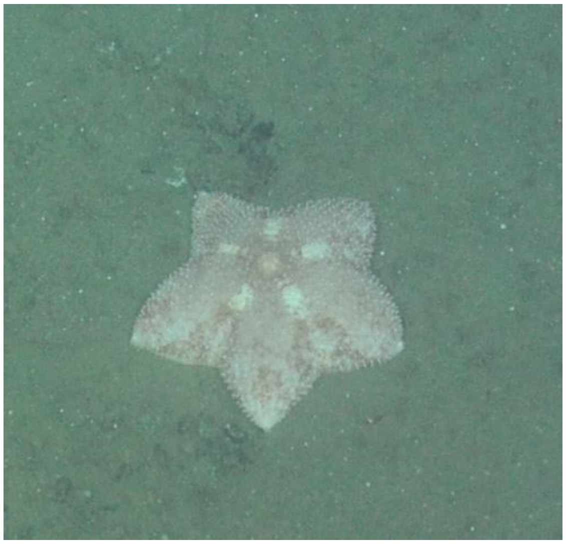
Comments: Has ‘finger-like’ projections and is often found growing in association with *Farrea occa*. Could be a demosponge.

Cookie star

Ceramaster sp.

Location	Farrea 2015
Dive	R1894
Photo ID	00989
Depth	169 m
Confidence	● ● ●

Comments: Could be *Ceramaster patagonicus*.



Cushion star

Culcita sp.

Location	Farrea 2015
Dive	R1894
Photo ID	00917
Depth	169 m
Confidence	● ○ ○

Comments

Blood star

Henricia sp.

Location	Farrea 2015
Dive	R1897
Photo ID	01573
Depth	170 m
Confidence	● ● ○

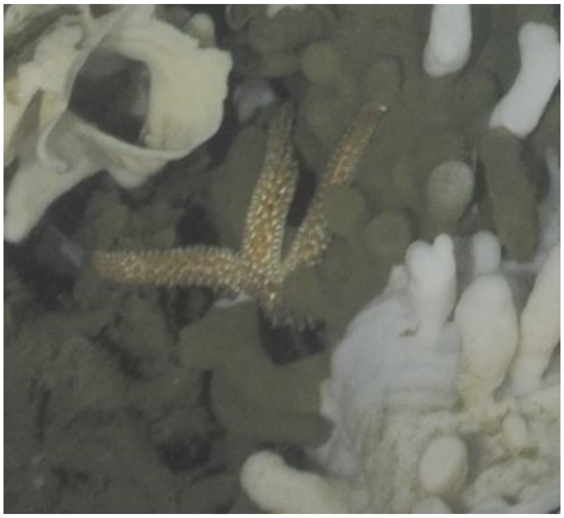
Comments

Vermillion star

Mediaster sp.

Location	Farrea 2015
Dive	R1999
Photo ID	02568
Depth	169 m
Confidence	● ● ○

Comments



Rainbow star

Orthasterias sp.

Location	Farrea 2015
Dive	R1894
Photo ID	00866
Depth	168 m
Confidence	● ○ ○

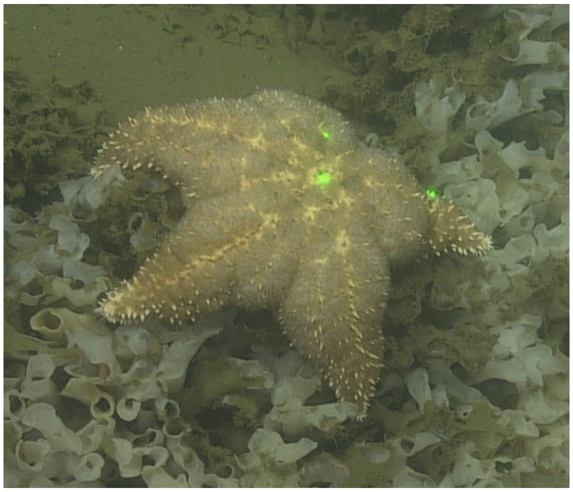
Comments

Slime star

Pteraster tesselatus

Location	Peloponnesus
Dive	R1895
Photo ID	01100
Depth	191 m
Confidence	● ● ○

Comments



Sea star (unidentified)

Location	Sponge Ridge West
Dive	R2001
Photo ID	01367
Depth	179 m
Confidence	○ ○ ○

Comments: Could be the species *Poraniopsis inflatus inflatus.* Common name Thorny star.

