Responsiveness of Glass Sponges to Suspended Sediments at Canada's Glass Sponge Reefs

by

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Abstract

Glass sponge reefs are globally unique ecosystems on Canada's western continental shelf that are susceptible to harm from fishing (e.g., bottom-contact trawling). In 2017, a marine protected area (MPA) was created to protect four of these reefs in Hecate Strait and Queen Charlotte Sound. Three sponge species form the reefs, *Aphrocallistes vastus, Heterochone calyx* and *Farrea occa*. Glass sponges are filter feeders, pumping water through their bodies to remove bacteria and oxygen and excrete wastes. Previous laboratory studies had shown glass sponges arrest their filtration in response to suspended sediment; this has never been studied *in situ*. Therefore the aim of this thesis was to determine whether glass sponge filtration is affected by resuspended sediments at the sponge reefs. The work was carried out at two reefs, one in the Strait of Georgia, BC and the other at the Hecate Strait and Queen Charlotte Sound Marine Protected Area. Using a remotely operated vehicle (ROV), current profilers and turbidity meters were deployed beside the glass sponge *Aphrocallistes vastus* on Fraser Ridge reef in the Strait of Georgia, BC, which is currently closed to bottom-contact fishing but which is not a MPA. Custom flowmeters were positioned into sponge oscula to record changes in filtration and changes in suspended sediment concentrations (SSC) were measured by changes in transmissivity using optical backscatter sensors. Sediment disturbances were created by the ROV. Increases in SSCs to 10 – 80 mg l^{-1} were correlated with decreased excurrent flow rate (r = -0.83 to -0.92). Both single arrests, lasting only 5 min in duration, and longer 'coughing' arrests lasting > 30 min were recorded, and together reduced feeding by up to 70%. *A. vastus* dominates Fraser Ridge reef, whereas two other species, *Heterochone calyx* and *Farrea occa,* comprise large portions of reef in the more northern Hecate Strait MPA. To determine whether species- or habitat-specific variations in the physiology of arrests in glass sponges, the responses of *H. calyx*, *F. occa* as well as a non-reef forming species, *Rhabdocalyptus dawsoni*, were studied in the MPA. Small sediment disturbances (< 5 – 10 mg l^{-1}) generated by the ROV triggered single arrests in both *H. calyx* and *R. dawsoni*. *H. calyx* appeared to clog following two hours of exposure to SSCs of 3.2 mg l^{-1} and *R. dawsoni* arrested all pumping activity following extend exposure to SSCs < 1 mg l^{-1} above natural levels of turbidity (2.71 mg l^{-1}). No arrests were recorded from *F. occa* but the low pumping rate of this sponge made it difficult to record flow out of this species. The distance suspended sediments could be transported was estimated using sediment collected from the reefs, and a settlement model. The model showed that a plume of sediment with <20 µm grain size has a range greater than the narrower portions of the MPA boundaries and would remain at high enough SSCs to induce arrests within the species studied. This study confirmed that different glass sponge species arrest filtration in response to elevated SSCs *in situ*. The thresholds for response varies between *A. vastus*, *H. calyx* and *R. dawsoni*, but all are significantly lower than those known to be generated by trawling (~ 100 – 500 mg l^{-1}). These results provide threshold and response data for use in current and future conservation of Canada's glass sponge reefs.

Preface

Chapter Two of this thesis has been published as: Grant, N., Matveev, E., Kahn, A.S., Leys, S.P., 2018. Suspended sediment causes feeding current arrests in situ in the glass sponge *Aphrocallistes vastus*. *Marine Environmental Research*, **137**, 111-120. I was responsible for data analysis and drafting the manuscript. E. Matveev and A.S. Kahn helped collect the data, advised on data analysis and edited the manuscript. S.P. Leys was the supervisory author and concieved the experiments, collected the data, advised on data analysis and edited the manuscript.

Chapter Three of this thesis was conceived by N. Grant with advice from E. Matveev, A.S. Kahn, S.P. Leys, and input on the final experimental design from A. Dunham, S. Archer (DFO). It is being prepared as a manuscript for journal publication. I was responsible for conceiving experiments, data collection, analysis and drafting the manuscript. Co-author contributions are as follows: data collection: E. Matveev, A.S. Kahn, A. Dunham, S. Archer, D. Eerkes-Medrano and R. Bannister; data analysis: E. Matveev, A.S. Kahn, S.P. Leys; manuscript editing: E. Matveev, AS Kahn, A. Dunham, D Eerkes Medrano, S.P. Leys.

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Chapter 1. Introduction

1.1 General Introduction

Earth's oceans are ever-changing environments that are constantly affected by the way humans interact with the planet (e.g., Sorte et al. 2011, Shine 2014, Clark et al. 2015, Crate and Nuttall 2016, de Souza et al. 2018). In particular, global fishing pressures have been recognized as one of the leading environmental and economic problems associated with the oceans for many decades (Davis 1921, Jackson et al. 2001, Lotze et al. 2006, Worm et al. 2009). While the majority of studies on the impacts of overfishing focus on pelagic species (e.g., Myers and Worm 2003, Pauly 2008, Worm and Branch 2012), the benthos is greatly affected as well (e.g., Kaiser et al. 2006, Clark et al. 2015, Hiddink et al. 2017). Non-motile animals, such as corals and sponges, are key members of many marine benthic communities and are threatened both directly and indirectly from bottom-contact fishing (Almany et al. 2009, Bell et al. 2015b, Hughes et al. 2017). Bottom-contact fishing, such as trawling, has been altering benthic ecosystems for as long as it has been in use (Davis 1921, March 1953, Jones 1992). It can destroy habitats and animals (Althaus et al. 2009, Ivanovic et al. 2011), release biocontaminants from seafloor sediments (Kaiser et al. 2002, Bradshaw et al. 2012) and resuspend large quantities of sediments into the water column, smothering and choking sessile animals that cannot escape (Newcombe and MacDonald 1991, Pilskaln et al. 1998, Freese et al. 1999, Ivanovic et al. 2011).

Despite this knowledge, animals like corals and sponges are not always given a protective designation, often due to their non-commercial status (Ludwig et al. 1993, Ban and Alder 2008, Howell 2010). Conservation of such ecosystems thus relies on the ecological importance or uniqueness of the community. This often leads to a policy first, science second approach based on the concept that conservation action should not be hindered in the face of insufficient science, particularly if human or environmental health is at risk (Santillo et al. 1998, Agardy et al. 2016). This precautionary tactic is initially beneficial, but is can lead to a conservation plan founded on a lack of knowledge about the habitat of concern. Where the science is partially available, it may not be strictly adhered to, such as what occurred with the Hecate Strait and Queen Charlotte Sound Glass Sponge Reef MPA, which was formed to protect the ecosystem of glass sponges (Figure 1-1) off the coast of British Columbia, Canada (Conway et al. 1991, Conway et al. 2001, Krautter et al. 2001). Only some of the research available at that time was represented in the establishment of the MPA. Before the creation of that MPA, and continuing since its creation, scientists have been striving to inform decisions about the conservation of sponges and the future of the sponge reefs in Canada. This thesis represents one avenue of that research and focuses on the sensitivities and behavioural reactions of reef sponges to sediments, such as those that might be resuspended by bottom-contact trawling.

1.2 Sponge Biology

Sponges (Porifera) are a phylum of sessile, aquatic animals that are considered one of the most basal branching groups of metazoans (Lendenfeld and von Lendenfeld 1915, Bergquist 1978, Müller 2003, Feuda et al. 2017). They are found globally, with 8500 accepted species (18,000 estimated) in both freshwater and marine environments, ranging in depth from a few meters to 8,800 m (Gage and Tyler 1992, Appeltans et al. 2012). With their asymmetrical body forms, sponges take on a wide variety of appearances and can range in size from centimeters to meters (Figure 1-1) (Lendenfeld and von Lendenfeld 1915, Fry et al. 1970, Hooper and Van Soest 2002). There are four taxonomic classes of sponges: the three cellular sponge classes are Calcarea, Demospongiae, and Homoscleromorpha and a fourth syncytial sponge class, Hexactinellida (Feuda et al. 2017). Calcarea, or calcareous sponges, are differentiated by their calcium carbonate spicules (rigid structural elements within sponges) and lack of spongin (flexible structural elements in sponges that are made of modified collagen). Demosponges contain spongin and can have either no spicules at all or many different siliceous spicules with a multitude of shapes and sizes. Homoscleromorpha sponges show little variation in their spicule type when they are present and do not contain spongin. Lastly, hexactinellids (Figure 1-1), or glass sponges, contain six-pointed siliceous spicules and lack spongin; a few can form rigid skeletons by secondary silicification. Sponges, regardless of class, generally play a critical role in their environment as they interact with nearly every organism around them by providing habitat, as food for predators, as competitors and consumers, hosting symbionts or altering ambient water conditions (Vacelet 1975, Rützler et al. 1990, Müller 2003, Goudie et al. 2013).

A common way used to distinguish sponges from other phyla is to state the traits they do not have, such as the lack of nervous, digestive, excretory, respiratory or circulatory systems seen in other taxa (Müller 2003). However, sponges possess their own set of characteristics that make them unique from other animals, primary among which being the aquiferous system, which is the series of fine canals and chambers through which the sponge pumps water. The majority of sponges are filter-feeders, pumping water through their bodies to obtain oxygen and food (Lendenfeld and von Lendenfeld 1915, Goudie et al. 2013). Porifera means “pore-bearer” and describes the numerous pores (ostia) found on the animal’s external surface (body wall) (Müller 2003, Leys et al. 2005). These pores mark the entry point for water into a sponge’s aquiferous system; water exits out a larger excurrent opening called the osculum (Figure 1-2 A-C) (Bergquist 1978, Müller 2003). Flagellated chambers in this system contain numerous flagellated cells (choanocytes) that are continuously beating, creating a current through the sponge body (Fry et al. 1970, Bergquist 1978). This continuous pumping action allows sponges to process up to 900 times their body volume in water each hour, drastically changing the content of the ambient water (Reiswig 1974, Kahn et al. 2015, Kahn et al. 2018). This flow-through system provides a crucial link between the pelagic and benthic food webs in aquatic environments and is one of the reasons sponges are considered an important part of their benthic communities (Rützler et al. 1990, Müller 2003).

By studying sponges, ecologists can piece together a greater understanding of the benthic ecosystems that sponges play such a crucial role in (Bergquist 1978, Müller 2003). Unfortunately, sponges are frequently forgotten in favour of more charismatic and seemingly more complex forms of life. However the extraordinary characteristics of glass sponges are often forgotten and are a part of what makes them an intriguing, not-so-simple animal to study.

1.3 Ecology of Glass Sponges

Glass sponges are differentiated from other sponges by their siliceous, glass skeletons and in having syncytial tissues that can propagate electrical signals. There are around 500 known species residing primarily in deep ocean waters below 300 m, though some do inhabit areas as shallow as 20 m (Leys et al. 2007). The relatively stable conditions found in these habitats are reflected in their slow growth rates (0.76 to 5.7 cm year^{-1}) and long life spans (220 year old estimates of 1 m in length specimen) (Leys and Lauzon 1998, Austin 2003, Austin et al. 2007). Throughout their long-life spans, glass sponges occupy an important ecological niche in their habitats. They are ecosystem engineers, animals that can directly modulate resource availability, significantly modifying a habitat (Jones et al. 1994). Glass sponges can alter the properties of the ambient water in their ecosystem and construct important habitats for many species (Leys et al. 2007).

Like other sponges, glass sponges filter bacteria and single-celled eukaryotes out of the water by pumping water through their aquiferous system. In areas where glass sponges flourish, such as the 29,242 m^2 of sponge cover on Fraser Ridge, they can filter over six billion liters of water per hour per (Kahn et al. 2015) and extract up to 95% of the most abundant bacteria in the water (Yahel et al. 2007). Glass sponges then excrete nitrogenous waste out of their osculum in the form of ammonium. Glass sponges also sequester large amounts of dissolved silicon from the water column (Chu et al. 2011).

Beyond altering the water contents, hexactinellids modify their environment due to their size and rigidity. Some glass sponge species are large, being propped up by their glass skeletons which provide extensive habitat for multiple other taxa, ranging from bryozoans to fish, in the otherwise featureless seascape of the deep sea (Figure 1-2 D-E). Their skeletons also act as scaffolding for the settling larva of other sponge and invertebrate species (Dayton et al. 1974, McClintock et al. 2005, Leys et al. 2007). Recruitment and settlement rates can be increased as a result of the way their large bodies alter bottom currents. It is suggested by Krautter et al. (2001) that dense aggregations of glass sponges decrease bottom current velocities which allows additional species to inhabit the spaces between glass sponge patches. Sediment is also believed to be baffled against the bodies of larger specimens, lowering the local turbidity (Krautter et al. 2001, Krautter et al. 2006). Lastly, their bodies can provide food for the few glass sponge predatory species that have been identified, like nudibranchs and some asteroid species (Leys et al. 2007, Chu and Leys 2012).

1.4 Canada's Glass Sponge Reefs

1.4.1 A Globally Unique Ecosystem

Our understanding of the ecology of glass sponges has primarily come from only a few populations as these animals live at depths not always accessible by SCUBA. The fjords of British Columbia, Canada, waters around Antarctica and some submarine caves in the Mediterranean are the areas commonly glass sponge research has been carried out (Leys et al. 2007). Recently, extensive glass sponge reefs, at depths of 80 to 200 m, were found on the continental shelf of British Columbia (Conway et al. 1991). They are not known elsewhere and are therefore a globally unique ecosystem (Figure 1-3). The exact reasons why glass sponge reefs only occur in such a limited global distribution is still unknown, but it is thought that they are restricted by a unique combination of water conditions. Low light levels, temperatures around 9 to 10 ºC, low suspended sediments and high dissolved silica concentrations as well as bottom currents that trap food and nutrient particulates near the reefs are all factors believed to play a role in the limited distribution of glass sponge reefs (Leys et al. 2004, Leys et al. 2007, Kahn et al. 2015).

The reefs were first seen as anomalies on sidescan sonar images by K.W. Conway, J.V. Barrie, and J.L Luternaur (Geological Survey of Canada) in 1986 (Conway et al. 1991). Sediment cores and photographs confirmed these anomalies as sponge mounds in 1987-88 (Conway 1999). This was followed by more extensive multibeam bathymetry and backscatter mapping in 1999-2003 (Conway et al. 2005a). Sponge reefs would come to be defined by the dark, shaded regions they make in multibeam acoustic images, which are surrounded by sediments that appear as lightly shaded areas. This is the result of the low acoustic reflectivity of the sponge-rich clay sediments and siliceous sponge skeletons of the reefs compared to the highly reflective boulder and gravel glaciomarine sediments in the area (Conway et al. 2005a). This distinctive signature made by sponge reefs is the criterion by which sponge reefs are still defined.

Sponge reefs are formed in iceberg scours, where rocky outcrops have been exposed above the seafloor (Krautter et al. 2001, Conway et al. 2005b, Krautter et al. 2006). Glass sponges settle on solid substrates, creating the patchy distribution of the reefs as they need the solid foundation to grow. When the sponges die, their fused siliceous skeletons are left behind, forming the substructure on which the rest of the reef is built (Krautter et al. 2006). These skeletal frameworks can be 21 m high and are cemented together through baffled sediment. Over time, sediments will bury these skeletons and new glass sponge recruits settle on top of them, increasing the growth of the reef outward and upward, often leaving only 1 – 2 m of live sponge visible above the seafloor. By aging cores through the reef, studies have found certain areas of the reefs are between 6000 and 9000 years old (Krautter et al. 2001, Conway et al. 2005b). Only three species are known to form the underlying reef architecture (Figure 1-1): *Aphrocallistes vastus, Heterochone calyx* and *Farrea occa* (Conway et al. 1991, Conway et al. 2001, Krautter et al. 2001). Additional sponge species like the glass sponge *Rhabdocalyptus dawsoni* and many species of demosponge inhabit the reefs but are not ‘reef-forming’ species (Conway et al. 2005b, Chu and Leys 2010).

Glass sponge reefs provide an extensive habitat for many species across a variety of taxa. Species important to Canada’s commercial fishing industry have been found in and around the reefs, including Pacific halibut, Dover sole, Lingcod, rockfish (multiple species), king crabs and prawns, among others (Jamieson and Chew 2002, Boutillier et al. 2013, Law 2018). The reefs act as nursery and spawning grounds for these species, provide refuge from predation and attachment points for larval and sessile invertebrates (Cook et al. 2008, Chu and Leys 2010). This concentration of commercially important species attracted fishing pressure to the reefs for many years. Following the discovery of the reefs, numerous trawl tracks and damage caused by trawling were noted at the reefs (Conway 1999, Conway et al. 2001, Krautter et al. 2001). This led to concerns about the future of the reefs and prompted the goal to make the reefs a Marine Protected Area (MPA).

1.4.2 Hecate Strait and Queen Charlotte Sound Glass Sponge Reef MPA

Canada’s glass sponge reefs face a myriad of threats owing to their placement on the heavily fished continental shelf. It is thought that due to their slow growth and long-life spans, continuous uninterrupted growth was necessary for the reefs to reach their current sizes of greater than 100 km^2 of reef patches extending up to 2 m above the muddy bottom (Krautter et al. 2001). As in other deep-water environments, the recovery rate of the sponges is expected be on the scale of hundreds of years (Kahn et al. 2016, Malecha and Heifetz 2017). This is why the observations of extensive bottom-contact trawling scars at the reefs by Conway et al. (1991) during their initial discovery was of such great concern. Since that time, more reports have confirmed extensive trawling damage across numerous portions of the reefs (e.g., Conway 1999, Conway et al. 2001, Krautter et al. 2001, Jamieson and Chew 2002) (Figure 1-4). Following these studies, an appeal for the protection for these globally unique ecosystems was accompanied by voluntary fishing closures around the reefs in 1999 (Fisheries and Oceans Canada 2010, 2014a, 2016). This led to mandatory fishing closures in 2002 and eventually, in February 2017, to the creation of the largest marine protected area (MPA) in Canadian waters at that time, the Hecate Strait and Queen Charlotte Sound Glass Sponge Reef MPA (Figure 1-3C) (Fisheries and Oceans Canada 2017c).

The Hecate Strait and Queen Charlotte Sound Glass Sponge Reef MPA includes four reef complexes along the Pacific coast, totaling 2410 km^2 of protected ocean habitat (Fisheries and Oceans Canada 2017b, c). The MPA limits the disturbances that can occur directly at or adjacent to the reefs through two levels of protective boundaries (Figure 1-3C). The first boundary is the core protection zone (CPZ), which provides the highest level of protection, preventing fishing, anchoring or industrial activity of any kind at the reefs. This boundary includes the reef itself, the seabed down to 100 – 150 m and 20 m of water above the reefs (Fisheries and Oceans Canada 2017b). The second layer of protection is the adaptive management zone (AMZ) consisting of both a horizontal and vertical aspect. The vertical AMZ extends from the top of the CPZ to the sea surface while the horizontal AMZ varies in size, from 400 m to a few kilometers, out from the CPZ of each reef complex. The AMZ currently allows the installation and maintenance of undersea cables and scientific research, but is closed to all commercial bottom-contact fishing and midwater hake trawls. The CPZ is closed to all levels of disturbance without express permission from Fisheries and Oceans Canada, which includes approved scientific research (Fisheries and Oceans Canada 2017b, c). For those reef discovered outside the current MPA, in areas like the Strait of Georgia, fishing closures can and have been implemented (Fisheries and Oceans Canada 2017d).

1.5 Primary Threats to Sponges

The purpose of the sponge reef MPA is to protect glass sponge reefs from damage caused by anthropogenic activities. Bottom-contact trawling has left marks in the reefs and in some areas there are barren stretches of muddy seafloor staggered with broken fragments and ‘stumps’ of sponge skeletons (Conway 1999). Even when voluntary fishing closures were instigated, trawling continued in the vicinity of the sponges (Boutillier et al. 2013) (Figure 1-4). However, destruction via trawling is not the only threat faced by Canada’s sponge reefs. The Geological Survey of Canada reports that the MPA’s northern and southern reefs reside in areas with high petroleum potential (Hannigan and Dietrich 2012). Interest in offshore oil and gas exploration within Hecate Strait and Queen Charlotte Sound would be accompanied by numerous environmental considerations for the reefs (Jamieson and Chew 2002, Hannigan and Dietrich 2012). Additionally, undersea cables were found have a 100% mortality rate for glass sponges directly in their path and 15% up to 1.5 m out from the cable (Dunham et al. 2015). While sponges in the CPZ of the MPA are protected from these activities, any sponges found in the AMZ or outside the MPA can be exposed to any of these impacts. The primary way this happens is through suspended sediments. Bottom-contact fishing, like trawls, re-suspends large quantities of sediments into the water column, at concentrations of 20 to 500 mg l^{-1} (Churchill 1989, Puig et al. 2012, Mengual et al. 2016) (Figure 1-4F); these concentrations are above those found to affect glass sponges in laboratory studies (Tompkins-MacDonald and Leys 2008).

Suspended sediments are a common factor that affects sponges and can be extremely damaging for these primarily filter-feeding animals (Leys 2013, Grant et al. 2018; Chapter 2, this thesis). While sponges are capable of excreting some inorganic detritus, such as clays, that enter their aquiferous system (Yahel et al. 2007, Kahn et al. 2015), too much can be detrimental (Reiswig 1974, Bell et al. 2015a). Suspended particles can settle on the exterior of a sponge, smothering it or causing tissue necrosis (Pineda et al. 2017), and if a sponge becomes completely smothered by deposited sediments, it will likely not be able to continue pumping as the sediment will block the incurrent pores (Ilan and Abelson 1995, Tompkins-MacDonald and Leys 2008). Smaller grain sizes can clog the pores, canals or flagellated chambers, preventing the sponge from filtering water at full capacity. All these effects reduce a sponge's ability to filter-feed, thus the need to protect themselves from suspended sediments is crucial in sponges.

1.5.1 Responsiveness of Sponges to Sediments

As sponges rely on their ability to process water to survive, the ability to sense changes in the water, such as increases in turbidity, is crucial. The ability to sense changes in the environment is often coupled with the capacity to respond to them in measurable, repeatable ways. These responses have been noted across many sponge species (e.g., Warburton 1966, Leys and Degnan 2001, Lavrov and Kosevich 2018). In many other animals, sensing and responding to increases in suspended sediments would require nerves and muscles. Sponges can accomplish both despite lacking a conventional nervous system or muscular tissues. In sponges, these responses generally occur across a longer time-scale than what is traditionally noted in other animals, often being too slow for human eyes and requiring other methods of detection (Leys and Meech 2006, Ludeman 2015).

Responses to environmental conditions are seen in larval and adult sponges. In larval sponges, movement and orientation has been associated with light intensity. Large quantities of sediments in the water can vary the light intensity of the habitat, affecting where larva may choose to settle (Newcombe and MacDonald 1991, Ilan and Abelson 1995, Maughan 2001). Phototaxis allows sponge larvae to coordinate movement and settle in more optimum locations, like other metazoan larvae (Leys et al. 2002, Elliott et al. 2004, Collin et al. 2010). Some adult sponges can also move minimally (Nickel 2004a, Lavrov and Kosevich 2018). While adult sponges are often considered sessile animals, slow locomotion has been observed in Calcarea, Demospongiae and Homoscleromorpha sponges in both freshwater and marine species inside aquaria (Fishelson 1981, Nickel 2010, Lavrov and Kosevich 2018). While the complete combination of factors driving these movements in not clear, it is believed that they are related to changes in aquaria water conditions such as increased particulates (Bond and Harris 1988, Nickel 2006, Lavrov and Kosevich 2018).

Sponge responses to sediments do not have to be locomotory in nature as whole body and tissue contractions have been noted in demosponges and are thought to be in response to seasonal changes or unwanted particles in the water (Reiswig 1971a, Nickel 2004b, Elliott and Leys 2007). These contractions can forcefully move water and any unwanted particles out and away from the sponge, protecting the sponge from retaining harmful particles within its body. Contractions help protect demosponges from damage from unwanted particles but are only seen in sponges that possess flexible, contractile tissues (Prosser et al. 1962, Prosser 1967, Elliott and Leys 2007). While demosponges can use these contractile responses to block or forcefully move sediments out and away from them (Elliott and Leys 2007), glass sponges, like those that make up the reefs, have evolved an entirely different strategy as the ability to contract has not yet been observed in glass sponges. Hexactinellids can arrest their pumping activity through coordinated responses when exposed to harmful particles in the water (Leys et al. 1999, Tompkins-MacDonald and Leys 2008).

1.5.2 The Glass Sponge Filtration Arrest

Laboratory studies on the glass sponge *Rhabdocalyptus dawsoni* showed that it propagates action potentials throughout its tissues in response to mechanical and electrical stimulation (Mackie et al. 1983, Leys and Mackie 1997). Electrical signalling has only been recorded in *R. dawsoni* because of that species is more readily collected by SCUBA than any other species. It is assumed all glass sponges can propagate electrical signals because the action potential are what triggers an arrest of filtration. Action potentials cause a complete cessation of pumping and filtration activity throughout the sponge (Figure 1-5) (Lawn et al. 1981, Mackie et al. 1983, Tompkins-MacDonald and Leys 2008). Arrests of filtration prevent the glass sponge from drawing in suspended sediments, but they also halt the sponge's feeding and respiration, which suggests this response, while protecting tissues from damage by sediments, has a 'trade-off' energetic cost.

Hexactinellids, like all sponges, lack nerves, and instead have multinucleated syncytial tissues, with no distinct cellular boundaries, which allow electrical signals to propagate throughout the whole sponge. The electrical impulses propagate as an all-or-none signal, traveling at 0.27 cm s^{-1} ± 0.1 (Lawn et al. 1981, Leys and Mackie 1997, Leys et al. 1999). Impulses, which are believed to be Ca^{2+}-based, can be initiated from one or multiple origin points within the tissues and are then propagated throughout the entire interconnected tissue. When an action potential is triggered by stimuli such as suspended sediments, the impulse travels throughout the sponge, arresting filtration. It is suggested that an influx of calcium ions ultimately arrests the beating of the flagella pumps (Mackie et al. 1983, Leys et al. 1999). This stops the flow of water into the sponge, reducing the potential for sediments to be drawn into the sponge.

While much of the early work was done on *Rhabdocalyptus dawsoni* (e.g., Mackie et al. 1983, Leys and Mackie 1997, Leys et al. 1999), Tompkins-MacDonald and Leys (2008) confirmed that another glass sponge, *Aphrocallistes vastus,* arrests filtration in response to suspended sediments in flow-through tanks. Prior to my thesis, no work had studied if sponges respond similarly at the reefs as they do in the laboratory studies, or if the concentrations triggering responses *in situ* were equivalent to those noted by Tompkins-MacDonald and Leys (2008). This is concerning as smothering, clogging and damage from large quantities of suspended sediments are all possible consequences in and around the glass sponge reef MPA. High concentrations of suspended sediments generated by trawling take time to dissipate, during which they could cover a large distance. How long and how far they travel is not well known, but was estimated for the implementation of the MPA using the available data (Boutillier et al. 2013). Members of the fishing industry called attention to at the lack of field-based results that the MPA has been designed around as a point of concern (Fisheries and Oceans Canada 2014b). As the settling time of a sediment plume increases, the potential amount of time a sponge exposed to it could be arrested will increase as well. Despite the protective nature of the glass sponge's ability to arrest their filtration, if it were to continue for long enough it could be fatal, primarily because glass reef sponges' daily energy budgets are balanced for continuous pumping (Yahel et al. 2007, Kahn et al. 2015). Spending large time periods arrested reduces their time spent feeding and respiring (reviewed in Leys 2013). Given that sponges make up the base of the reef and perform important ecological processes that alter their local habitat, the deaths of reef-building individuals would likely lead to the end of the only known glass sponge reef ecosystems in the world.

1.6 Thesis Objectives

The overall focus of this thesis is to assess whether suspended sediment causes reef-building glass sponge species to arrest filtration. My first objective was to determine whether *Aphrocallistes vastus* responded to experimental sediment disturbances in the field by arresting filtration, similar to the ex situ results found by Tompkins-MacDonald and Leys (2008). My second objective was to determine whether the other two reef-building glass sponge species, *Heterochone calyx* and *Farrea occa*, at the Hecate Strait and Queen Charlotte Sound MPA also arrested filtration in response to experimentally generated increases in suspended sediment. The studies described in this thesis provide the first *in situ* experiments to test responsiveness by all three primary reef-building glass sponge species to suspended sediments. The analyses and conclusions drawn will help improve current and future legislation to protect glass sponges and glass sponge reefs.

Chapter Two describes experiments to assess feeding current arrests on *A. vastus* at a glass sponge reef in the Strait of Georgia, British Columbia in 2015. My analysis demonstrated that *A. vastus* does arrest filtration in response to SSC increases *in situ*. Arrests can be categorized as single 'on-off' arrests, or coughing arrests (repeated attempts to filter after arrest), each with unique defining characteristics. *A vastus* arrests were trigged by SSCs which are above the natural turbidity levels of Fraser Ridge reef but the lowest concentrations were much lower than those found to trigger arrests in the laboratory studies. The characteristics of the arrests, the effect of the arrests on sponge health and the management implications of the results are discussed in this chapter. These findings illustrate the sensitivity of one reef-building species and the importance of studying glass sponge responsiveness *in situ*.

In Chapter Three, experiments carried out in 2017on three glass sponge species in the Hecate Strait and Queen Charlotte Sound Glass Sponge Reef MPA are described. Each species was found to possess different thresholds of response to SSCs compared to *A. vastus*. At Hecate Strait, *R. dawsoni* and *H. calyx* were found to arrest filtration in response to minimal SSC increases while no arrests could be observed in *F. occa*. This chapter discusses the species-specific differences in glass sponge arrest behaviours, highlighting the unique sensitivities of glass sponges in the MPA. The effectiveness of the current MPA boundaries are discussed in terms a sediment transport model.

In Chapter Four, I discuss the implications of my findings for our understanding of the relationships sponges have with sediment, cumulative impacts that the reefs may experience and the future protection of sponge-based ecosystems. I explore directions this research may be taken in the future as well as the benefits and limitations of field-based studies as they pertain to conservation and sponge research.

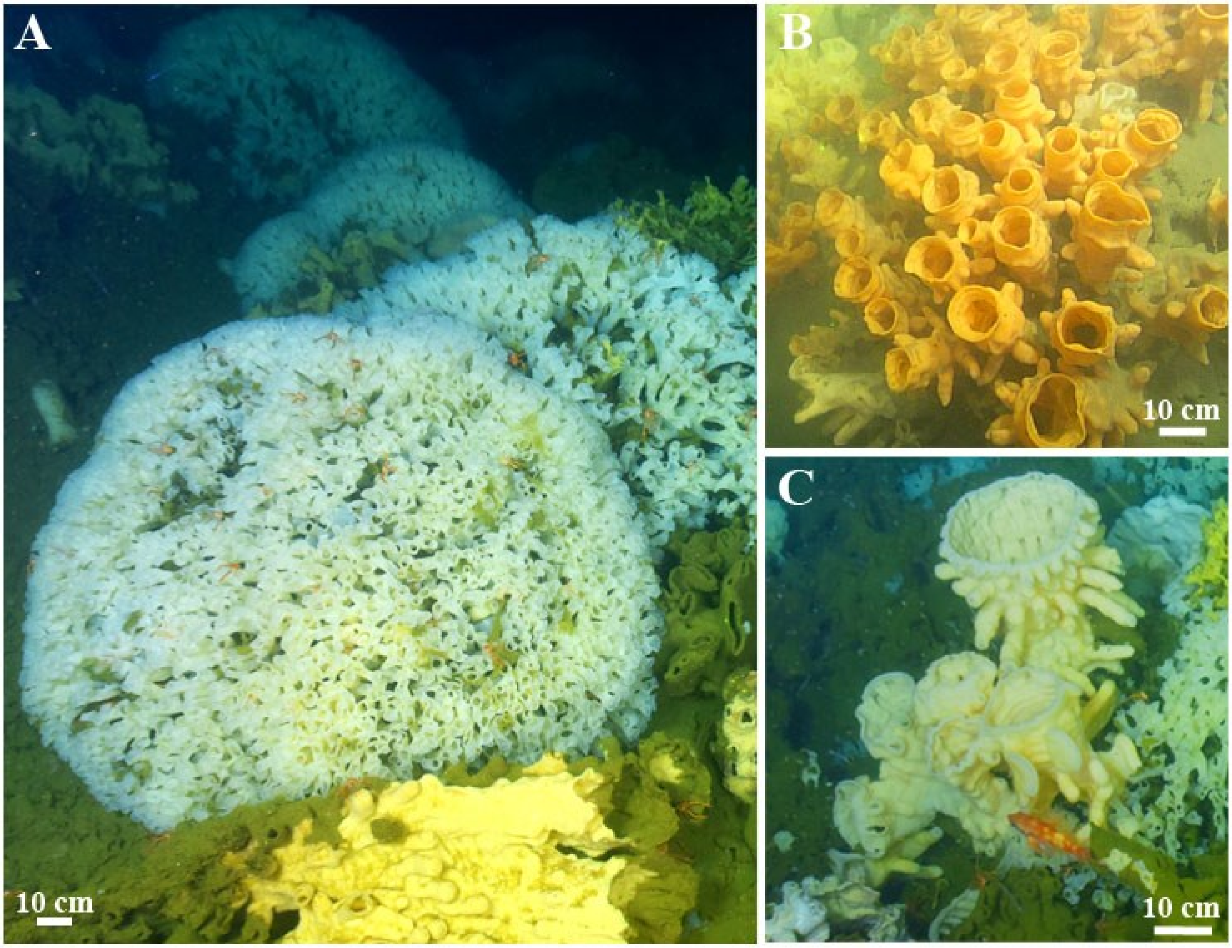

Figure 1-1: *In situ* photographs of each of the three reef-building glass sponge species. *Farrea occa* (A) (the bush sponge) has a large bush-like shape with multiple smaller oscula. *Aphrocallistes vastus* (B) (the cloud sponge) shows mitten-like projections and a single, central osculum. *Heterochone calyx* (C) (the fingered goblet sponge) has smaller finger-like projections leading to a large, central osculum.

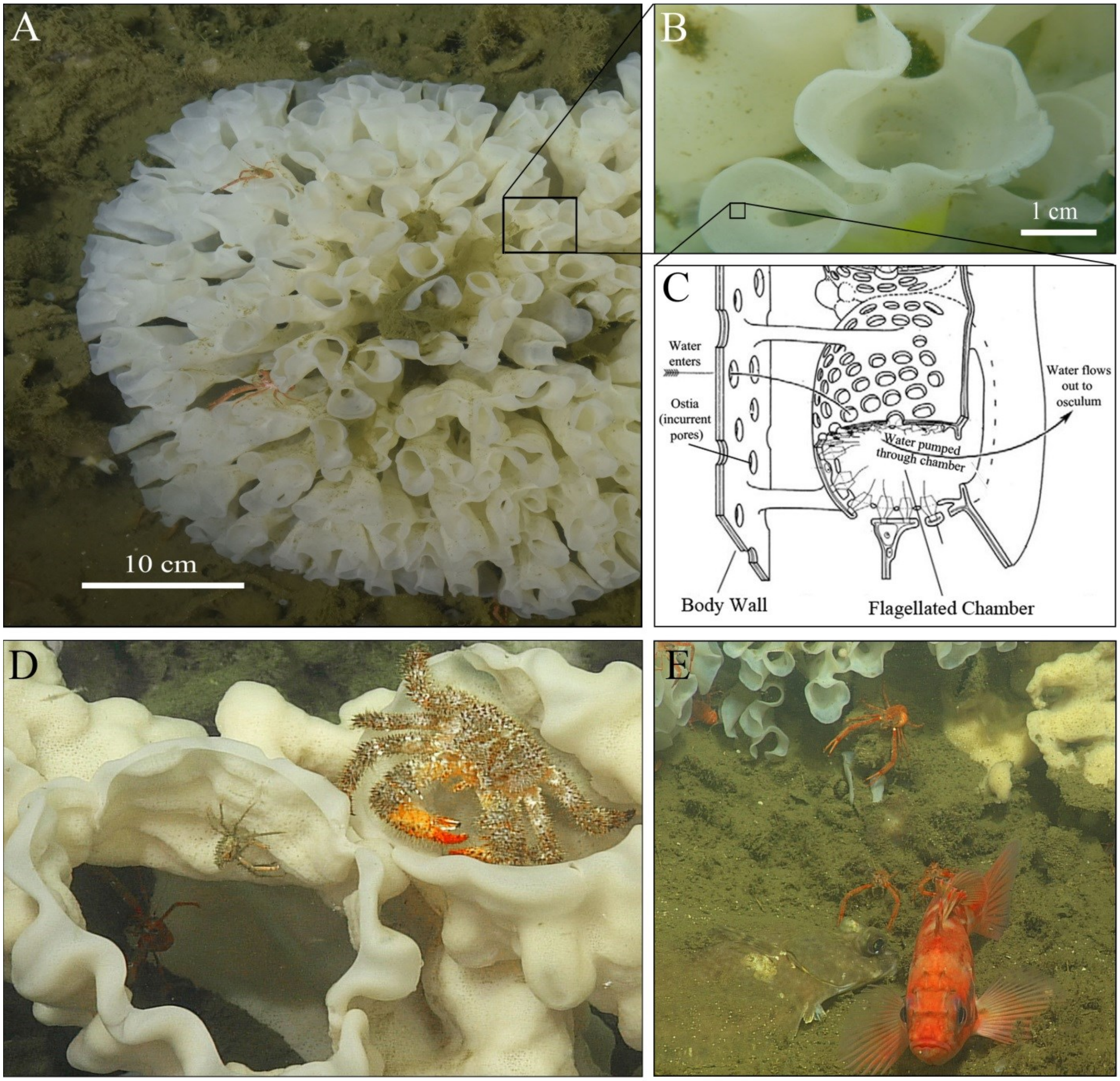

Figure 1-2: Aspects of the biology and ecology of reef-building glass sponges. (A) The glass sponge, *Farrea occa*, which houses multiple organisms within and around its body structure. (B) A closer look at one of the many *F. occa* oscula and its body wall. (C) A diagram of how water is pumped through a sponge. Water enters through the ostia in the body wall and exits out the centralized osculum. Adapted from Figure 4A Reiswig and Mehl (1991). (D-E) Examples of benthic biota that rely on glass sponge reefs for survival.

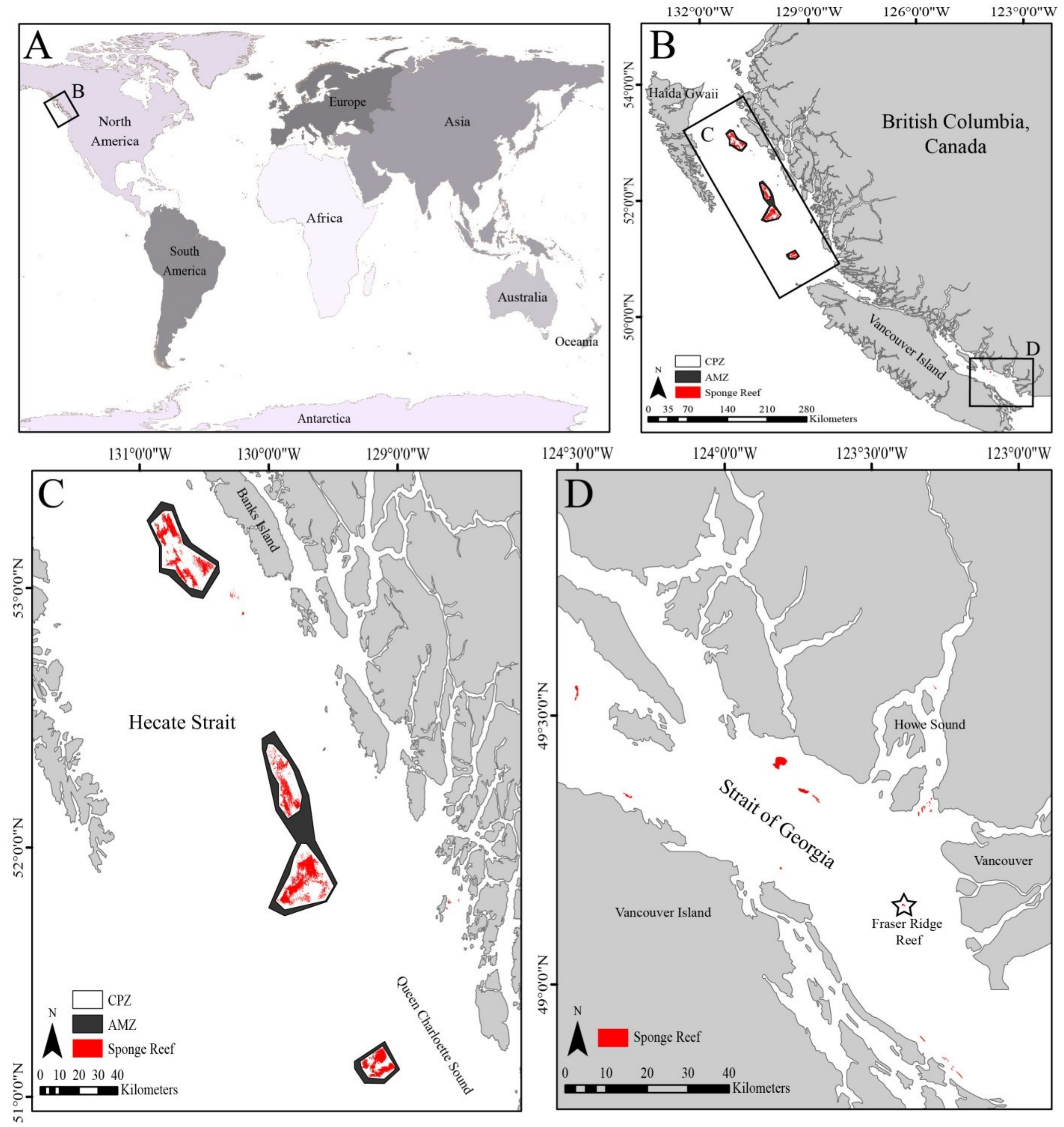

Figure 1-3: The location of glass sponge reefs on Canada's Pacific coast. (A) The only known location of glass sponge reefs globally. (B) Locations of glass sponge reefs in waters off the coast of British Columbia, Canada. (C) Four reef complexes make up the Hecate Strait and Queen Charlotte Sound Glass Sponge Reef Marine Protected Area. MPA boundaries around the sponges are the core protection zone (CPZ) and the adaptive management zone (AMZ). The northern most complex was an area of study in this thesis. (D) Reefs located in the Strait of Georgia and Howe Sound, some of which have been included within legislation mandating fishing closures. The star indicates Fraser Ridge Reef, one of the areas of study in this thesis. Maps were produced using ArcGIS from shapefiles provided by Fisheries and Oceans Canada.