Sea star (unidentified)

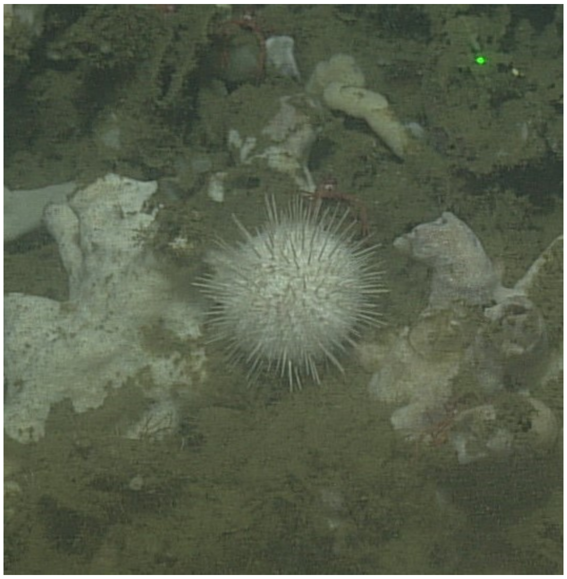
Location	Farrea 2015
Dive	R1897
Photo ID	01624
Depth	171 m
Confidence	○ ○ ○

Comments: Could be the species *Stylasterias forreri.* Common name Velcro star.

Sea star (unidentified)

Location	Farrea 2015
Dive	R1897
Photo ID	01624
Depth	171 m
Confidence	○ ○ ○

Comments



Sea urchin (unidentified)

Class Echinoidea

Location	Farrea 2015
Dive	R1996
Photo ID	17444
Depth	169 m
Confidence	○○○

Comments: Could be the species *Allocentrotus fragilis* (*Strongylocentrotus fragilis*). Common name Fragile urchin.

Whitespotted sea cucumber

Parastichopus leukothele

Location	Sponge Ridge West
Dive	R1989
Photo ID	00623
Depth	178 m
Confidence	● ● ●

Comments

Giant red sea cucumber

Parastichopus californicus

Location	Sponge Ridge West
Dive	R1989
Photo ID	00636
Depth	177 m
Confidence	●○○

Comments

Papillose sea cucumber

Synallactes challengeri

Location	Peloponnesus
Dive	R1895
Photo ID	01082
Depth	191 m
Confidence	● ● ○

Comments

Brittle stars (unidentified)

Ophiura sp.

Location	Peloponnesus
Dive	R1895
Photo ID	01064
Depth	189 m
Confidence	● ● ○

Comments

Hermit crab

Superfamily Paguroidea

Location	Farrea 2015
Dive	R1894
Photo ID	00932
Depth	167 m
Confidence	● ○ ○

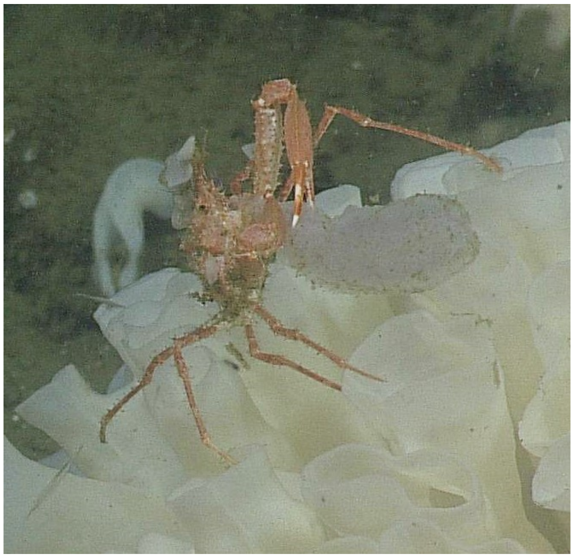
Comments

Spiny lithode crab

Acantholithodes hispidus

Location	Farrea 2015
Dive	R2000
Photo ID	02952
Depth	170 m
Confidence	● ● ●

Comments



Longhorn decorator crab

Chlorilia longipes

Location	Farrea 2015
Dive	R1996
Photo ID	10491
Depth	172 m
Confidence	● ● ●

Comments: Has sponge decorated on to its carapace.