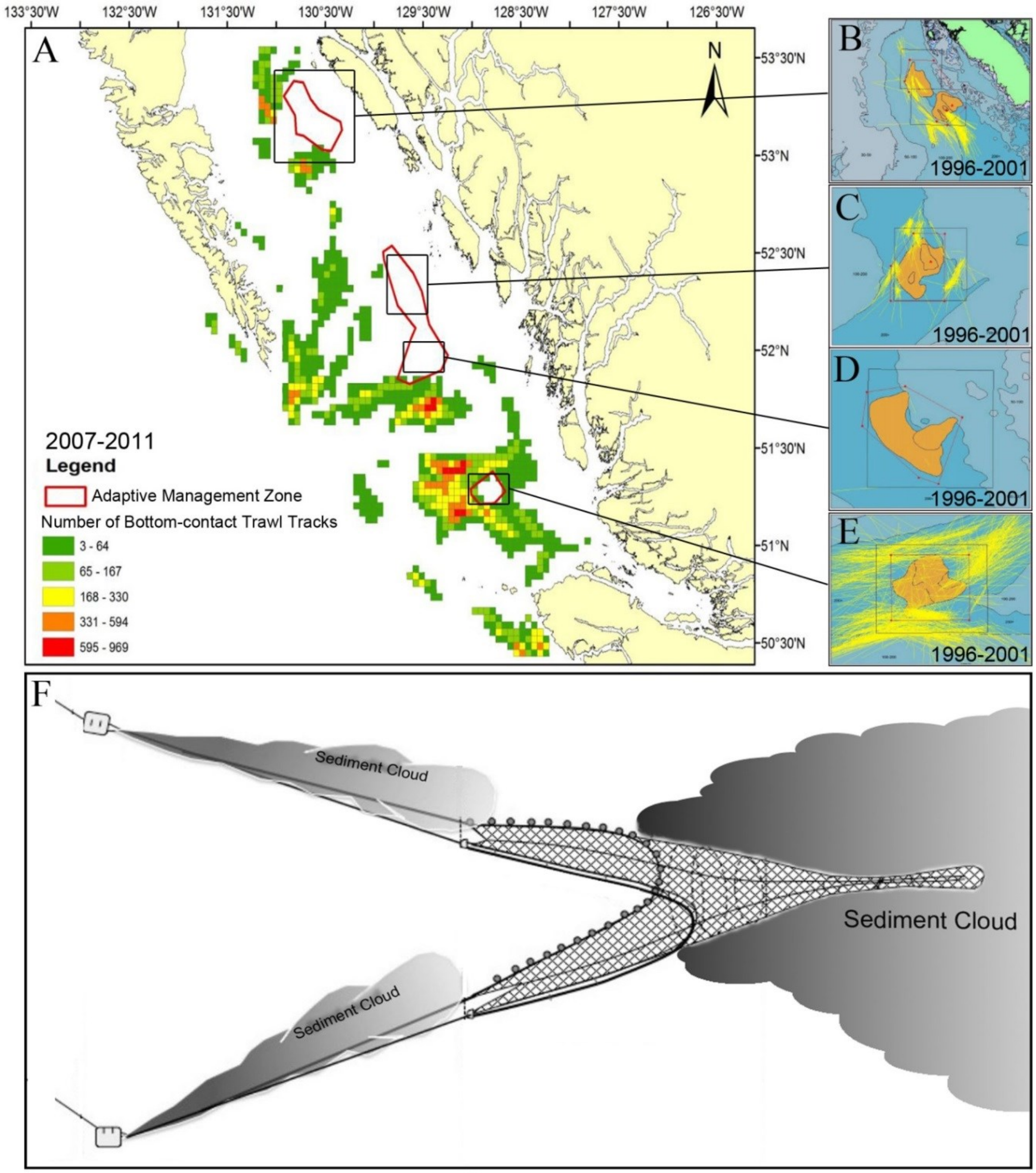

Figure 1-4: Bottom-contact trawl fishing on the four reef complexes that make-up the Hecate Strait and Queen Charlotte Sound Glass Sponge Reef Marine Protected Area. (A) The number of bottom contact trawls that occurred within Hecate Strait during 2007-2011, a time when sponge reefs were protected through voluntary fishing closures. Adapted from Figure 6 Boutillier et al. (2013). (B-E) Trawl tracks (yellow lines) on each reef complex that occurred prior to the establishment of any protective planning. Fishing closures for groundfish (red boxes) and shrimp trawls (black boxes) began in 2002. Adapted from Figures 7-10 Jamieson and Chew (2002). (C) Diagram of how a bottom-contact trawl suspends sediment into the water column. Adapted from Figure 3 He (2015).

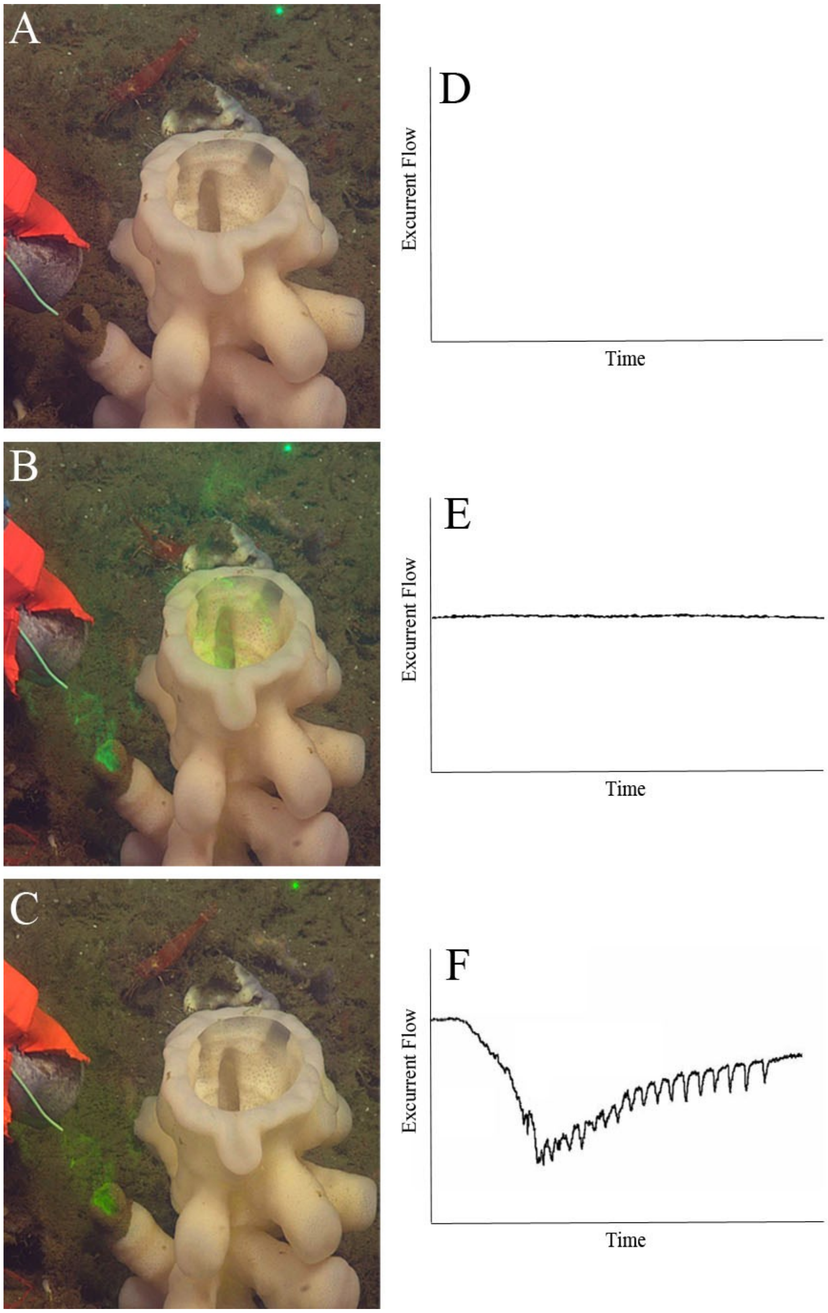

Figure 1-5: The pumping activity of *H. calyx* and a demonstration of arrested filtration using fluorescein dye. (A) *H. calyx* prior to fluorescein addition. (B) Fluorescein is being drawn through the body wall and travelling out the osculum indicating that the sponge is actively pumping. (C) The lack of fluorescein dye coming out of the osculum simulates an arrest of the excurrent flow out of the sponge. (D) No flow being recorded from a sponge. (E) Steady pumping activity (sponge in undisturbed conditions) is approximated by the flat line of the flow record. (F) An arrest of filtration followed by a recovery of pumping activity as it would be observed in a flow record. (B, D, F) Graphs do not represent recordings from this sponge and are redrawn from Figure 5D Tompkins-MacDonald and Leys (2008) as examples of how arrests appear within flow records.

Chapter 2. Suspended sediment causes feeding current arrests *in situ* in the glass sponge *Aphrocallistes vastus*[1]

2.1 Introduction

Bottom trawling equipment has been damaging deep-water benthic habitats since its inception (Grant 1826, Malecha and Heifetz 2017). Direct impacts such as physical damage to substrates and the resulting declines in local density and diversity of benthic biota are often highlighted (e.g., Tuck et al. 1998, Althaus et al. 2009). Less has been said about the effect of suspended sediments, which are one product of bottom trawling on benthic habitats (Puig et al. 2012). So many animals are affected by increased suspended sediment concentrations (SSCs) that Newcombe and MacDonald (1991) suggested sediment should be considered an environmental contaminant. In particular, for non-motile benthic animals such as corals and sponges, the impacts of suspended sediments can be extensive and include declines in growth, respiration and feeding, and increased mortality rates (Rogers 1983, Miller and Cruise 1995, Bell et al. 2015a).

As filter feeders, sponges are particularly susceptible to variations in SSCs. Sponges feed by pumping water through their bodies, filtering up to 900 times their body volume each hour (Reiswig 1971a, Kahn et al. 2015). Suspended sediments that are pumped through the aquiferous system of a sponge could clog or damage their flagellated chambers and canals. Larger grains could even block the 20 µm diameter incurrent openings (Kilian 1952, Maldonado et al. 2008, Leys 2013).

Sponges are a diverse phylum and have different behavioural responses to increased SSCs. Many demosponges contract to expel particles from their aquiferous system (Storr 1976, Elliott and Leys 2007). Peristaltic-like contractions travel across the sponge's tissues causing a sneeze-like response which can force water, sediments and unwanted particles out of and away from the sponge (Elliott and Leys 2007). Glass sponges (class Hexactinellida) show a different

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response to undesirable particles in the water in that they temporarily arrest their pumping activity (Leys et al. 1999). The arrests are triggered by electrical signals that travel across the syncytial tissues of the whole sponge shutting down the flagella pumps (Leys and Mackie 1997, Leys et al. 1999). Arrests are thought to be protective, but they also limit the total time available for feeding (Tompkins-MacDonald and Leys 2008). Given that sponges pump continuously to feed and excrete wastes, reductions in the volume of water filtered are expected to have negative effects on metabolism and health.

Until recently, field-based studies on the effect of suspended sediments on sponges were limited to shallow, tropical species, with a focus on demosponges. Early work showed that the pumping rate of *Aplysina lacunosa* (formerly *Verongia lacunosa*), a Caribbean demosponge found at 14 m depths, decreased in response to suspended clay applied *in situ* (Gerrodette and Flechsig 1979). More recently, Bannister et al. (2007) studied two demosponge species on the Great Barrier Reef that are adapted to differing levels of suspended sediments. Whereas *Coscinoderma* sp. was found to be fairly tolerant of sediment, *Rhopaleoides odorabile* was more sensitive to sediment. Because of the variable sediment regime across the Great Barrier Reef, these species were determined to have become adapted to habitat ranges that are, in part, limited by SSCs. Bannister et al. (2007) suggested that exposure beyond their native sediment regimes would result in reduced survival.

Less is known about the response of deep-water sponges to increased SSC because they are more difficult to observe than shallow-water sponges. However, increased use of remotely operated vehicles has allowed specimens to be brought from depth for laboratory experiments. *Geodia barretti*, a demosponge found throughout the northern Atlantic, has been the focus of recent studies examining the effect of suspended sediment, mine tailings and drilling muds on benthic organisms. Kutti et al. (2015) found that oxygen consumption was reduced with both acute and long-term exposure to these types of industrial sediments, while another study found that drilling muds can have toxic effects on *G. barretti* (Edge et al. 2016). Both studies recommended that the effect of suspended particles on habitats dominated by sponges should be considered when designating marine protected areas. *G. barretti* is a highly abundant species (Kutti et al. 2013) yet remains a secondary concern in protection efforts throughout the north Atlantic. The primary focus of policy makers tends to be the accompanying ecosystem, primarily cold-water corals and fishing grounds (Davies et al. 2007). The high abundance yet low protection concern of *G. barretti* is in stark contrast to the deep-water reef-building hexactinellid sponges found in northeastern Pacific, which are of primary concern for protection in Canada.

Glass sponges (class Hexactinellida) are found worldwide in deep cold water. As few glass sponge populations occur shallower than 40 m (Vacelet et al. 1994, McClintock et al. 2005) they are difficult to reach by SCUBA, and most are studied by submersible or remotely operated vehicle (ROV). Glass sponges are often found on steep rocky substrates where little suspended sediment settles; fewer glass sponges occupy flat shelves (Farrow et al. 1983, Maldonado and Young 1996). However, on the northwestern coast of North America, from British Columbia, Canada to Alaska, USA, glass sponges form the only known sponge reefs on the rocky outcroppings of the muddy continental shelf at depths of approximately 80 - 200 m (Conway et al. 2001, Krautter et al. 2001). The reefs are composed of glass skeletons that have been cemented together by sediments over the last 6000 - 9000 years (Conway et al. 1991). Three species form the reefs, *Aphrocallistes vastus, Heterochone calyx,* and *Farrea occa*, and in Queen Charlotte Sound and Hecate Strait, British Columbia, they cover 100s of kilometers of seafloor (Krautter et al. 2001, Conway et al. 2007).

With such expansive coverage and density of pumping units, sponge reefs are estimated to filter up to 6 billion liters of water per hour, altering regional water content (Kahn et al. 2015). While they recycle carbon and nitrogen in the water column, glass sponge reefs also provide a complex habitat for fish and invertebrate species, some of which are commercially important (Cook et al. 2008, Chu and Leys 2010). This has attracted bottom-contact trawling which has caused visible damage throughout the reefs (Conway et al. 1991, Conway et al. 2001). In response to this, and taking their ecological importance and endemic nature into account, in February 2017 Fisheries and Oceans Canada established a 2410 km^2 region as a Marine Protected Area (MPA) for the protection of glass sponge reefs in Hecate Strait and Queen Charlotte Sound (Fisheries and Oceans Canada 2017c). Additionally, there are closures to bottom-contact fisheries in the Strait of Georgia and Howe Sound, British Columbia, Canada, but neither these, nor the MPA, provide protection against influences directly adjacent to the reefs such as sediments resuspended via trawling (Fisheries and Oceans Canada 2016). Understanding the effect that increased SSCs have on glass sponges is crucial for determining whether the present boundaries provide adequate protection to the reefs and this will be important to know for designating future MPA boundaries.

We carried out experiments at a sponge reef in the Strait of Georgia, Canada, to determine whether suspended sediments affect glass sponge pumping and filtration. We describe arrests of filtration *in situ*, examine the relationship of arrests to increased SSCs, and compare arrest behaviours seen *in situ* with those reported from previous laboratory studies.

2.2 Methods

2.2.1 Study Area

This study was carried out at 170 m depth at the Fraser Ridge glass sponge reef in the Strait of Georgia, Canada during two cruises in November 2014 and October 2015 aboard the Canadian Coast Guard Ships *CCGS Vector* and *CCGS JP Tully* (Figure 2-1A). The remotely operated vehicle (ROV) ROPOS (http://ropos.com) carried out five dives in 2014 and four in 2015. The principal reef-building sponge species in this area, *Aphrocallistes vastus*, was the target of this study. An attempt was made to place instruments at the same location each year to reduce variability between years and orientations of sponges on the reef (49° 09′22.9″N 123° 22″57.4″W (2014), 49° 09′23.0″N 123° 22′56.8″W (2015)).

2.2.2 In situ Recordings

We used custom-built thermistor-flowmeters (referred to hereafter as ‘thermistors’ or ‘flowmeters’) to record excurrent flow from the sponges. Thermistors were used because they provide constant point velocity measures (LaBarbera and Vogel 1976, Vogel 1977). The thermistors were calibrated *in situ* in undisturbed ambient flow using an acoustic Doppler velocimeter (Vector ADV, Nortek, Rud, Norway) for three calibration periods totaling 5 hrs for each flowmeter. The thermistors had two measuring probes, one for ambient flow and one for the excurrent flow from a sponge. Thermistors were placed adjacent to sponges and the excurrent probes positioned by ROPOS directly into the sponge osculum (Figure 2-1B) such that the probe was completely in the osculum and did not touch the wall of the sponge (Figure 2-1C). An ‘Aquadopp’ acoustic Doppler current profiler (ADCP, Nortek, Rud, Norway) was placed 17 m upstream of the thermistors (Figure 1a). An optical backscatter sensor (OBS, Campbell Scientific, Edmonton, Canada), paired with the Aquadopp, quantified suspended sediment concentrations (SSCs). Once the thermistors were in position, the ROV left the area. During November 2014, thermistors recorded the excurrent flows of two sponges and the area was disturbed as little as possible to record a baseline of their natural pumping cycles. In 2015, experimental sediment disturbances were created by ROPOS near the Aquadopp (Figure 2-2), allowing the plume of sediment to flow over three thermistor-paired sponges. However, two thermistors were not positioned correctly or recorded poorly and were not used in the final analysis. Thus, in 2015 excurrent flow from a single sponge was recorded and related to multiple experimental sediment disturbances.

2.2.3 Data Analysis

Thermistors recorded onto Omega data loggers (Laval, Canada) as voltage, which was converted to cm s^{-1} using the calibrations made with the Vector ADV. Both the Vector and ADCP recorded velocity in m s^{-1}, and the latter was compass calibrated to provide flow direction relative to North. OBS data recorded SSCs as counts and was converted to mg l^{-1} using calibrations carried out in the lab at the University of Alberta. For calibrations, sediment was collected using core tubes on the ROV from Fraser Ridge, frozen and transported to the University of Alberta. A calibration curve was generated from the absorbance of a serial dilution of a stock solution measured using a Beckman Coulter (UV/VIS) spectrophotometer. In a tank circulated by an aquarium pump, the OBS recorded in counts during consistent additions of a sediment solution. Samples (15 ml, n = 10) were collected at each sediment addition; the absorbance of those samples was measured, and sediment concentration was calculated using the calibration curve. This process was repeated twice, and the resulting equation was determined as SSC = 0.0358*OBS counts + 0.1542 ($R^2 = 0.99$). Periods when ROPOS was handling the instruments, disturbing the flow or was within the immediate vicinity of the experiment were annotated during the dive via notes in the Integrated Real Time Logging Software (IRLS), and excluded from analysis.

Arrest responses were identified by a decrease in excurrent velocity (the arrest phase) followed by a return to normal excurrent velocity (the recovery phase) (Figure 2-3A, C). Normal excurrent flow can be defined as the excurrent velocity measured during periods of uninterrupted pumping. The boundary between the arrest and recovery phase is when the excurrent flow reaches the lowest velocity in the arrest. Arrests of sponge filtration were isolated in flow records first manually and subsequently by comparing the point-to-point variation across the flow record. This allowed us to narrow the manual inspections to periods in the record where reductions in excurrent flow were greater than 1.0 cm s^{-1} and lasted longer than 30 s, indicating possible arrest of filtration. We used the following criteria to identify arrests within these periods: a reduction of > 1.0 cm s^{-1} in excurrent velocity with no concurrent reduction in ambient flow; an arrest phase lasting > 30 s, and a staggered or stepwise return to normal excurrent flow taking more than 1 min. This was differentiated from small variations in the record caused by local turbulence by smoothing the data with 10 s medians. The method described above was based on criteria derived from descriptions of recordings by Mackie et al. (1983) and Tompkins-MacDonald and Leys (2008). All arrest behaviours were confirmed by visual inspections of the data. This conservative approach ensured that the decline in excurrent flow represented a sudden and complete arrest of sponge pumping and not random variations of flow due to small scale turbulence.

After confirming an arrest of the feeding current had occurred, the behaviours were separated by the length of the arrest phase. Through this separation two types of arrests were described, 'single' and 'coughing' arrests. Arrest phases lasting < 5 min were called single arrests as they showed a shorter recovery phase. Several of these could occur in succession. The second type of response, 'coughing', involved prolonged behaviours, with arrest phases lasting > 5 min (Figure 2-3B, D). The clear defining feature of a coughing response was the prolonged recovery phase with an inconsistent rate of increase (or return to normal filtration levels).

Recordings of arrest behaviours were paired with the Aquadopp current profiler and OBS records. Changes in SSCs and excurrent flow were compared using Pearson's correlation coefficients during each phase of all arrest responses. Tidal cycles during those periods were downloaded from Fisheries and Oceans Canada's observed tidal records for Vancouver, B.C. (http://www.pac.dfo-mpo.gc.ca/science/charts-cartes/obs-app/observed-eng.aspx?StationID=07735). Tidal cycles were included in a separate correlation to determine whether increased ambient flow affected natural SSC.

2.3 Results

2.3.1 Arrests of Sponge Filtration

A total of 23 arrests of filtration (19 single and 4 coughing, Figure 2-3, Table 2-1) were identified in 29 hrs of excurrent recordings from a single sponge The single arrests identified during this study lasted 2 - 5.5 min (4.25 ± 1.3 min (mean ± SD), n = 19) with arrest phases measuring 0.5 - 3 min (1.91 ± 0.96 min, n = 19) and recovery phases of length 1 - 4 min (2.34 ± 0.62 min, n = 19). The rate of change of the arrest phase ranged from -0.007 to -0.056 s^{-1}. The four coughing arrests occurred when concentrations of sediment in the water column did not dissipate. The coughing responses were highly variable, lasting 11 - 54 min (31 ± 22.89 min, n = 4). Arrest phases averaged 4 - 15 min (10.46 ± 5.26 min, n = 4) while recovery phases lasted 6 - 40 min (20.54 ± 18 min, n = 4). The maximum rate of change for the arrest phase during a coughing response was -0.01 s^{-1} while the minimum rate of change was -0.0002 s^{-1}.

2.3.2 Relationship between Arrests and Sediment

Of the 23 arrests that were identified in the 2015 experiment, 14 arrests of filtration were correlated with increased SSC (r = -0.83 to -0.92) (Figure 2-4). In contrast, the periods of excurrent flow before the arrest, comparable in duration to the arrest phase, showed no correlation with SSC (r = -0.49 to 0.75) (Figure 2-4). Five arrests occurred outside of the OBS recordings and were therefore not analyzed for correlation with SSC. Of the remaining 18 arrests, 14 differed significantly from the pre-arrest flow as determined by a Fisher's r-to-z transformation followed by two-tailed independent group test ($p < 0.05$). The final four were not correlated with changes in SSC and were consistent with the spontaneous arrests defined in Tompkins-MacDonald and Leys (2008). The 23 arrests occurred under comparable conditions to those observed in a laboratory study (Tompkins-MacDonald and Leys 2008); the arrest responses seen in 2015 occurred between SSCs of 10 to 80 mg l^{-1}, whereas arrests occurred in the laboratory study at 36 mg l^{-1}.

Recordings in 2014 from sponges that were not disturbed showed three single arrest responses and two coughing events over 39 hrs (Table 2-1). The onset of two single arrests coincided with the start of high tide; a third arrest occurred during the transition period from high tide to low tide (Figure 2-5B). The coughing events occurred during periods of higher tidal flow (Figure 2-5B). For two of the single arrests, the excurrent flow record during the arrest phases was negatively correlated with increases in suspended sediment (r = -0.86 and -0.89) ($p < 0.05$). This was not the case for the two coughing responses, which were not correlated with SSC.

2.3.3 Natural Sediment Resuspension

The changes in SSCs recorded during 2014 roughly corresponded to the tidal cycle, indicating that the tides can increase the suspended sediment at the sponge reefs (Figure 2-6A). The concentration of suspended sediment at Fraser Ridge reef, between tides, was 4.4 mg l^{-1} (± 0.7 mg l^{-1}). Tidal resuspension in 2014 generated a slight increase in suspended sediments to 5.3 mg l^{-1} (± 0.9 mg l^{-1}), but levels did not reach the 10 to > 40 mg l^{-1} generated by our experiments. Periods of increased and decreased SSC were correlated with high and low tides, respectively ($r = 0.8 - 0.99$), and lasted for up to 50 min in 2014. The experimental recording from 2015 showed arrests across high and low tides, following no tidal pattern (Figure 2-6B). No correlation was found between tide and SSC in 2015. The strength of the tides was noted for each year with greater tidal fluxes occurring in 2014.

2.4 Discussion

This study provides the first evidence that glass sponges arrest their feeding currents in response to experimentally increased SSC *in situ*. Furthermore, the arrest behaviours we recorded *in situ* from reef-building sponges are comparable to those reported by Tompkins-MacDonald and Leys (2008) in tank studies. The arrests in sponge feeding current are significantly correlated with increases in suspended sediment concentration (SSC) (Figure 2-4). This study only aimed to assess the effect of increased SSC on feeding currents, the arrests of which are thought to protect the sponge filter from damage. It was not possible to study the prolonged effect of sediment on these sponges *in situ* at the reefs.

2.4.1 Arrest Behaviours

In 2014 the sponges' excurrent flow was recorded for 39 hrs without disturbance; that period included a full tidal cycle. Higher tidal flows were found to increase SSCs to a limited degree: over 39 hrs, four out of five arrests coincided with increases in tidal flow. In contrast, the experimental conditions generated in 2015 induced frequent arrest behaviours as well as multiple longer coughing responses (Figure 2-5A). The frequency of arrests in 2014, five total over 39 hrs, indicates that they are not a common behaviour, often only being triggered when necessary to prevent potential harm from tidally suspended sediments (Figure 2-5B). In contrast, the 2015 tidal cycle had no correlation with SSC or when arrest behaviours occurred. Instead, arrests occurred primarily during times of experimentally increased SSC indicating that suspended sediments trigger arrest behaviours *in situ*. The majority of arrests, across both years, were correlated with sediment resuspension and tidal flow. Overall, few arrests were not correlated with experimental or tidal resuspension. Previous studies have shown that arrests can be induced by mechanical stimuli in addition to suspended sediments (e.g., Mackie et al. 1983, Tompkins-MacDonald and Leys 2008). The few arrests that were independent of increased SSC in this study could have been due to mechanical stimuli such as contact with fish.

Arrests are presumed to be protective behaviours that reduce the risk of damage caused by suspended sediments, but arrests of filtration result in reduced feeding by the sponge. Many sponge species have multiple ways to generate energy (e.g., via phototrophic or chemotrophic microbial symbionts), and for those species continuous filtration may not be as necessary for capturing heterotrophic bacteria for food as it is in *A. vastus* (Leys et al. 2011). *Aphrocallistes vastus* gains all its energy from filtering heterotrophic bacteria from ambient water (Yahel et al. 2007); therefore, time spent filtering water is crucial for its health. The majority of this feeding, up to two thirds, occurs during flood tide at the reef (Leys et al. 2011). Leys (2013) estimated that if arrests are triggered during periods of increased ambient flow there would be a 30% reduction in daily food intake. We found that during arrests, the excurrent flow was reduced by 70% but was variable. SSC levels at the sponge averaged 40 mg l^{-1}during a disturbance (range 10 - 80 mg l^{-1}). During a 1.5 hr sediment disturbance event, the sponge filtration was arrested for 56% of the time, including one coughing and two single arrests.

To gauge the effect of arrest behaviours on the sponge energetics, we estimated the loss of carbon uptake by *A. vastus* that results from arrest behaviours. Using measurements reported by Kahn et al. (2015), we calculate that a single sponge ingests 16.20 µg or 1.34 µMol carbon per liter pumped (from Table 2, Kahn et al. (2015); 3.4 g C m^{-2} d^{-1} consumed from 210 m^3 m^{-2} d^{-1} of water filtered). Whereas a sponge osculum would normally filter 763 µMol of carbon in 1.5 hr (from Table 2, Kahn et al. (2015)), a 1.5 hr sediment disturbance would lead to a loss of 70% or 534 µMol carbon per osculum. It is hard to estimate the true loss in energy because a concurrent reduction in the amount of energy expended by pumping would also occur. However, because *A. vastus* has a balanced daily energy budget, this substantial loss of food energy for every non-tidally induced sediment disturbance is expected to negatively influence the health of a sponge. This estimate does not account for any additional potential metabolic costs associated with removing sediment, for example by production of mucus. Mucus production by demosponges in response to sedimentation has also been noted where sediment is high (Turon et al. 1999, Bannister et al. 2012). The production and replacement of mucus due to sloughing may be energetically costly (Bell et al. 2015a, McGrath et al. 2017). A study on phototrophic and heterotrophic demosponges has shown decreased survival and energy reserves and increased necrosis for sponge exposed to suspended sediments for 28 days (Pineda et al. 2017). If the same applies to glass sponges, then a reduction in feeding caused by continually resuspended sediments will have negative consequences on the health of reef-building glass sponges. As trawling transects are rarely individual events, but occur multiple times in succession (Puig et al. 2012), the reduced feeding would be compounded over each pass of the trawling equipment.

2.4.2 Trawling-Induced Suspended Sediments

Deep-water hexactinellid sponge reefs are not typically exposed to large volumes of suspended sediments naturally and so trawling, which has become a common practice in seafloor ecosystems, is a primary concern. Estimates of resuspension by trawling activities vary with the grain size and trawling equipment used. Mengual et al. (2016), using bottom otter trawls, recorded SSCs as high as 200 mg l^{-1} behind what they termed a ‘classical’ trawl (two Thyboron doors in constant contact with the seabed). An ‘alternative’ trawl using Jumper doors (having intermittent contact with the seabed) generated an average of 20 mg l^{-1} SSC but reached peaks of 110 mg l^{-1}. Shrimp trawls have generated SSCs of 100 - 550 mg l^{-1} (Churchill 1989). Using a bottom trawl with "rockhopper" gear, Durrieu De Madron et al. (2005) recorded maximum SSCs between 150 and 300 mg l^{-1} behind the path of the trawl. The turbidity of 10 - 80 mg l^{-1} we recorded during arrest behaviour of the glass sponges was a magnitude higher than the normal conditions found at Fraser Ridge reef of 4.4 mg l^{-1}, yet those levels did not reach SSCs which can be generated by trawling activities. If the SSCs at Fraser Ridge reef were to reach the levels generated by trawling activities, our data suggests that the sponge’s arrests and coughing behaviours would become frequent if not incessant, and smothering would be likely.

The deposition rate of sediment in a plume is an important factor that influences how long the animals are exposed to sediment. Grain size and current velocity are two primary factors determining deposition rates of suspended sediments (Pilskaln et al. 1998, Puig et al. 2012, Mengual et al. 2016). SSCs can remain elevated for an hour to 5 days after initial trawls in some instances, the time they remain in suspension increasing as grain size decreases and decreasing as current velocity increases (Churchill 1989, Palanques et al. 2001). The sponges we recorded filtration behaviour from at the Fraser Ridge reef were exposed for a short time. The longest duration of elevated SSCs was ~ 80 min, yet we still saw multiple coughing responses. As exposure times increase, arrest behaviours become more frequent and total time available to feed and respire decreases (Tompkins-MacDonald and Leys 2008). Grain sizes of sediments that remain in suspension at the Fraser Ridge reef are not known. However, the highest frequency of arrests occurred during the lower range of ambient flows, which happen at the change of tidal flow, and this may have caused the suspended sediment plume to remain around the sponges.

The size of the sediment plume caused by a trawl is also highly variable. The size and type of the equipment used as well as grain size influence the resulting cloud of resuspended particles. Plume size can determine the amount of sediment suspended and the maximum resuspension height influences how far particles will travel before settlement (Churchill 1989). Transit distances of suspended sediments within the Strait of Georgia vary between 45 m to a few kilometers (Hill et al. 2008). Measurements of trawl plume sizes vary from 2 - 10 m high and as wide as 200 m from the central trawl line (Durrieu De Madron et al. 2005, Mengual et al. 2016). This greatly increases the likelihood that the glass sponge reefs can be exposed to trawl-induced suspended sediments even when trawling activities are not immediately adjacent to the reefs.

The residence time and size of the plume are not the only ways that grain size affects reef sponges. Variable grain sizes can have differing effects on a sponge. Smaller grain sizes (< 20 µm) can be inhaled through ostia, damaging the sponges internally while larger grain sizes clog and smother the sponges (Tompkins-MacDonald and Leys 2008, Leys 2013). Sediments at Fraser Ridge reef include sand and clays (2 - 2000 µm) (Thomson 1981a, Whitney et al. 2005). The large variation in grain size means that sponges at Fraser Ridge reef must face sediment induced damage, clogging and smothering from large plumes with long resident times, even when trawling does not physically touch the reef. With so many potential effects, the need for appropriate protection is clear.

2.4.3 Management Implications

The immediate response to potential damage by trawling to the Hecate Strait and Queen Charlotte Sound glass sponge reefs has been legislation creating a Marine Protection Area surrounding the reefs. As of 2017, the MPA boundaries are divided into a core protection zone (CPZ) and an adaptive management zone (AMZ) (Fisheries and Oceans Canada 2017c). The AMZ for the Hecate Strait reefs varies from 0.6 to 1.6 km in breadth. According to data obtained by trawling experiments (e.g., Mengual et al., 2016), sediments generated by trawling activity can be transported across this distance. This means that the glass sponge reefs in the CPZ could be impacted by activities that may suspend sediments outside of the AMZ. This should be confirmed before future MPA designations are made. The Fraser Ridge reef is closed to bottom-contact fishing (Fisheries and Oceans Canada 2016) but the existing 150 m buffer region may not provide a large enough buffer to protect the sponges from the transport of suspended sediments onto the reef.

Distinct sponge reefs may be affected differently depending on species, local environmental conditions, fishing pressures and industrial activities present in the vicinity of each reef. For example the waters of Fraser Ridge reef are considered siliciclastic compared to those of Hecate Strait (Conway et al. 2007), and therefore more sediment is resuspended tidally than at Hecate Strait. While early descriptions of sponge reefs noted large areas of damaged reefs caused by direct contact with trawling equipment (Conway et al. 1991, Krautter et al. 2001), trap fishing has become more commonplace in the Strait of Georgia (Fisheries and Oceans Canada 2017d). Little work has been done on the sediment resuspension caused by trap fishing gear and so quantifying this will be important to keep protective legislation up-to-date. Additionally, laying undersea cables and resource exploration are other activities that should be considered for their direct mortality effects and resuspension ability (Dunham et al. 2015). Dunham et al. (2015) showed 100% mortality under the direct path of marine power transmission cables and 15% mortality in areas adjacent to the cables, 3.5 years after installation. Should an AMZ be designated for any MPAs chosen to protect glass sponge reefs, species-specific tolerances to suspended sediments, the distance from the reef, type of resuspension activity and equipment used, and the local current regime should all be considered.

2.5 Conclusion

The arrests of sponge filtration we recorded from *A. vastus* on the Fraser Ridge glass sponge reef were consistent with those previously recorded in laboratory studies. Arrests occur occasionally under natural conditions but much more frequently when sediment concentrations in the water column are elevated. The arrests noted here were highly correlated with increased concentrations of suspended sediments even though experimentally generated concentrations of resuspended sediments did not reach the levels known to be generated by trawling activities. We contend that the arrest behaviours likely place *A. vastus* in an energetic deficit after a sediment disturbance. Glass sponge reefs provide a habitat that supports commercially important species, such as fish. Efforts to extract the fish may incidentally damage sponges either with direct contact or indirectly via sediment deposition. Safeguarding sponges from activities that increase suspended sediment should be a priority when determining protective buffer zones around glass sponge reefs and potentially also around other sponge grounds.

Table 2-1: Kinetics of single and coughing arrests of filtration from recordings showing the length and rates of arrest and recovery phases. Figure 2-3 shows examples of response types and phases of the arrest.

Type of Response	Year	Total Number	Length (min) (mean ± SD)			Rate (s^{-1})	
			Arrest Phase	Recovery Phase	Total	Arrest Phase	Recovery Phase
Single Arrest	2015	19	0.5 – 3 (1.91 ± 0.96)	1 – 4 (2.34 ± 0.62)	2 – 5.5 (4.25 ± 1.3)	-0.0 – -0.06	≤ 0.01 – 0.04
	2014	3	0.98 – 1.9 (1.53 ± 0.4)	2.1 – 6.45 (3.78 ± 1.91)	3 – 8.3 (5.3 ± 2.2)	-0.03 – -0.09	0.02 – 0.05
Coughing Arrest	2015	4	4 – 15 (10.46 ± 5.26)	6 – 40 (20.54 ± 18)	11 – 54 (31 ± 22.89)	≤ -0.01	< 0.01
	2014	2	9 – 23 (16.1 ± 7.4)	19 – 69 (43.8 ± 25.1)	19 – 69 (43.8 ± 25.1)	≤ -0.02	< 0.01

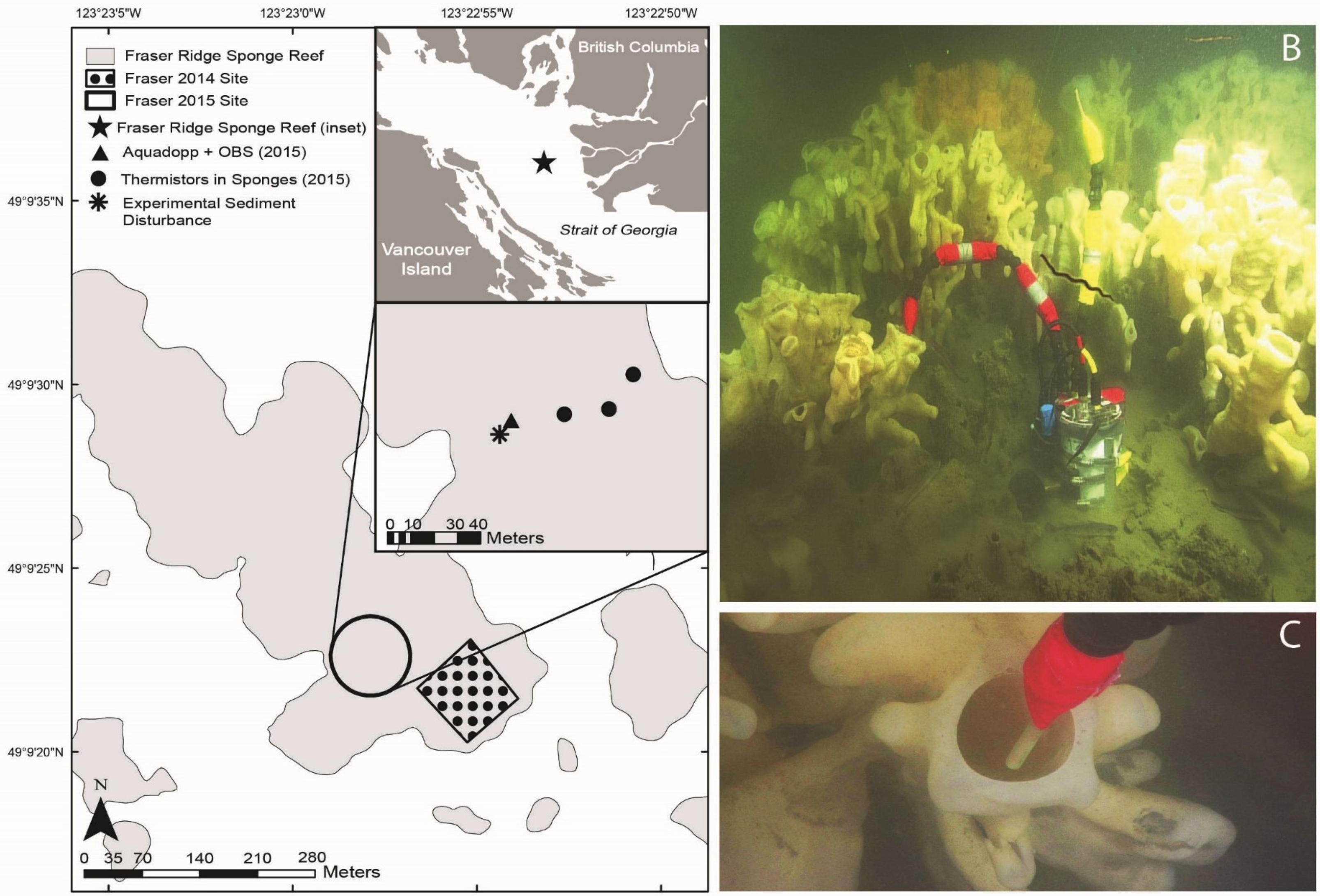

Figure 2-1: Map of the 2014 and 2015 research sites located on Fraser Ridge reef, Strait of Georgia (A). (B) A thermistor-flowmeter positioned in the osculum of *Aphrocallistes vastus*. (C) View of the tip of the thermistor probe inserted into osculum of *A. vastus*.