Squat lobster

Munida quadraspina

Location	Farrea 2015
Dive	R1897
Photo ID	01661
Depth	172 m
Confidence	● ● ●

Comments

Spot prawn

Pandalus platyceros

Location	Farrea 2015
Dive	R1996
Photo ID	01709
Depth	170 m
Confidence	● ● ●

Comments: Has two distinct white spots on its tail.

Sea spiders (unidentified)

Order Pantopoda

Location	Farrea 2015
Dive	R1894
Photo ID	00958
Depth	170 m
Confidence	○ ○ ○

Comments

Clams (unidentified)

Order Veneroida

Location	Farrea 2015
Dive	R1895
Photo ID	01070
Depth	188 m
Confidence	○○○

Comments

Giant Pacific octopus

Enteroctopus dofleini

Location	Farrea 2015
Dive	R1996
Photo ID	01709
Depth	171 m
Confidence	●●○

Comments

Pacific bobtail squid

Rossia pacifica

Location	Farrea 2015
Dive	R1897
Photo ID	01645
Depth	172 m
Confidence	●●○

Comments

Dovesnails (unidentified)

Family Columbellidae

Location Sponge Ridge West
Dive R1989
Photo ID 00644
Depth 180 m
Confidence ○○○

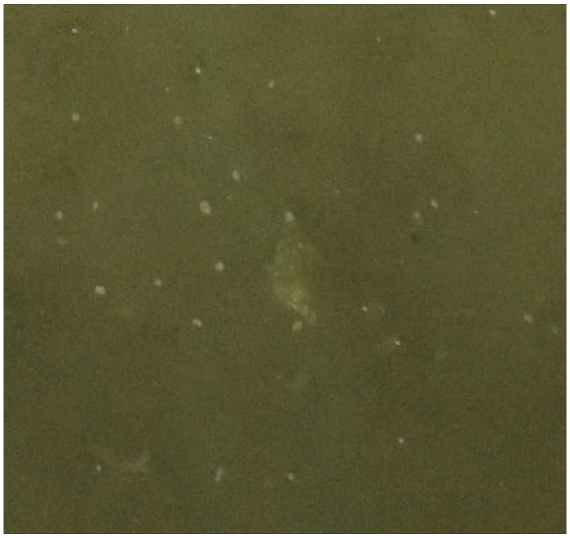
Comments

Topsnails (unidentified)

Calliostoma sp.

Location Farrea 2015
Dive R1897
Photo ID 01571
Depth 171 m
Confidence ○○○

Comments



Oregon hairy triton

Fusitriton oregonensis

Location Sponge Ridge West
Dive R1989
Photo ID 00657
Depth 180 m
Confidence ●●○

Comments

Dorid nudibranch

Peltodoris lentiginosa

Location	Farrea 2015
Dive	R1996
Photo ID	01967
Depth	170 m
Confidence	● ● ●

Comments

Anemone (unidentified)

Order Actinaria

Location	Farrea 2015
Dive	R1894
Photo ID	00845
Depth	168 m
Confidence	○○○

Comments

Anemone (unidentified)

Order Actinaria

Location	Farrea 2015
Dive	R1894
Photo ID	00885
Depth	170 m
Confidence	○○○

Comments

Sculpin (unidentified)