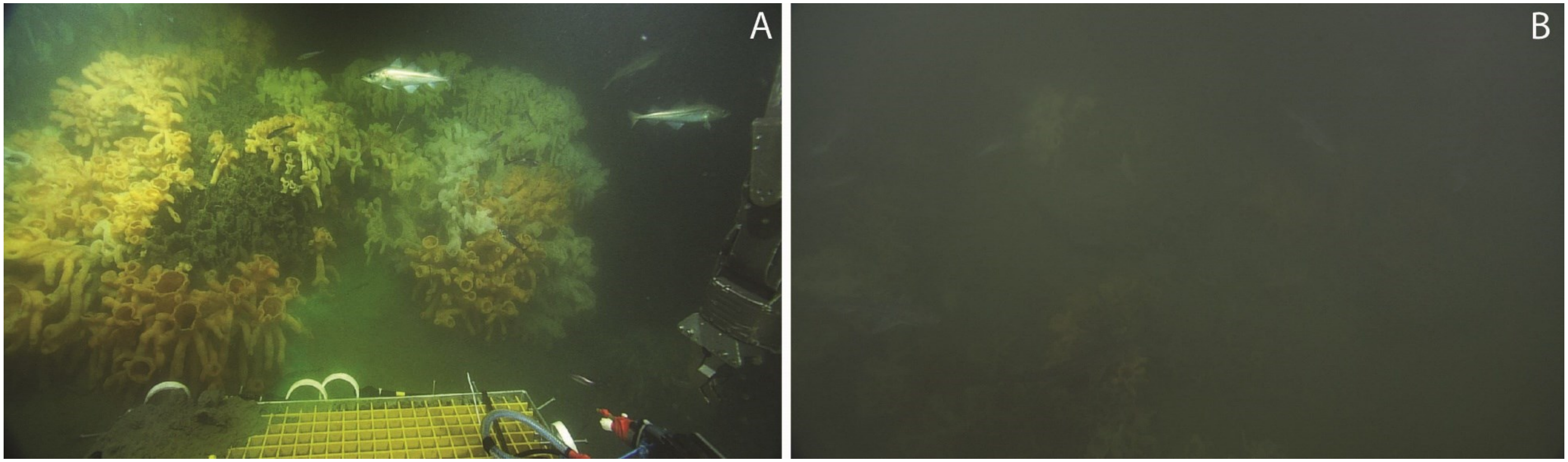

Figure 2-2: View of sponge reef before (A) and after (B) an experimental sediment resuspension event created using ROPOS

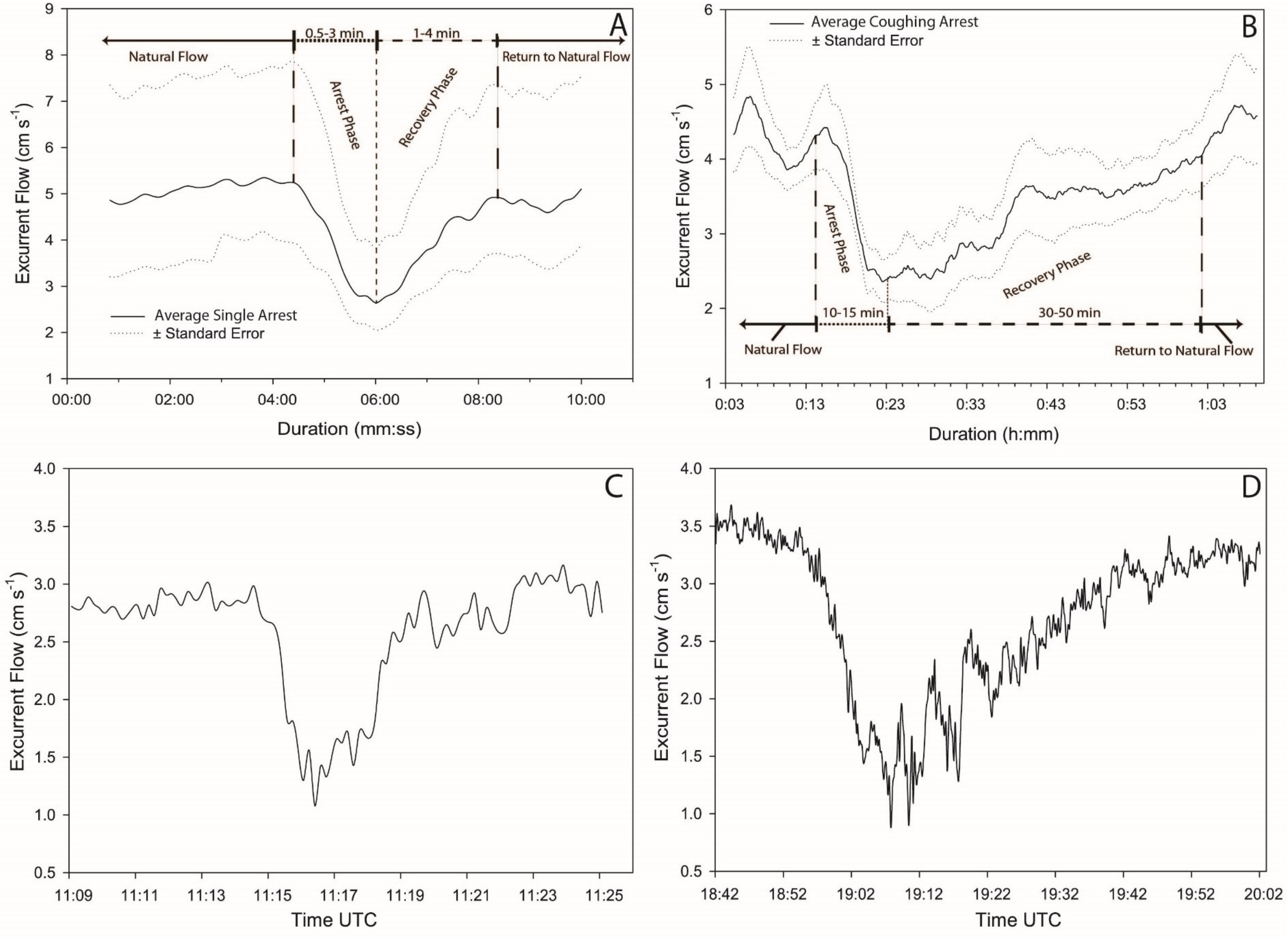

Figure 2-3: Descriptive characteristics of a single and coughing arrest of the feeding current of *A. vastus*. (A) The average profile of a typical single arrest of the feeding current (mean +/- SD, n = 18), and (C) an actual single arrest. (B) The average profile of a typical coughing arrest (n = 4) and (D) an actual coughing arrest. The kinetics of each arrest type is provided in Table 1.

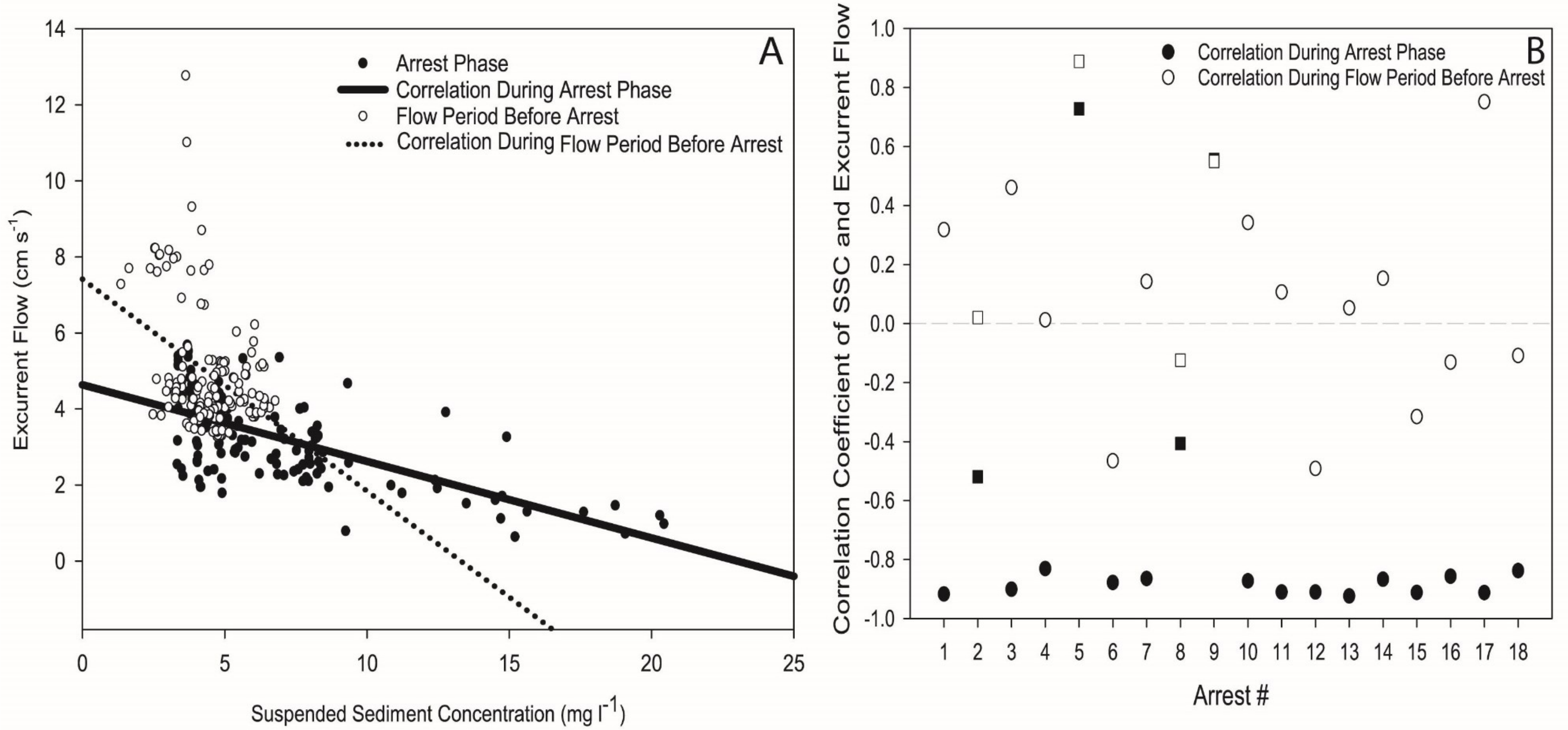

Figure 2-4: The correlation between the onset of the arrest and increases in SSC. (A) Prior to the arrest phase, there is no discernible relationship between excurrent flow and SSC (white) (r = -0.38). During the arrest phase (black), there is a negative relationship between SSC and excurrent flow (r = -0.66). (B) Correlation coefficients of SSC and excurrent flow during the arrest phase and natural flow periods for each individual arrest. Strong negative correlations indicate that excurrent flow decreases with increasing SSC. Circles represent those arrests where the correlation during the arrest phase was significant and squares represent spontaneous arrests that were not correlated with suspended sediments.

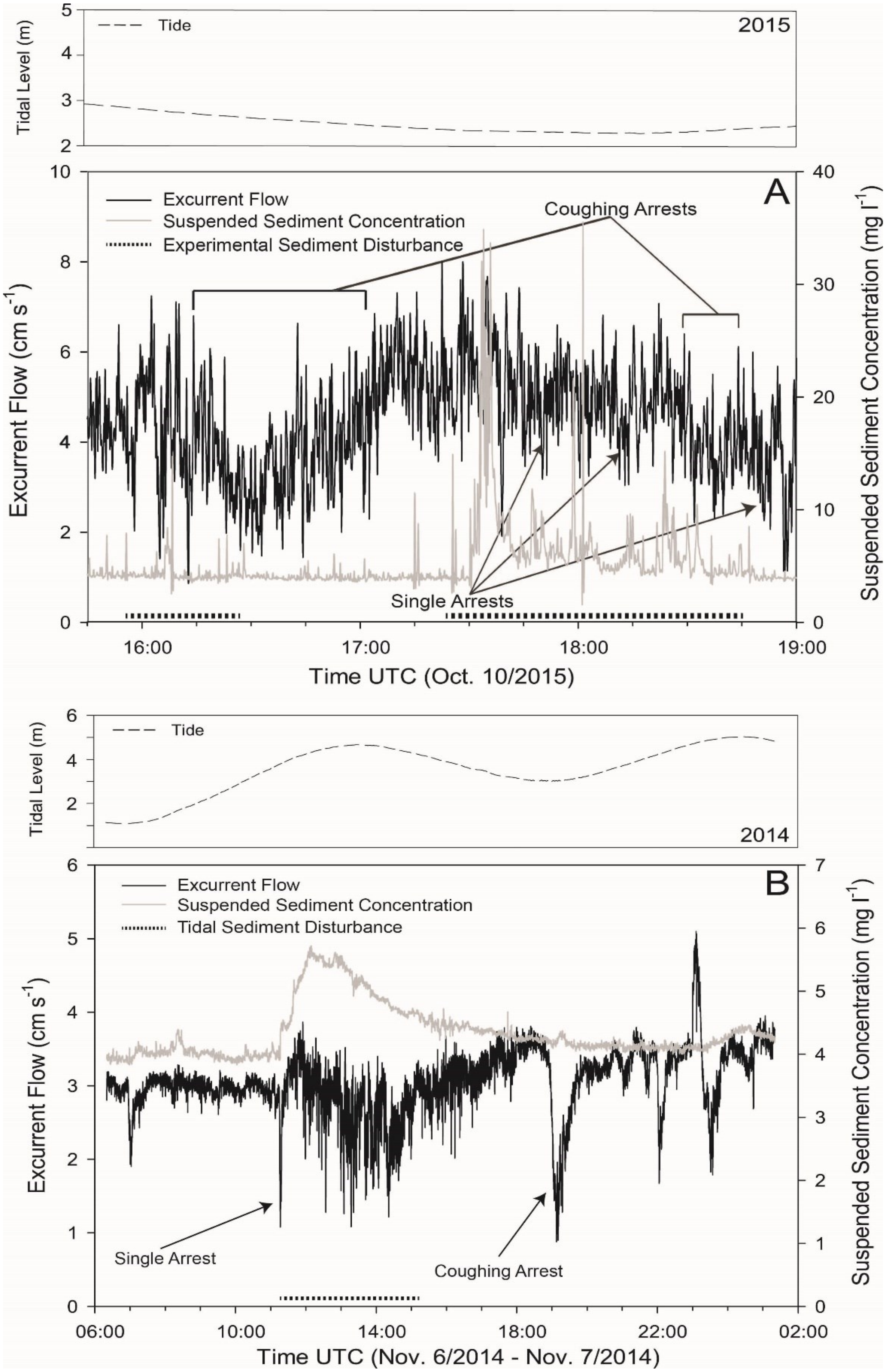

Figure 2-5: A record of filtration behaviour and arrests of filtration within *A. vastus*. (A) Arrests in filtration seen in the excurrent flow recording from a single sponge in 2015 occurred across a range of SSCs (from 10 to 80 mg l-1). (B) A recording from a sponge in 2014 shows both single and coughing arrests occurred during small tidal resuspensions ~5 mg l-1. The frequency of both single and coughing arrests was higher in 2015.

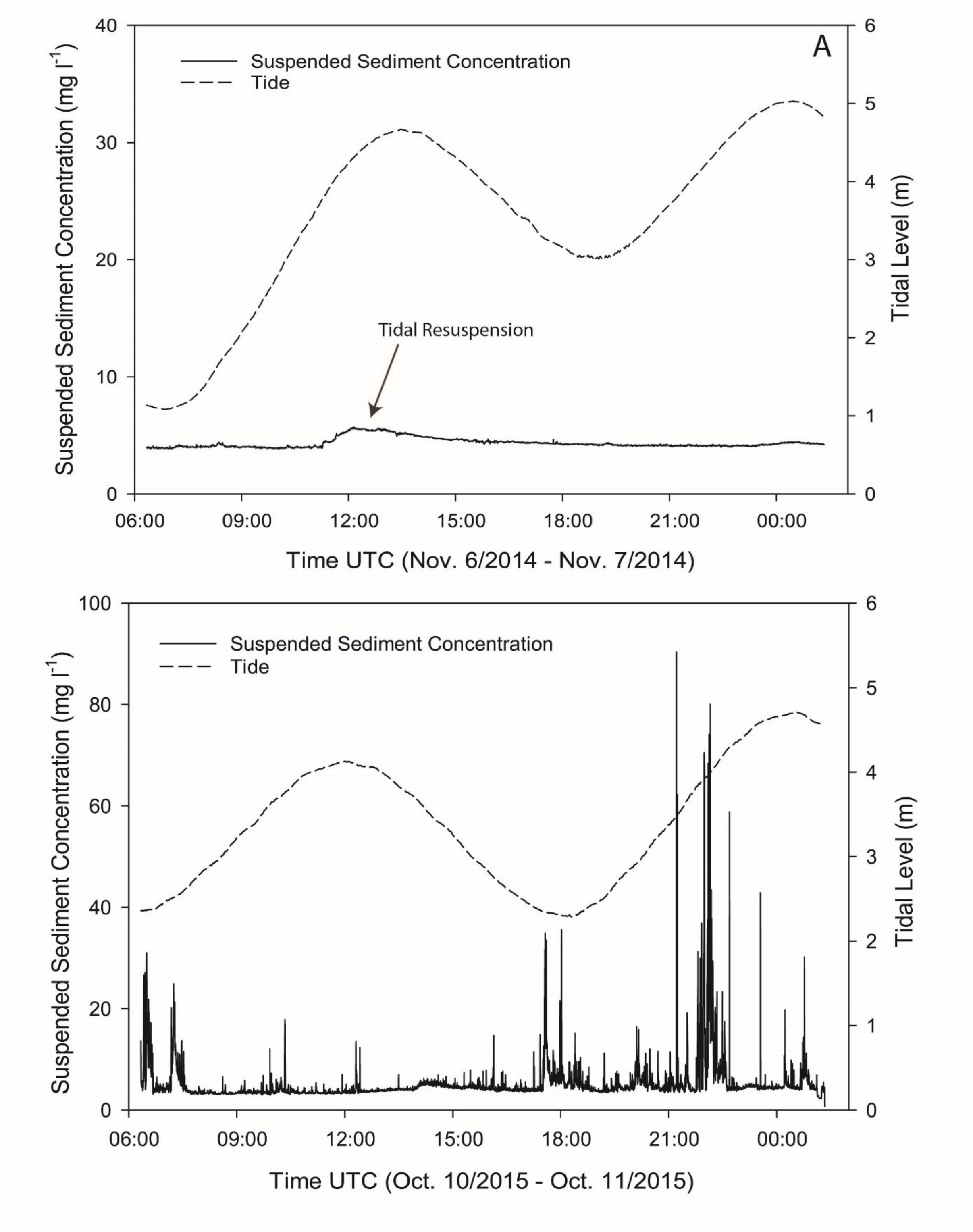

Figure 2-6: Tidal flow and suspended sediment records for 2014 and 2015 from Fraser Ridge reef. In 2014 (A), when tidal strength was highest during this study, there was notable resuspension of sediment corresponding with high tide. This relationship was not detectable in 2015 as experimental sediment disturbances caused increased SSCs to last across each tidal phase. The SSC increases in 2015 (B) reached higher concentrations than was possible through tidal resuspension alone (A).

Chapter 3. The Effect of Suspended Sediments on Filtration of Three Species of Glass Sponge *In situ*

3.1 Introduction

Globally, marine ecosystems are challenged by multiple human-based stressors (Wilber and Clarke 2001, Cote and Darling 2010, McCauley et al. 2015). In response, the United Nations has set targets to protect 10 percent of the ocean by 2020 and more thereafter (MacKinnon et al. 2015). Establishing Marine Protected Areas (MPAs) is fundamental to meeting these targets, but how the areas are chosen and how boundaries are set and managed is critical for effective conservation. One example is Canada's recently established Hecate Strait and Queen Charlotte Sound Glass Sponge Reefs MPA (Fisheries and Oceans Canada 2017c).

Glass sponge reefs are globally unique ecosystems that occur in depths of 30 – 200 m on the continental shelf of British Columbia, Canada and Alaska, U.S.A. (Conway et al. 1991, Conway et al. 2001, Krautter et al. 2001). The reefs are built by three glass sponge species that provide extensive habitat for many commercially important fish and invertebrates, such as Pacific halibut, rockfish, and spot prawn (Conway et al. 2001, Cook et al. 2008, Chu and Leys 2010); this has brought fishing pressure, including bottom-contact trawl fishing, to the sponge reefs resulting in visible physical damage prior to MPA establishment (Conway et al. 1991, Conway et al. 2001, Jamieson and Chew 2002, Austin et al. 2007). Bottom-contact fishing also resuspends large amounts of sediment but the impact of these sediment plumes on the glass sponges is still unknown.

In February of 2017, Fisheries and Oceans Canada established a 2410 km^2 MPA around four glass sponge reef complexes in Hecate Strait and Queen Charlotte Sound (Fisheries and Oceans Canada 2017c). The MPA consists of a core protection zone (CPZ), which excludes all human activities, and an adaptive management zone (AMZ), a buffer zone bordering the reef complexes, which is currently closed to fishing activity but may be opened in the future. However, it is currently unclear if these measures protect the reefs from indirect impacts of trawling (e.g., resuspended sediments) when such activities occur adjacent to the AMZ.

Sponges are highly efficient water filters capable of processing up to 900 times their body volume in an hour (reviewed in Yahel et al. 2003). Generally, they filter constantly and take in both organic and inorganic particles alike. While they can excrete inedible detritus (Wolfrath and Barthel 1989, Yahel et al. 2007, Kahn et al. 2018), too much of it can be detrimental (reviewed in Bell et al. 2015a). Sponges are sensitive to minute changes in the water quality and have been found to respond to changes in seasonal characteristics of the water column (Reiswig 1971a), food availability (Reiswig 1975, Kahn et al. 2012), ocean acidification (Bates and Bell 2017) and suspended sediments (Gerrodette and Flechsig 1979, Carballo 2006, Tompkins-MacDonald and Leys 2008). Sediments can smother and clog a sponge (Airoldi 2003, Pineda et al. 2017) but smaller grain sizes can fit through the incurrent pores on the sponge surface (< 20 µm) (Kilian 1952, Reiswig 1974) potentially damaging the aquiferous structure. Most demosponges contract either to prevent entry of sediment or to expel already ingested sediments (Prosser et al. 1962, Elliott 2004, Elliott and Leys 2007); others can secrete mucus to slough sediments off their surface (Kowalke 2000). Of all sponges however, glass sponges (Class Hexactinellida) are the only group that respond instantly to sediments by using electrical signalling to arrest filtration (Leys et al. 1999, Tompkins-MacDonald and Leys 2008, Grant et al. 2018; Chapter 2, this thesis).

Arrests of filtration are triggered by action potentials travelling throughout the glass sponge's syncytial tissues (Mackie et al. 1983, Leys et al. 1999). Two species of glass sponge *Rhabdocalyptus dawsoni* and *Aphrocallistes vastus*, have been found to arrest filtration in response to sediment in laboratory experiments (Tompkins-MacDonald and Leys (2008). One of these, *A. vastus*, has also been studied *in situ.* Previous work in the naturally turbid waters of the Strait of Georgia, British Columbia found that *A. vastus* stopped filtration in response to suspended sediment concentrations far lower than those generated by trawling (Grant et al. 2018; Chapter 2, this thesis).

Reefs in the northern section of the Hecate Strait MPA are comprised of different species and live in a less turbid environment than reefs in the Strait of Georgia (reviewed in Leys 2013). To determine whether other reef-building glass sponges are also affected by suspended sediments, we conducted experiments *in situ* at the northern sponge reef complex in the Hecate Strait and Queen Charlotte Sound MPA. Our specific aim was to determine whether the sponge species at the reef are adapted, through variations in arrest responses and their thresholds to sediment disturbance, for specific environments and environmental conditions. We hypothesized that either glass sponges in Hecate Strait would be sensitive to smaller increases in suspended sediment concentrations than those in the Strait of Georgia, or alternatively, that Hecate Strait sponges would not be used to higher suspended sediment concentrations and thus would not respond.

We also studied the size fractions of sediment found at the northern reef complex in Hecate Strait as well as current velocities above the sponges at the reef. These parameters were used to model the projected reach of sediment plumes under different transport scenarios. Our analyses underscore the importance of understanding the biology of animals to be protected by an MPA. They also highlight the importance of protective buffer zones around the conservation targets within MPAs.

3.2 Methods

3.2.1 Study Site

Experiments were carried out on a sponge reef at approximately 170 m depth in the Hecate Strait and Queen Charlotte Sound Glass Sponge Reef Marine Protected Area (MPA), British Columbia, Canada during two cruises of the Canadian Coast Guard Ship (CCGS) *JP Tully* in October 2015 and May 2017 (Figure 3-1) (53º 11’37.2”N 130º 28”27.7”W (2015), 53º 11”38.0”N 130º 28”29.4”W (2017)). Dives were conducted using the remotely operated vehicle (ROV) ROPOS (http://ropos.com) in the northern reef complex. Sediment experiments were carried out at the eastern corner of this complex, at a site dominated by large, patchily distributed bushes of *Farrea occa*. *Heterochone calyx* sponges were found growing between and on top of *F. occa* bushes while tube-shaped *Rhabdocalyptus dawsoni* were found on the seafloor between bushes.

3.2.2 Instrumentation

We used both an acoustic Doppler velocimeter (‘Vector’ ADV, Nortek, Rud, Norway) and an acoustic Doppler current profiler (‘Aquadopp’ ADCP, Nortek, Rud, Norway) mounted on a flat frame to measure changes in ambient flow velocity and direction either at a single point (Vector) or for a 5 m profile above the bottom (Aquadopp) (Figure 3-2A and C). The Aquadopp and the Vector were each paired with optical backscatter sensors (OBS, Campbell Scientific, Edmonton, Canada) to record suspended sediment concentrations (SSCs) (Figure 3-2C). The Aquadopp was compass calibrated prior to the expedition. The OBS instruments were calibrated with sediment samples obtained from a previous trip to the sponge reefs in Hecate Strait following the calibration process outlined in Grant et al. (2018) (Chapter 2, this thesis). The resulting calibration curves used to convert OBS data from ‘counts’ to mg l^{-1} resulted in the following equations ($R^2 = 0.92$): SSC = 0.0113 * OBS counts + 1.3021 for the Aquadopp-paired OBS and SSC = 0.0103 * OBS counts + 1.9302 ($R^2 = 0.99$) for the Vector-paired OBS.

Custom-built thermistor-flowmeters (hereafter referred to as ‘thermistors’) recorded constant point velocities of flow both out of the osculum (excurrent openings) of sponges (i.e., excurrent flow rates) and adjacent to the sponges (i.e., ambient flow rates) (Figure 3-2A, C and E). Each thermistor pair recorded both excurrent and ambient current velocities simultaneously. Thermistors were calibrated *in situ* using the Vector in an area of undisturbed ambient current for at least 8 hr. Thermistors were then placed directly beside a sponge and the probes positioned by mechanical arms of the ROV into the sponge osculum, the chimney-shaped opening which all filtered water exits from; care was taken to prevent the probe from contacting the body wall of the sponge (Figure 3-2B, D and F). Probes were re-positioned if any camera view showed that the probe was not inserted into the osculum deep enough or was touching the body wall. Either an Aquadopp ADCP or Vector ADV was positioned with the OBS as close to the sponge as possible to capture the turbidity around the sponge during the experiments.

3.2.3 In situ Experiments

We positioned instruments over a total of 10 sponges: six *F. occa,* three *H. calyx* and one *R. dawsoni*. Although *R. dawsoni* is not a reef-building sponge, previous work in flow-through seawater tanks found it arrests filtration in response to suspended sediments (Leys et al. 1999, Tompkins-MacDonald and Leys 2008) and therefore it was used as a positive control. Additionally, we obtained another control by recording flow in the osculum of a dead *F. occa* specimen. Once a sponge was paired with a set of thermistors, ROPOS left the area to allow recordings of undisturbed filtration activity; these recordings ranged from 6 to 24 hr (20 ± 6.5) (mean ± SD) depending on instrument availability and battery charge.

After recording undisturbed pumping activity, we returned to each sponge to carry out sediment resuspension experiments (Figure 3-3). Sediments were suspended near sponges using the ROV manipulator arm and a modified ice scoop. We positioned the ROV upstream from the sponge to ensure that resuspended sediment would move towards the sponge. Because the action of the

ROV manipulator arm to lift the sediment up and towards the sponge could also push water towards the instruments and affect the recordings, we first used control ‘scoops’ in which the ROV operators caused the manipulator arms to swing an empty scoop in the direction of the sponge (Figure 3-3B). Following the control scoops, sediment was scooped up from the seafloor and shaken into the water column in the direction of the target sponge (Figure 3-3C). The number of scoops suspended for each experimental disturbance varied from a single scoop to 15 min of continuous scooping in order to record sponge responses across a range of SSCs (Figure 3-3D). A total of 13 experimental sediment disturbances were conducted (Supplemental Table 1). All instrument placements, experimental disturbances and ROPOS activity near the sponges were recorded in the Integrated Real-Time Logging System (IRLS) to allow for quality control checking of the data during the analysis process.

3.2.4 Arrest Response Analysis

Filtration arrests were identified in sponge excurrent recordings using the criteria outlined in Grant et al. (2018) (Chapter 2, this thesis) with a modification based on descriptions of arrests in *R. dawsoni* by Tompkins-MacDonald and Leys (2008). Briefly, an arrest was defined as a decrease from the average excurrent velocity (the arrest phase) followed by the gradual return to average excurrent velocities (the recovery phase); the minimum recovery phase length was 20 s. As *R. dawsoni* has shorter arrests than those of *A. vastus,* these criteria ensured filtration arrests could be identified from all species.

In general, arrests were categorized as follows: single arrests, coughing arrests, prolonged arrests or clogging events. Single arrests and coughing arrests differ in both their overall duration and the slope of the recovery phase (Grant et al. 2018; Chapter 2, this thesis). Single arrests of filtration are short, off and on events, with little variation in recovery phase slope. Coughing arrests are slightly longer and have a staggered recovery phase involving several attempts to increase pumping rate prior to reaching the full pumping rate. The duration of single and coughing arrests differ for different species: for *A. vastus*, the two arrest types have a characteristic ‘V-shape’ (see Grant et al. 2018; Chapter 2, this thesis) and the same was expected for *H. calyx*; for *R. dawsoni* both arrest types show a more ‘U-shaped’ pattern (see Tompkins-MacDonald and Leys 2008). Prolonged arrests were distinguished by the length of the arrest, with flow completely arrested for over 40 minutes. Clogging events appeared as incomplete arrests where excurrent flow rates reduced but did not completely stop.

For analysis, each excurrent flow record was first visually assessed to identify filtration arrests. After this, a moving average of the variance was carried out on the time series at 10 s intervals to detect any additional points during which the variance in excurrent flow decreased more than 0.25 over a 10 s interval, indicating a possible arrest of pumping. This was followed by two additional manual inspections to ensure no arrests were missed in each record. A Spearman's rank correlation was calculated between the arrest phases identified by the above procedure and ambient velocities measured during that period. The final count of 'arrests of sponge filtration' only consisted of those in which the decrease in excurrent velocity was independent of the ambient current. To determine whether increases in SSC were correlated with decreases in excurrent flow a Spearman's rank correlation was used. Changes in SSC caused either by experimental disturbances immediately preceding an arrest or by natural events within the 2 minutes preceding the arrest were compared to the excurrent flow rate during the arrest phase. These analyses were carried out using STATISTICA 13 (Statsoft, 2017).

3.2.5 Sediment Collection and Analysis

Sediment cores were collected from the northern reef complex. Areas selected for sediment cores were open, sponge-free portions of the reef where sediment had naturally settled, within a 50 m radius of the instrument-paired sponges. Push cores 7.6 cm in diameter were pressed into the sea floor to a depth of 60 cm. Cores were frozen on board of the ship and transported to the University of Alberta for further analysis. Sediments from Fraser Ridge reef in the Strait of Georgia, British Columbia were collected in traps placed at the height of the sponges in 2011. Collection and storage of those traps was described previously (Kahn et al. 2016).

3.2.5.1 Grain Size and Transportation Modelling

Sediment cores (n = 4) were thawed and dried in a 60ºC oven for three days prior to analysis. We did not retain distinct depth fractions. Dried sediments were placed in a W.S. Tyler's RO-TAP® RX-29 sieve shaker and shaken 100 g at a time for 5 min or until sediment no longer passed between sieves (Table 3-1). Dried sediment samples were weighed before and after entering the sieve shaker to calculate the proportion of each grain size by weight. Each core was analyzed separately and the means of all four calculated. Z-tests were used to test for differences in the proportion of different grain sizes between the two reefs.

Settling rates, time spent suspended, maximum distance travelled and the height of suspension needed to maximize the distance travelled in a single tidal cycle were calculated using the grain sizes in Table 3-1 and variables defined in Table 3-2. Settling rate was calculated using the Stokes settling equation:

Equation 1

$$V_t = \frac{gd^2(\rho_p - \rho_m)}{18\mu}$$

The maximum distance that could be travelled by a particle in a single 6 hr tidal cycle was modelled by:

Equation 2

$$X_{D\,Max} = U_{To}\frac{1}{\omega_T}[-cos[\omega_T(T_{Fall\,Max} - t_o)] + cos(\omega_T\,t_o)]$$

The maximum travel distance of a particle was modeled at different heights above seafloor. The total settling time of a particle suspended at a given height above the seafloor was calculated for each grain size using:

Equation 3

$$T_{Fall} = \frac{H_0}{V_t}$$

Sediments were analyzed and modelling was completed for all sediment collected from the northern Hecate Strait reef complex in May 2017. This model assumes that all particles are spheres and does not account for particle flocking, turbulence, or stratification of the water column. This was duplicated using sediments collected previously from the Fraser Ridge sponge reef.

3.3 Results

3.3.1 Ambient Conditions of the Study Site

Ambient currents at one meter above bottom (mab) averaged 12.01 cm s^{-1} (± 6.39) (4 hr average ± SD) during flood tides and 6.31 cm s^{-1} (± 3.63) during slack tides (Sup. Figure 3-1). The ambient current velocity increased with increasing height above the seafloor. At 5 mab, current during flood tides averaged 27.4 cm s^{-1} (± 12.12), and 19.3 cm s^{-1} (± 9.37) during slack tides. The ambient current over the reef alternated in an east-west direction during flood tides while during the slack tide we recorded a short duration of north-south movement. Background levels of suspended sediment concentrations (SSCs) showed little variation over the 6 to 24 hr (20 ± 6.5) (mean ± SD) duration of our recordings, averaging 2.71 mg l^{-1} (± 0.09) at all instrument placements (Sup. Figure 3-1, Appendix 2).

3.3.2 Rhabdocalyptus dawsoni

R. dawsoni (n = 1), our positive control, showed the greatest number of filtration arrests in response to experimentally increased SSC but also in response to natural increases in suspended sediments. A total of eight single and one prolonged arrest were identified throughout the 21.5 hr recording. Single arrests matched previous descriptions of arrests in *R. dawsoni* (Tompkins-MacDonald and Leys 2008). The prolonged arrest lasted for more than 5 hr (Figure 3-4A and B); instruments were collected before the sponge began pumping again and so the duration of the arrest was undetermined. Single arrests lasted 0.65 – 9 min (2.12 ± 2.64) (mean ± SD) in total duration, with arrest phases lasting 0.32 – 3.55 min (0.91 ± 1.01), and recovery phases 0.33 – 5.5 min (1.21 ± 1.64) (Table 3, Figure 3-4A). In seven of the eight single arrests the decrease in excurrent velocity was correlated with increases in SSC of < 7 mg l^{-1} ($r = -0.81$ to -0.87, $p < 0.05$) that occurred in the 2 minutes prior to the onset of the arrest phase (Figure 3-4C). The sediment suspension events linked to these arrests corresponded with movement of ROPOS at or near the sponge that generated plumes of sediment that remained around the sponge for between 9 and 307 s (65 ± 92) (mean ± SD). The ambient SSCs before filtration arrests varied from 2.55 to 2.67 mg l^{-1} and increased very slightly to between 2.85 and 6.41 mg l^{-1} at the time of the arrests. The average excurrent velocity from the sponge before arrests was 2.56 cm s^{-1} (± 0.88) (± SD) during flood tides and 0.42 cm s^{-1} (± 0.06) at slack tides (Figure 3-4D).

A single prolonged arrest was shown by *R. dawsoni* following a long sediment disturbance caused by ROPOS moving in the area. The sponge stopped filtering for more than 6 hr (Figure 3-4B and E), and the reduction in excurrent velocity was correlated with the increases in SSC (r = -0.85, $p < 0.05$). The sediment remained elevated around the sponge for 2.45 hr, with a peak concentration of 3.20 mg l^{-1} (average, 2.74 mg l^{-1}). Prior to this disturbance, the SSC averaged 2.64 mg l^{-1} (± 0.17). An experimental sediment disturbance was carried out 5 hr into this extended cessation of pumping and may have prolonged the duration of the arrest. Because the thermistor flowmeter was collected before the sponge began pumping again, it is not known exactly how long the sponge remained without filtering. No coughing events were observed in *R. dawsoni.*

3.3.3 Heterochone calyx

We recorded excurrent flow from three *Heterochone calyx.* Two bowl-shaped sponges were each exposed to a single experimental sediment disturbance *in situ,* and both showed single arrests in response to increased sediment concentrations as well as reductions in filtration rate over longer periods than single arrests, which looked like clogging events (Figure 3-5A, B). In the third *H. calyx* there were no spontaneous arrests over a 24 hr recording although no experimental disturbance was carried out. No coughing events were observed in *H. calyx.*

Single arrests (n=5) ranged in duration from 1.2 – 7 min (3.76 ± 2.5). Arrest phases lasted 0.47 – 2.97 min (1.30 ± 1.03) (mean ± SD) and recovery phases took 0.75 – 4.03 min (2.46 ± 1.56) (Table 3, Figure 3-5A). In all five single arrests, the decrease in excurrent flow was correlated with increased SSC in the 2 minutes prior to the arrest (Figure 3-5C). The first sponge underwent three single arrests, which occurred after a single experimental sediment disturbance event. The decreased excurrent velocity was correlated with increased SSC prior to the arrest (r = -0.89 to -0.92, $p < 0.05$). The second *H. calyx* individual carried out two single arrests, and in both cases the decrease in excurrent velocity was correlated with increased SSC prior to the arrests caused by a second sediment disturbance by ROPOS (r = -0.81 to -0.97, $p < 0.05$).

Prior to experimental disturbances, the mean excurrent velocity during non-arrest periods from all three *H. calyx* was 1.75 cm s^{-1} (± 0.44) (± SD) during flood tide and 0.48 cm s^{-1} (± 0.15) at slack tide (Figure 3-5D). The SSCs around the *H. calyx* individuals during periods when the ROV was not in the area was on average 2.75 mg l^{-1} (± 0.03). Our experimental disturbances increased the SSC to between 5.07 and 10.1 mg l^{-1}. The residence time of these plumes of sediment over the sponges was between 54 s and 2.35 min.

Two clogging events were recorded from *H. calyx.* During slack tides, twice the excurrent velocity dropped to between 0.2 - 0.73 cm s^{-1} (Figure 3-5B) immediately after a slight increase in sediment concentration that was smaller than those caused by our experimental disturbances. The slightly elevated SSC persisted in water around the sponges due to the lower ambient current seen at slack tide. Clogging events were different from the 'prolonged' arrest seen in *R. dawsoni* because they did not result in the complete cessation of excurrent flow from the sponge, but instead the record showed a persistent decline in excurrent flow rate much as seen by (Tompkins-MacDonald and Leys 2008). The first clogging event lasted 3.41 hr and came after an extended period of increased SSC lasting 2.53 hr, with a peak concentration of 4.53 mg l^{-1} and average of 2.98 mg l^{-1} (± 0.08) following this initial peak (Figure 3-5E). The second clogging event lasted 0.79 hr and followed an increase in SSC with a peak concentration of 4.10 mg l^{-1} and average of 3.01 mg l^{-1}. While we do not know what caused these increases in SSC, the manipulation of nearby instruments and activity of fish are possible explanations. Decreases in excurrent velocity from the sponge were correlated with the increases in SSC prior to the clogging events ($r = -0.86$, $p < 0.05$).

3.3.4 Farrea occa

The excurrent velocity from *F. occa* did not drop in a way that appeared to be an arrest either following sediment experiments or at any time when the sponges were left undisturbed. The record for *F. occa* naturally fluctuated and experimentally-induced changes in excurrent velocity were not distinguishable from this natural variation. There was no significant correlation between changes in excurrent velocity and experimental increases in SSC (Figure 3-6C).

Nine experimental sediment disturbances were carried out on six different *F. occa*, increasing the SSC from 3.5 to 57 mg l^{-1} (average 32 mg l^{-1}). None of the experimental disturbances resulted in an arrest or slowing of excurrent flow. It is uncertain if the flow records accurately represent the pumping activity of *F. occa,* because the excurrent velocity increased with increased ambient current ($r = 0.83$, $p < 0.05$), independent of changes in SSC (Figure 3-6D). Undisturbed flow out of the sponge bushes averaged 1.54 cm s^{-1} (± 1.81) (± SD) during flood tide and 0.32 cm s^{-1} (± 0.22) at slack tides. Recordings from a dead bush gave comparable excurrent velocities to the live bushes, 2.58 cm s^{-1} (± 1.02) during flood tide and 0.49 cm s^{-1} (± 0.39) at slack tides. The comparable flow rates between live and dead sponge bushes may be an indication that flow rates are too small to be detected. To determine how much flow was generated by the sponge pump in *F. occa* and how much might be caused by ambient currents disturbing the water around the flow probes in the sponge oscula, we collected two individuals and immediately after the ROV arrived on deck put fluorescein dye beside the wall of the sponge. In one case the sponge did not appear to take in any dye, but in the second sponge moved dye through the body wall extremely slowly prior to stopping, as though the sponge was irritated by collection. This demonstrates that *F. occa* can actively pump, but does not confirm whether or not our flow measurements accurately captured pumping behavior in *F. occa*.

3.3.5 Sediment Grain Size

Four push cores of sediment from the Hecate Strait MPA and four sediment traps from Fraser Ridge reef were analysed for grain size, a total of 1150 g and 432 g (dry weight), respectively. Only two grain size categories differed significantly between the two reefs (Table 3-4). First, Hecate Strait samples contained significantly more grains larger than fine sand (> 212 μm), 69% in Hecate Strait to 50% at Fraser Ridge reef ($Z = 3.26$, $p < 0.01$). Second, Fraser Ridge reef had a larger portion, by weight, of medium silts (20 – 45 μm), 24% at Fraser Ridge reef compared to 6% at Hecate Strait ($Z = 5.02$, $p < 0.001$). There was no significant difference between the two locations for the remaining grain sizes.

3.3.6 Sediment Transportation

The model we used in this paper is a conservative model that excludes additional factors such as bottom current turbulence and possible resuspension. Particles are suspended into the water column at the beginning of a tidal shift and are transported continuously in a single direction for the entire 6 hr flood tide or until they would have settled out of suspension. For example, when suspended 3.5 mab, a < 20 μm particle would be in ambient flow of ~ 20 cm s^{-1} and travel 2.77 km (Figure 3-7A and B) in 3.8 hr before settling out of suspension. As the ambient current velocity increases with increasing height above the sponges (until the boundary layer is exited), the maximum possible distance sediment could be carried also increases. At 5 mab, the same sized particles could travel 5.94 km, passing over even the largest portions of the adaptive management zone (AMZ) (4.5 km). As larger particles settle out of suspension, the concentration of the plume will decrease as well (Figure 3-7C). The initial SSC, grain size of the sediments and suspension height of a plume can be used to predict the total area and individual species that will be affected by a plume. For example, when suspended to 5 mab, a sediment plume with an initial SSC of 500 mg l^{-1} will remain above the thresholds of response for *H. calyx* and *R. dawsoni* even when the sponges are 2.11 and 2.39 km away from the initial disturbance, respectively (Figure 3-7C).

As seen in Figure 3-7C and 3-7D, each grain size has a maximum range, with larger sand grains settling out of suspension within a few meters and smaller sizes travelling further. In Hecate Strait, between 1 and 6% of sediments, silts and clays, can travel up to 5.94 km when suspended to 5 mab, surpassing MPA boundaries, which range from 600 m to 4.5 km (Figure 3-7C and D). Larger grains, those > 212 µm (69.5% of sediment collected), will travel up to 50 m, fine sands (15.8%) up to 100 m, very fine sands (5.37%) up to 360 m, and coarse silts (2.94%) up to 800 m.

The amount of time a single particle will remain suspended in the water column will vary depending on the initial height of suspension (Table 3-5) and so the range of dispersal is expected to increase the higher sediments are resuspended. If sediments were suspended as high as 10 mab, larger particles could remain in suspension for 6 min, and the smallest grain sizes measured would remain in suspension for more than 11 hrs (Figure 3-7E). Therefore, smaller particles (< 20 µm) would remain in suspension for longer than the 6 hr tidal cycle and could be transported in multiple directions as they experience multiple tidal cycles.