Family Cottidae

Location	Farrea 2015
Dive	R1894
Photo ID	00972
Depth	168 m
Confidence	○ ○ ○

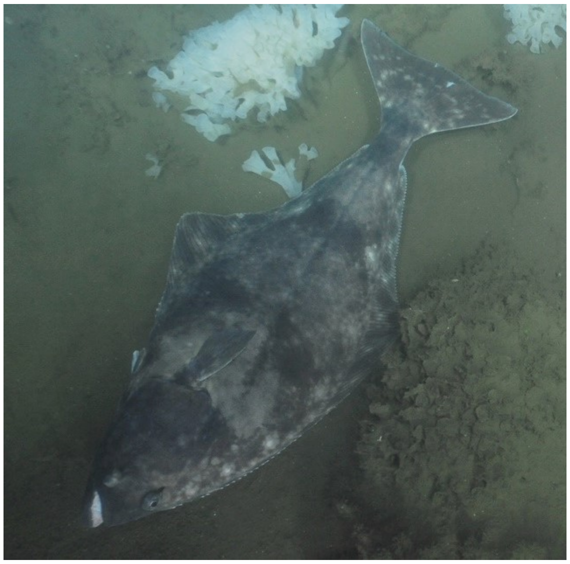
Comments

Sculpin (unidentified)

Family Cottidae

Location	Farrea 2015
Dive	R1894
Photo ID	00952
Depth	172 m
Confidence	○ ○ ○

Comments



Flatfish (unidentified)

Family Pleuronectidae

Location	Peloponnesus
Dive	R1895
Photo ID	01072
Depth	193 m
Confidence	○ ○ ○

Comments: This species is *Hippoglossus stenolepsis* (Pacific halibut). All flatfishes were grouped together for image analysis and not distinguished by species.

Pricklebacks

Family Stichaeidae

Location	Farrea 2015
Dive	R1894
Photo ID	00957
Depth	170 m
Confidence	○ ○ ○

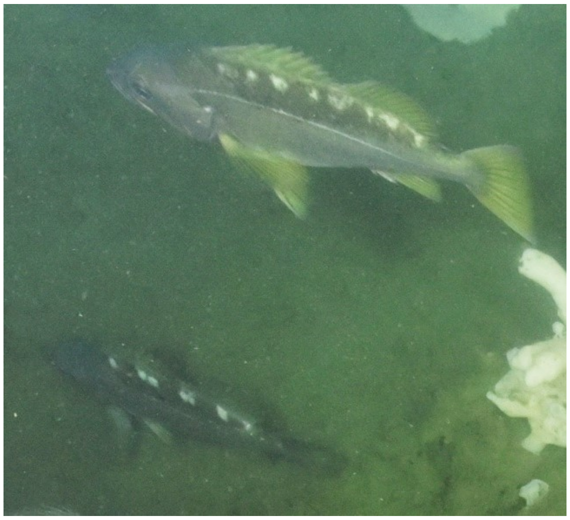
Comments

Walleye pollock

Gadus chalcogrammus

Location	Farrea 2015
Dive	R1991
Photo ID	00891
Depth	170 m
Confidence	● ● ●

Comments: Sometimes confused with *Gadus microcephalus* (Pacific cod). Pacific cod has a large chin barbel, whereas walleye pollock have little to no chin barbel.



Yellowtail rockfish

Sebastes flavidus

Location	Sponge Ridge West
Dive	R1989
Photo ID	00565
Depth	178 m
Confidence	● ● ●

Comments

Splitnose rockfish

Sebastes diploproa

Location	Sponge Ridge West
Dive	R1989
Photo ID	00586
Depth	176 m
Confidence	● ● ●

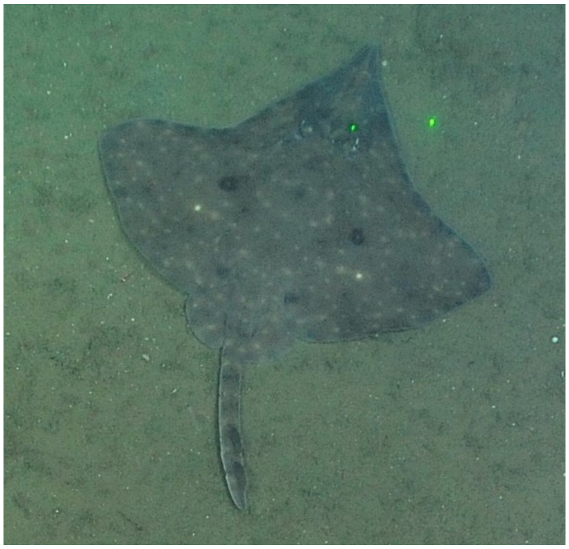
Comments: Upper jaw is split with two knobs on either side.