Sediment grains may be continuously settling but the model shown in Figure 3-7 does not account for turbulent bottom currents which could cause continued suspension of the smaller grain sizes throughout the 6 hr tidal period. A predictive 'worst-case scenario' model using resuspension by bottom currents and limited settling of particles can be seen in Supplemental Figure 2, Appendix 2. This model is only included as a point of comparison for the model seen in Figure 3-7.

3.4 Discussion

Arrests of filtration in response to elevated concentrations of suspended sediment were recorded for the first time from glass sponges *in situ* in Hecate Strait, British Columbia, Canada.

Our data showed that not only do different species of glass sponge have different tolerances to suspended sediment, but that the sensitivity of the glass sponge filtration system seems to be adapted to the relative turbidity of its habitat.

3.4.1 Sensitivity of Hecate Strait Sponges to Suspended Sediments

Our previous work in the Strait of Georgia showed that *A. vastus* arrests filtration at 10-40 mg l^{-1} SSC, well above the natural turbidity (4.4 mg l^{-1}), but it also arrests each time the tidal flow resuspends sediment (Grant et al. 2018; Chapter 2, this thesis). Strait of Georgia reefs are typically fairly turbid, with a transmissivity often below 30% (Johannessen et al. 2006). In contrast, Hecate Strait waters are less turbid with a transmissivity around ~ 55% (greater transmissivity is associated with fewer particles in the water) (Conway et al. 2005b). We hypothesized that either glass sponges in Hecate Strait would be sensitive to smaller increases in SSC as they are not naturally exposed to many suspended sediments unlike those in the Strait of Georgia which naturally experience higher SSCs, or alternatively, that Hecate Strait sponges would be unaccustomed to increased SSCs and would therefore be adapted to continual feeding without responding. Our results suggest that both may be correct.

At the northern Hecate Strait reef *R. dawsoni* and *H. calyx* are more sensitive to suspended sediments than *A. vastus* studied in the Strait of Georgia reefs or *R. dawsoni* studied in laboratory settings. *H. calyx* arrested filtration when concentrations of sediment reached 4 to 10 mg l^{-1}, a relatively small increase from the average turbidity of 2.71 mg l^{-1} (± 0.09) recorded for the northern reef complex in Hecate Strait and well within the ambient SSCs observed in the Strait of Georgia. In comparison, *A. vastus*, which is found in the naturally more turbid environment of Fraser Ridge reef (4.4 mg l^{-1} ± 0.7), arrests filtration in response to SSC of 10 – 40 mg l^{-1} (Grant et al. 2018; Chapter 2, this thesis). This suggests that in the Strait of Georgia, *A. vastus* is slightly more tolerant to changes in the natural SSCs than *H. calyx* is at Hecate Strait. The sediment composition was similar between these two locations but tidal resuspension and the natural turbidity varied. We recorded no change in turbidity associated with tides at the Hecate Strait northern reef and indeed no natural variation was found in the SSC recordings. In contrast, sponges at Fraser Ridge reef experience frequent tidal resuspension, increasing SSCs to 5.3 mg l^{-1} (± 0.9) (Grant et al. 2018; Chapter 2, this thesis) and seasonal increases up to 7 to 8 mg l^{-1} due to deposition from the Fraser River (Thomson 1981b, Hill et al. 2008). Interestingly, *H. calyx* can be found at both locations (Conway et al. 2001, Krautter et al. 2001) but imagery captured by the ROV indicates that this species may be more common in the northern reef complex of Hecate Strait.

R. dawsoni, commonly called the ‘boot’ sponge, appears to be the most sensitive glass sponge studied at the reefs. At the Hecate Strait reef, the boot sponge carried out multiple arrests in response to SSC increases of only 0.5 or 1 mg l^{-1} above the normal levels of 2.71 mg l^{-1} (± 0.09). This small change in SSC was an order of magnitude lower than concentrations found to trigger arrests of filtration by *R. dawsoni* in previous tank experiments (Tompkins-MacDonald and Leys (2008). *R. dawsoni* may indeed be more sensitive to sediment, as suggested by Mackie et al. (1983) and Mackie and Singla (1983) who found it would arrest pumping activity in response to nearly any disturbance. A higher sensitivity in this species is also consistent with observations that *R. dawsoni* is not found at Fraser Ridge reef (Krautter et al. 2001, Conway et al. 2007, Dunham et al. 2018) nor near the turbid regions of the upper fjords in British Columbia (Farrow et al. 1983). This is possibly because it cannot survive such a turbid habitat. The absence of *R. dawsoni* at Fraser Ridge reef and the presence of the marginally more tolerant *H. calyx* at both Hecate Strait and Fraser Ridge reefs suggests that the presence of different species of glass sponge at different reef complexes depends in part on their sensitivities to the environmental conditions (Conway et al. 2001, Dunham et al. 2018). However, if suspended sediments were the only limiting factor, we would expect to see species with high sediment tolerances, like *A. vastus,* to be common both at the low turbidity site in Hecate Strait and in areas with higher turbidity. While *A. vastus* is found in the northern Hecate Strait reef complexes, it appears to be more abundant on the westward portion of the reef where it, together with *H. calyx*, may be the more dominant species (Law 2018). This indicates that sedimentation is likely not the only factor that determines what reef-building species are present at a given reef patch (Leys et al. 2004, Kahn et al. 2015). Evaluating differences in the water column properties between the western and eastern sides of the northern Hecate Strait reef complex could provide insight into the variables that influence sponge species distribution at the reefs.

3.4.2 Species-Specific Differences in Glass Sponge Responses

In situ recordings from this study and Grant et al. (2018) (Chapter 2, this thesis) show three classifications of filtration arrest: simple ‘off-on’ responses (single), arrests with intermittent attempts to restart (coughing) and what we have termed ‘prolonged’ arrests as well as ‘clogging events’. Prolonged arrests may be a longer version of a simple arrest or may reflect clogging of the filter. As all the species share the same ability and mechanism to arrest filtration, we did not expect to find the inter-species variations noted within this study. Arrests are triggered by electrical signals that travel throughout the sponge at 0.27 cm s^{-1} (recorded in *R. dawsoni*) (Leys and Mackie 1997, Leys et al. 1999). Action potentials are followed by a refractory period of 29 s, which limits the number of sequential, individual responses a sponge can undergo (Mackie et al. 1983, Leys and Mackie 1997, Leys et al. 1999). If a second action potential is propagated during this period, the arrest will be prolonged (Leys et al. 1999, Tompkins-MacDonald and Leys 2008). The relationship between repeated signals induced by sediments and the refractory period is a possible cause for the differences between single and prolonged arrests.

H. calyx and *R. dawsoni* both had single arrests like those previously described for *A. vastus* (Tompkins-MacDonald and Leys 2008, Grant et al. 2018; Chapter 2, this thesis), but the concentrations of resuspended sediment that trigger the arrests are unique to each species. *R. dawsoni* arrested all excurrent flow for more than 6 hr following a minimal increase of SSCs of 0.1 to 0.6 mg l^{-1}, in what is referred to here as a ‘prolonged arrest’. It is unlikely this concentration caused clogging. In *H. calyx* in contrast, the sponges showed a reduction in excurrent velocity lasting of 0.79 to 3.41 hr, and these looked like clogging events rather than complete ‘single arrests’ since there was never a complete cessation of flow out of the osculum. These events had very similar characteristics to those reported as clogging in *A. vastus* (Tompkins-MacDonald and Leys (2008), but if these do reflect clogging, then in *H. calyx* clogging occurred after sustained but very slight increases in SSC of only 1 to 2 mg l^{-1} above natural conditions. This demonstrates that glass sponges have a range of physiological responses to increased SSCs. These results, along with the remarkably high sensitivity of *R. dawsoni* to extended sediment exposure suggest that the concentration threshold may not be the only variable that determines whether a species will respond. Sensitivity may be influenced by the concentration of suspended sediments, the duration of exposure, and even the number of disturbances of a given threshold.

It is not completely unexpected to find specific tolerances to sediment concentrations of a given region and variation in the responses of individuals that reside in different environments as environmental adaptations are seen in many animals (Levinton 1991, Somero 2002, Chiba et al.

2016, Stickle et al. 2017). Our findings suggest that variation seen within the response of reef glass sponges is partially driven by environmental factors. Comparing the responses of species that reside in different regions with different environmental conditions (i.e., *H. calyx* or *A. vastus* in Hecate Strait and the Strait of Georgia) could offer insight as to whether the differences we see are species-driven or environmentally-driven.

3.4.3 Farrea occa

A large portion of the reef we studied is built by *Farrea occa* and so we carried out several sediment experiments on this species. However, in none of our six recordings and 10 sediment experiments did we see a clear arrest of filtration. Pumping activity in these bush-shaped sponges appeared to be so minimal that we were unable to distinguish excurrent flow generated by the sponge pump from changes caused by ambient flow around the bush of oscula. Brief observations of collected specimens moving fluorescein dye through their body walls indicated extremely low levels of pumping but this was only observed once, for a very short period of time before the sponge ceased pumping completely. Because of this, if arrests do occur in this species, we were unable to detect them.

One hypothesis about the limited pumping activity we observed is that *F. occa* relies heavily on current being induced to flow through the tubes by ambient current over the bush. The body wall of *F. occa* is often less than 1 mm thick, and these wafer-thin walls form ‘flutes’ (Figure 3-8) as described by Krautter et al. (2001). We studied one of these small bushes using computed tomography (CT) at the University of Alberta (Diagnostic Imaging, University of Alberta Hospital) and discovered that the tubes are hollow from the osculum to the base of the bush potentially allowing water to be drawn from the base of the sponge. Krautter et al. (2001) suggest that *F. occa* is an important species for baffling sediments at the reef due to its large size. The hollow interior of *F. occa* could be adapted for using induced-flow to assist feeding while still baffling sediments on the reefs. If the sponge is baffling sediments, the continuous exposure to low-levels of sediments may render filtration arrests inefficient within this species. This could suggest that the hollow body form of *F. occa* may be an adaptation to sediment exposure, allowing the sponge to rely more heavily on induced currents rather than generating its own through pumping activity. Elucidating whether this is the case will help build a better understanding of this unique species.

3.4.4 Suspended Sediments Influencing the Hecate Strait Marine Protected Area

Understanding the extent to which anthropogenic activities influence abiotic conditions like suspended sediments is crucial for management of reefs and species in the Hecate Strait MPA. Resuspension of sediments is a well-known consequence of bottom-contact fishing (Schubel et al. 1978, Puig et al. 2012, Mengual et al. 2016), an activity that is common near the sponge reefs (Fisheries and Oceans Canada 2017b). The sediment concentrations known to be resuspended by trawl gear are condiserably greater than levels that cause arrests in glass sponge reef species (Figure 3-9). Large clouds of suspended sediments can be generated by a trawl, resulting in plumes that are 200 m wide, 10 m tall and 1.5 km long depending on the substrate (Churchill 1989, Durrieu De Madron et al. 2005, Boutillier et al. 2013, Mengual et al. 2016). The model in this study suggests that plumes of this size could easily pass over the current protective boundaries of the Marine Protected Area (MPA). We calculated how far trawl-induced resuspended sediment could travel (Figure 3-7). Our model indicates that, within a single tidal cycle, smaller grained sediments generated outside of the MPA boundaries could travel as far as 5.94 km, surpassing both the AMZ and CPZ boundaries. Smaller sized sediments will remain in suspension for longer and therefore have a greater potential of causing repeated or longer arrests of filtration. Multiple arrests were previously calculated to reduce the daily energy uptake of *A. vastus* by up to 70%, which can negatively affect the health of a sponge and could potentially be fatal (Leys 2013, Grant et al. 2018; Chapter 2, this thesis). When estimates such as these are scaled up to the number of sponges and species making up a reef, the impacts on a reef could be substantial. However, the long-term effects of repeated filtration arrests and sediment exposure on the health and population of reef-building species are yet to be studied and remain a knowledge gap in the future of conservation of the glass sponge reefs.

The threshold concentrations of suspended sediments that triggered filtration arrests in this study were all below 10 mg l^{-1}; in contrast those found previously at the Strait of Georgia (Grant et al. 2018; Chapter 2, this thesis) were greater, at 40 mg l^{-1}. Modern trawl equipment currently used near the reefs is known to cause plumes of sediment well above these thresholds. The two most commonly used bottom-contact trawls in the area are otter trawls and shrimp trawls (Boutillier et al. 2013). Otter trawls can generate SSCs of 200 mg l^{-1} while more targeted shrimp trawls have recorded concentrations as high as 500 mg l^{-1} (Figure 3-9) (Schubel et al.

1978, Mengual et al. 2016). Trawls designed to reduce the impact on and contact time with the seafloor, such as Jumper doors, can suspend 20 to 110 mg l^{-1} of sediments into the water column (Mengual et al. 2016). All of these methods generate sediment plumes with concentrations greater than what is currently known to induce arrests in glass sponges and would take considerable time and distance to dissipate to concentrations less than the thresholds of response reported in this study. Other industrial activities such as prawn trap fishing and laying undersea cables can resuspend smaller, localized clouds of sediments but concentrations of these clouds have not yet been reported (Puig et al. 2012, Boutillier et al. 2013, Dunham et al. 2015).

The extent to which reef sponges could be exposed to increased SSCs from trawling activity depends on proximity to the trawling disturbance, ambient currents, height at which the sediments are resuspended, as well as the grain sizes within the sediment plume and initial concentration of the sediment plume. At our study site, ambient current velocity increased with height above the reef, from 0.12 m s^{-1} at 1 mab up to 0.27 m s^{-1} at 5 mab (Figure 7). Sediments suspended by fishing trawls have been reported to reach ~ 5 to 10 mab (Durrieu De Madron et al. 2005). A sediment plume of 500 mg l^{-1} suspended 5 mab would have a radius of 2.39 km in which the SSC was greater than the threshold of response for both *H. calyx* and *R. dawsoni* (Figure 7C). A trawl on the edge of the narrowest portion of the AMZ, 0.6 km would allow such a sediment plume to remain above 10 mg l^{-1} up to ~1.35 km into the CPZ. In contrast, the largest AMZ section, 4.5 km, could protect the CPZ from most sediments, except for smaller silts and clays < 20 µm. The distance that a single particle, regardless of grain size or settling velocity, could be transported in a single direction is based on the average ambient current velocity during a flood tide and on the settling velocity of the particles.

Increased suspension height and faster ambient currents mean small grain sizes travel farther, and if sediments remain in suspension for more than a single tidal cycle, there is increased risk of a sediment cloud reaching far from the initial disturbance (Nafe and Drake 1961, Jones 1992). Smaller particles, like silts and clays found at the sponge reefs (~ 8% of sediments at Hecate Strait, see Table 3-4), are more easily resuspended, are more likely to suspend higher in the water column, settle more slowly than larger sand grains, and can be resuspended by bottom current turbulence before settlement occurs (Nafe and Drake 1961). Once in suspension, ambient currents move sediments away from the source. The distance between a sponge and the source of suspension allows SSCs to dissipate to lower concentrations that may not affect sponges. However, this distance increases for smaller grain sizes (Hill et al. 2008, Puig et al. 2012).The smallest grain sizes (< 20 µm) may have additional impact because they can enter the sponge aquiferous system (Kilian 1952, Reiswig 1974), potentially causing damage. As a result, reef sponges could be affected in some way by sediments unless the AMZ is adjusted in to a greater extent than suggested here to allow for the dissipation of high concentration sediment plumes.

The results of sediment dispersal reported here are based on conservative estimates made by our model, but in fact the problem could be beyond what has been calculated. Our calculations assume that all particles are spheres and does not account for particle flocking, turbulence or stratification of the water column. These almost certainly do not represent the natural conditions at the reefs. Boutillier et al. (2013) reported that silts and clays can constitute between 48% and 60% of the sediments on the western Canadian continental shelf. The sheet-like shape of natural clay particles will likely take longer to settle out of suspension than what we assume in our model, increasing their travel time. This may lead to an underestimation of the total dispersal distance of these smaller sediment grains. Additionally, our model assumes a constant ambient current velocity which may not reflect how currents move around the sponges. If the skeletons of sponges are decreasing local ambient currents, it would likely cause more sediment to settle out directly over or at the sponges themselves instead of continuing to move with the currents. These potential factors should be considered in future models of sediment dispersal around the reefs.

3.5 Conclusion

Two glass sponges, *Heterochone calyx* and *Rhabdocalyptus dawsoni*, from Canada's Hecate Strait and Queen Charlotte Sound Glass Sponge Reef MPA, show arrests of filtration in response to changes in suspended sediments *in situ*. The threshold concentrations of suspended sediments that induced these arrests are lower than those previously found for *Aphrocallistes vastus* in Fraser Ridge reef, and lower than previously reported for *R. dawsoni* in laboratory experiments. *R. dawsoni* appears so sensitive that several hours of reduced filtration was triggered by minimal changes in the concentration of suspended sediments, leading to a prolonged arrest. Glass sponge species in reefs clearly have different sensitivities and species-specific responses to changes in suspended sediment concentrations. The bush sponge *Farrea* *occa* appears to filter at such a low rate that it was not possible to reliably record filtration or responses to sediment disturbances. The distance sediments are predicted to travel in Hecate Strait suggest that bottom contact activities outside the current Core Protection Zone (CPZ) could generate SSC that would be damaging to sponges reefs within the CPZ. Our model suggests that activities which cause sediment resuspension should continue to be excluded from within the AMZ. Additionally, our data also suggest a larger buffer (AMZ) of >2.39 km would be beneficial by preventing any interaction of anthropogenically resuspended sediment with sponges. A future study running a numerical ocean model such as ROMS, and using the results of this paper, would be able to draw sediment dispersion risk contours around the reefs (as in Boutillier et al. 2013 and Chandler, DFO 2018), to adjust the shape of the Adaptive Management Zone to be wider in some areas. This study highlights that understanding the range of effects suspended sediments on different species of deep-water sponges is important for effective design of MPA boundaries and regulations.

Table 3-1. Mesh sizes, and their equivalent grain size classification, chosen for partitioning sediments sizes during analysis.

Mesh size (µm)	Grain Size Classification
212	> Fine Sand
106	Fine Sand
63	Very Fine Sand
45	Coarse Silt
20*	Medium Silt
>20	Fine Silt

Table 3-2. Variables utilized for modelling sediment transportation and settlement across all grain sizes recorded at the northern Hecate Strait glass sponge reef.

Variables	Description
V_t	Settling velocity of the particle (cm s^{-1})
g	Gravitational constant (m s^{-2})
d	Particle diameter, assuming a sphere (μm)
ρ_p	Particle density for a given grain size (kg m^{-3})
ρ_m	Density of seawater at depth (kg m^{-3})
μ	Dynamic viscosity (kg m^{-1} s^{-1})
$X_{D\ Max}$	Maximum distance travelled by a particle in one direction during a single 6 hr tidal cycle (km)
U_{To}	Average ambient current velocity (cm s^{-1})
ω_T	Tidal phase during suspension event
T_{Fall}	Time a particle spends falling in the water column from a given height of suspension (s)
$T_{Fall\ Max}$	Maximum time a particle can spend falling in a single 6 hr tidal cycle (s)
t_o	Initial time when particles are suspended into the water column (s)
H_o	Height of particle suspension above the seafloor (m)

Table 3-3. Numerical description of single and prolonged arrests, as well as clogging events, recorded in *Rhabdocalyptus dawsoni* and *Heterochone calyx*.

Sponge Species	Type of Response	Total Number	Length (min) (mean ± SD)			Rate (s^{-1})	
			Arrest Phase	Recovery Phase	Total	Arrest Phase	Recovery Phase
R. dawsoni	**Single Arrest**	8	0.32 – 3.55 (0.91 ± 1.01)	0.33 – 5.5 (1.21 ± 1.64)	0.65 - 9 (2.12 ± 2.64)	< -0.01 – 0.03	< -0.01 – -0.2
	Prolonged Arrest	1	61.5	N/A	> 360	0.03	N/A
H. calyx	**Single Arrest**	5	0.47 – 2.97 (1.30 ± 1.03)	0.75 – 4.03 (2.46 ± 1.56)	1.2 - 7 (3.76 ± 2.5)	-0.01 – -0.03	< -0.01 – -0.02
	Prolonged Clogging Event	2	19.37 – 89.35 (54.36 ± 49.49)	28.13 – 115.17 (71.65 ± 61.54)	0.79 – 3.41 (2.1 ± 1.85)	-0.01 – -0.06	< -0.01 – -0.04

Table 3-4. Grain size composition of sediments from the northern Hecate Strait sponge reef (n = 4) and Fraser Ridge reef (n = 4). Results are pooled from all cores collected. * Denotes significant difference between the two locations.

Classification	Grain Size (µm)	Hecate Strait Total Dry Weight (g)	Hecate Strait Composition by weight (%)	Fraser Ridge Total Dry Weight (g)	Fraser Ridge Composition by weight (%)
Total Sample	-	1150.45	-	432.28	-
> Fine Sand*	> 212	799.10	69.46%	224.25	51.88%
Fine Sand	212-106	181.79	15.80%	40.16	9.29%
Very Fine Sand	106-63	61.77	5.37%	35.68	8.25%
Coarse Silt	63-45	33.85	2.94%	29.11	6.73%
Medium Silt*	45-20	70.21	6.10%	102.86	23.79%
Fine Silt	< 20	8.29	0.72%	0.32	0.07%

Table 3-5. Time spent in suspension (T_{Fall}) of each grain size measured at Hecate Strait.