Spotted ratfish

Hydrolagus colliei

Location	Sponge Ridge West
Dive	R1989
Photo ID	00660
Depth	177 m
Confidence	● ● ●

Comments



Longnose skate

Raja rhina

Location	Farrea 2015
Dive	R1894
Photo ID	00908
Depth	169 m
Confidence	● ● ●

Comments: Sometimes confused with *Raja binoculata* (Big skate). Big skate have large multi-ringed eye spots on each pectoral fin, whereas longnose skate have small eye spots.

Appendix 2

Supplementary material for Chapter Four discussion

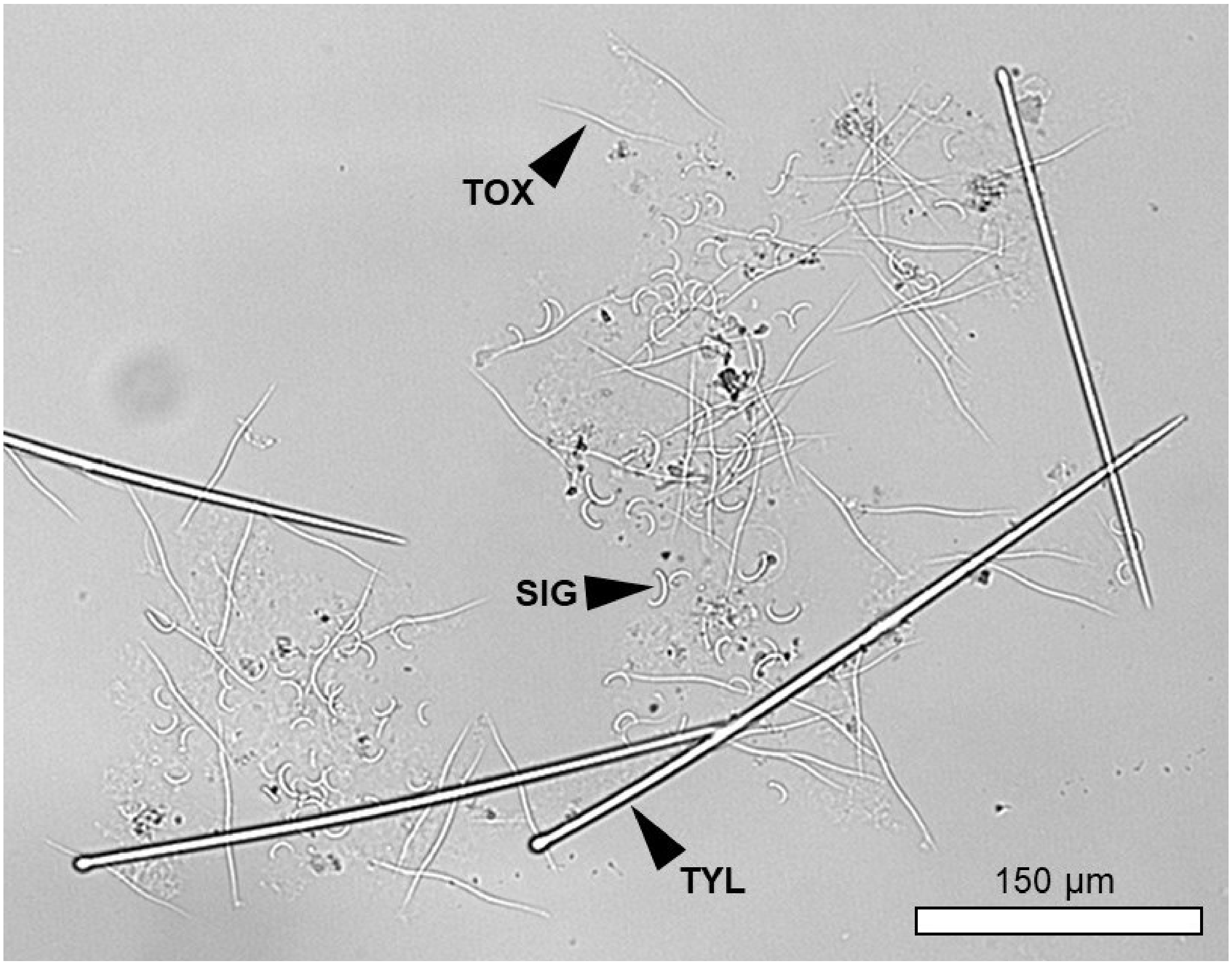


Figure A2-1. Spicule types in the non-reef forming UI 9 'finger' sponge. Megascleres of long, thin tylostyles (TYL) with one end pointed and an elliptical tyle (globular swelling) at the base. Microscleres of C-shaped sigmas (SIG) and long, thin, and wavy toxas (TOX). Image taken using the Zeiss Axioskop2 compound microscope with a QIcam camera using Northern Eclipse.

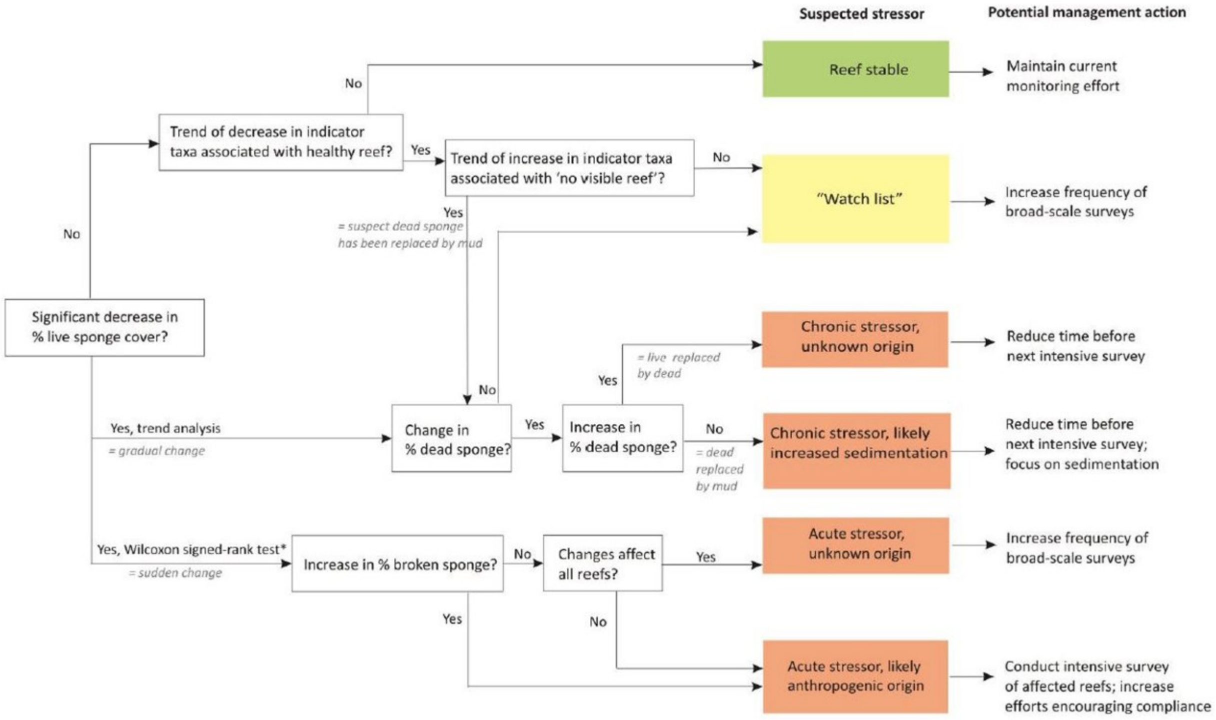


Figure A2-2. Diagnostic decision-tree for monitoring glass sponge reefs. Figure from (Dunham et al. In press).