Particle	**Settling velocity ($m\ s^{-1}$)**	**T_{Fall} (hr) when suspended to a height of 10 mab**	**T_{Fall} (hr) when suspended to a height of 5 mab**	**T_{Fall} (hr) when suspended to a height of 1 mab**
> Fine Sand	0.02607	0.11	0.05	0.01
Fine Sand	0.01470	0.19	0.09	0.02
Very Fine Sand	0.00415	0.67	0.33	0.07
Coarse Silt	0.00184	1.51	0.75	0.15
Medium Silt	0.00067	4.17	2.08	0.42
Fine Silt	0.00025	11.00	5.50	1.10

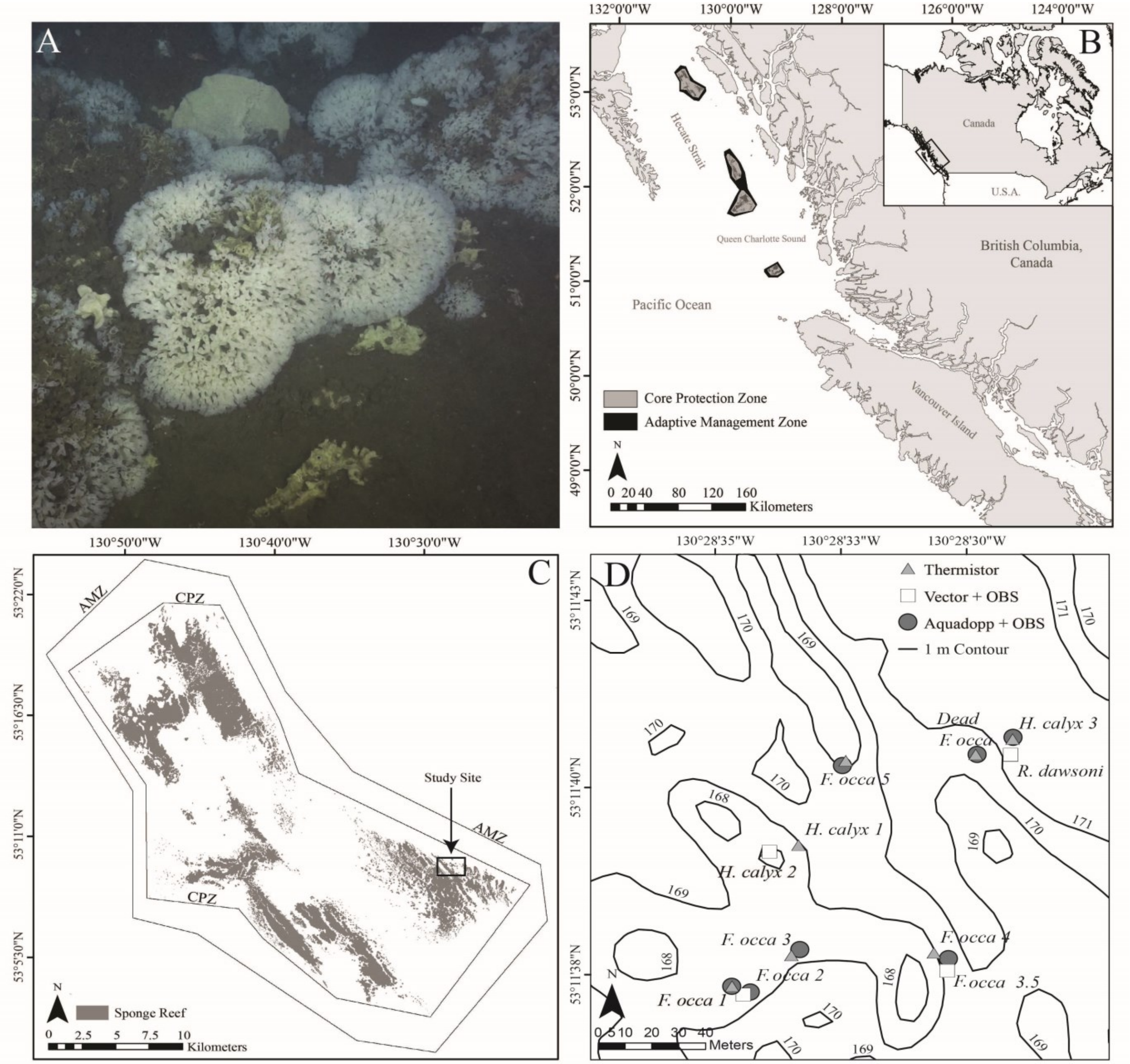

Figure 3-1: Location of the glass sponge reefs and MPA in northern British Columbia. (A) Sponges at the north-eastern portion of the northern reef complex. (B) Location of the Hecate Strait and Queen Charlotte Sound Glass Sponge Reef MPA. (C) Precise location of the northern sponge reef complex as delineated by multibeam bathymetry. Borders around the reef complex define the core protection zone (CPZ) and adaptive management zone (AMZ) boundaries. (D) Map showing the locations of individual sponges that were studied here.

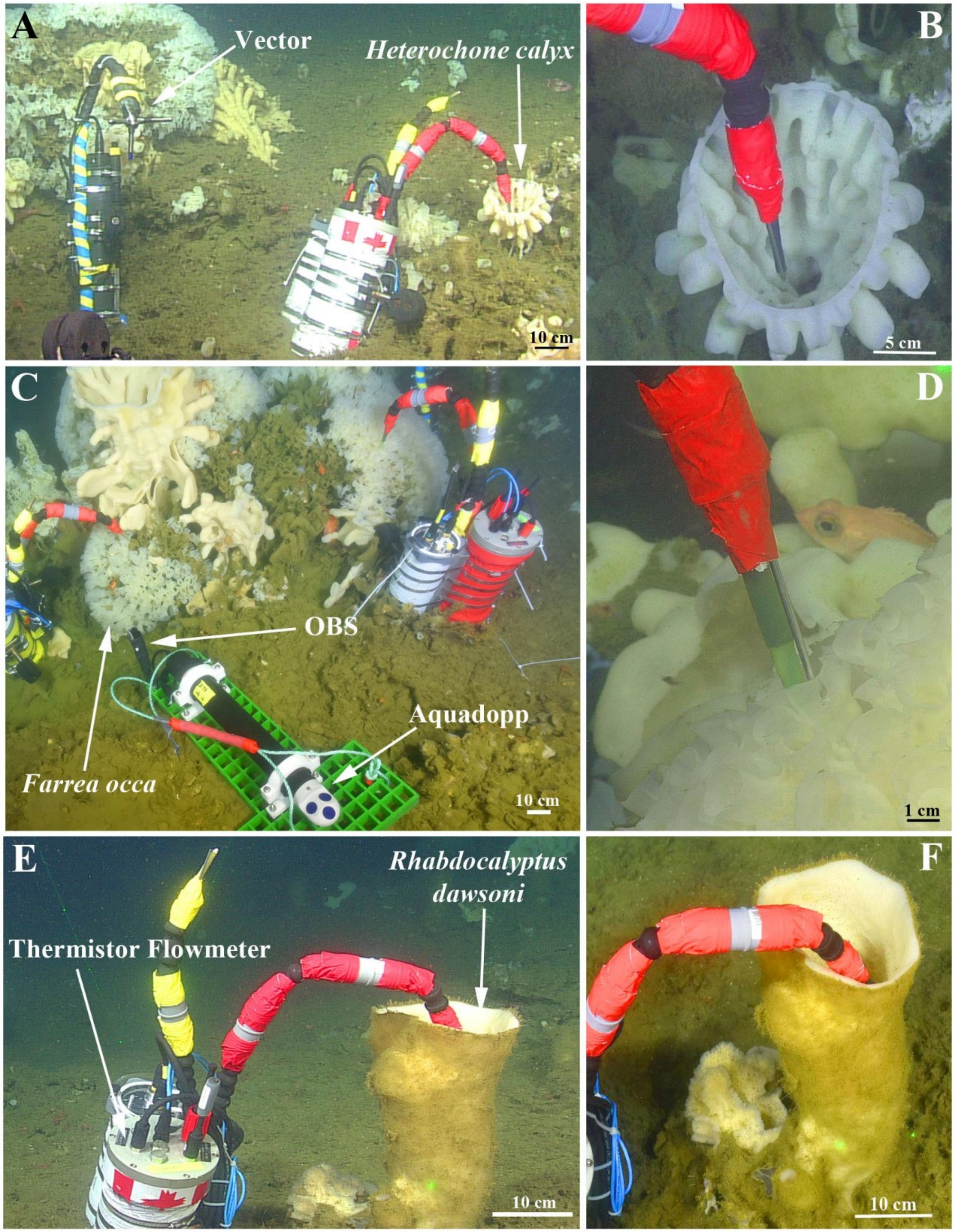

Figure 3-2: Overview of all sponge species and instrumentation used in situ (A, C, E). (B, D, F) Excurrent probes of the thermistor-flowmeters and oxygen sensors (red) were positioned into the center of the osculum without touching the body wall. Ambient sensors (yellow) were placed above the sponge oscula to record surrounding ambient current velocity.

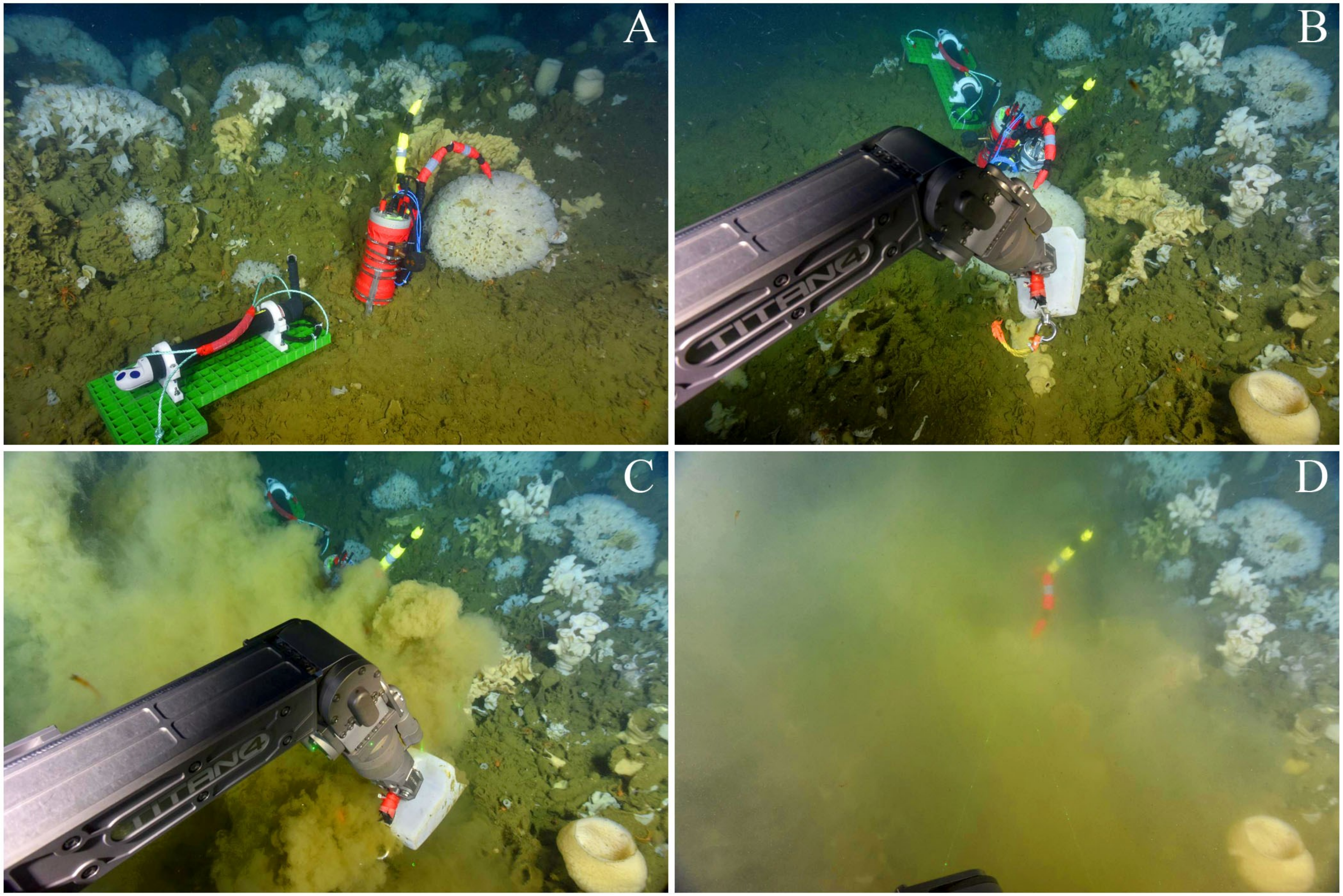

Figure 3-3: Experimental sediment disturbances were used to expose each species to increasing concentrations of suspended sediment. (A) Instruments were positioned adjacent to a sponge such that the optical backscatter sensor OBS would be down-stream from the sponge. (B) An example of the manipulator arm carrying out 'control scoops' of water with no sediment, towards *Farrea occa*. (C) An example a sediment disturbance generated by 'scooping' sediment towards the sponge and instruments. (D) A sediment plume engulfing the target specimen and instruments.

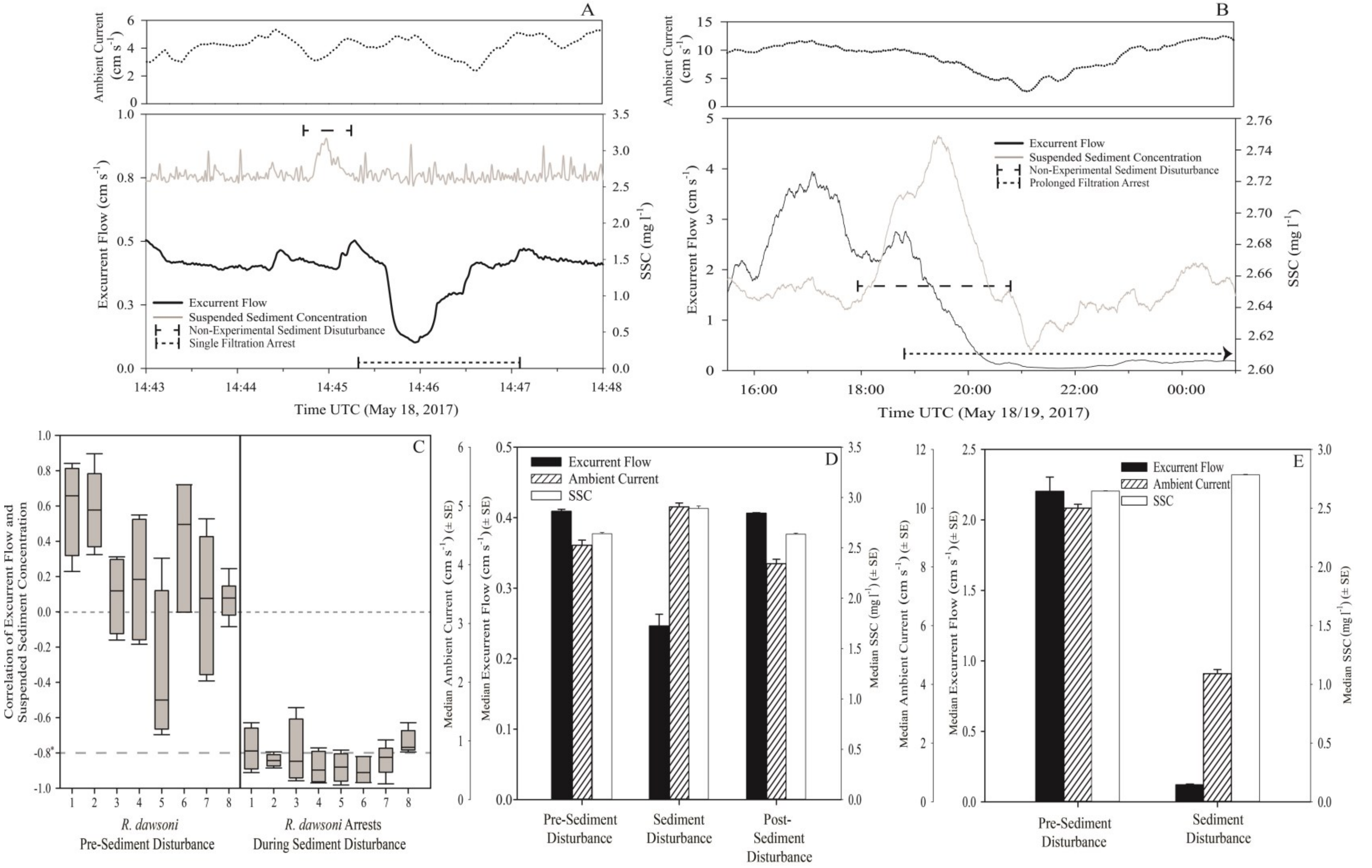

Figure 3-4: Filtration arrests by *Rhabdocalyptus dawsoni*. (A) A single arrest following a non-experimental sediment disturbance likely generated by the ROV. (B) A prolonged arrest associated with a 2.45 hr exposure to elevated suspended sediment concentrations (SSCs). (C) Correlation of SSCs and sponge pumping activity prior to and during filtrations arrests. (D) Median measurements of excurrent and ambient current velocity and of SSC prior to, during and after single arrests by *R. dawsoni*. (E) Median measurements of excurrent and ambient current velocity and of SSC before and during the prolonged arrest shown in (B). No measurements were made following this arrest.

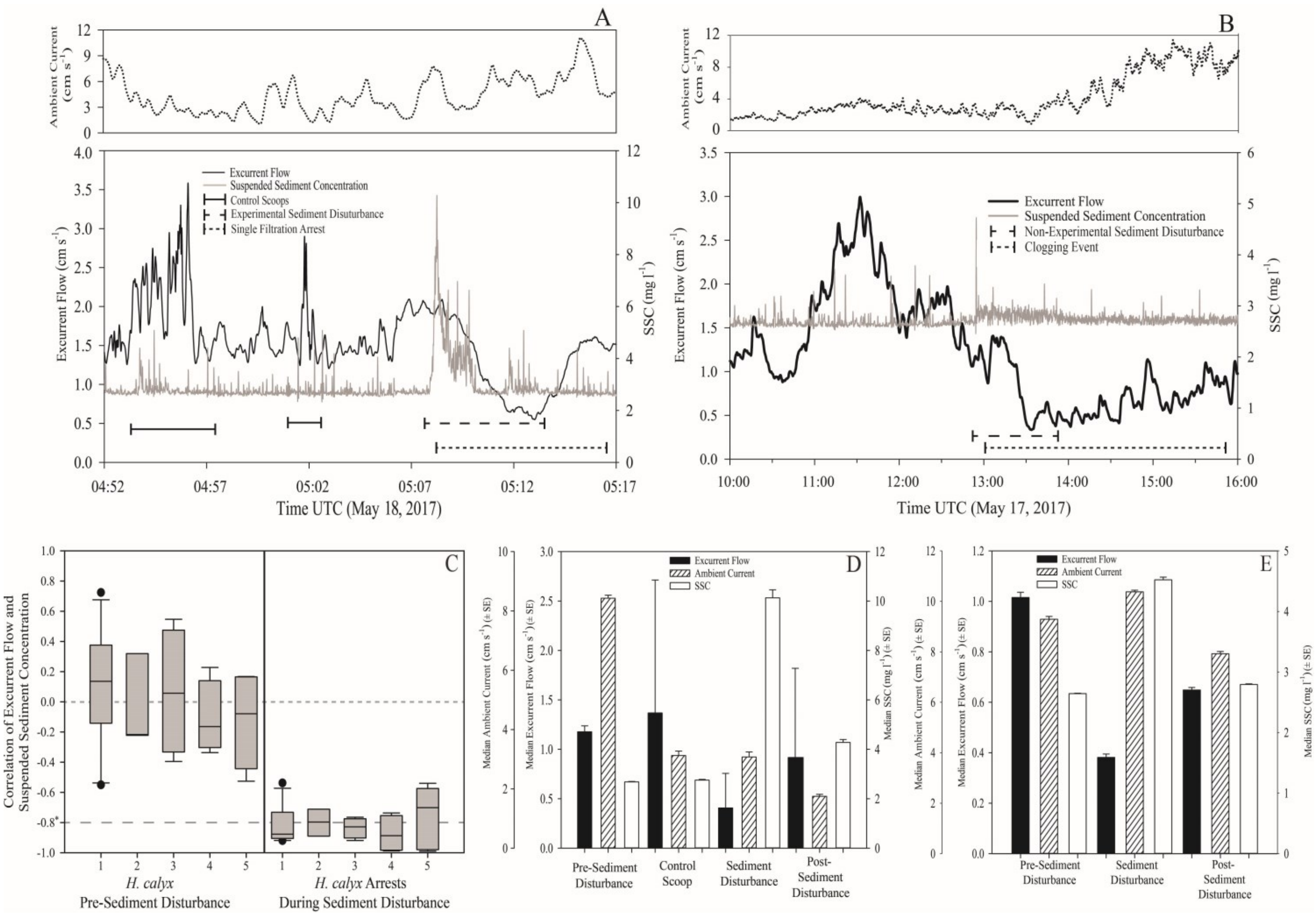

Figure 3-5: Filtration arrests by *Heterochone calyx*. (A) Two control scoops followed by an experimental sediment disturbance generated by the ROV ROPOS that induced a single arrest. (B) A clogging event associated with prolonged exposure (~0.8 hr), to elevated suspended sediment concentrations (SSCs). (C) Correlation of SSCs and sponge pumping activity prior to and during filtrations arrests. (D) Median measurements of excurrent and ambient current velocity and of SSC prior to and during the control scoop and single arrest and following the experimental sediment disturbance. (E) Median recordings of excurrent and ambient current velocity and of SSC before, during and after a clogging event.

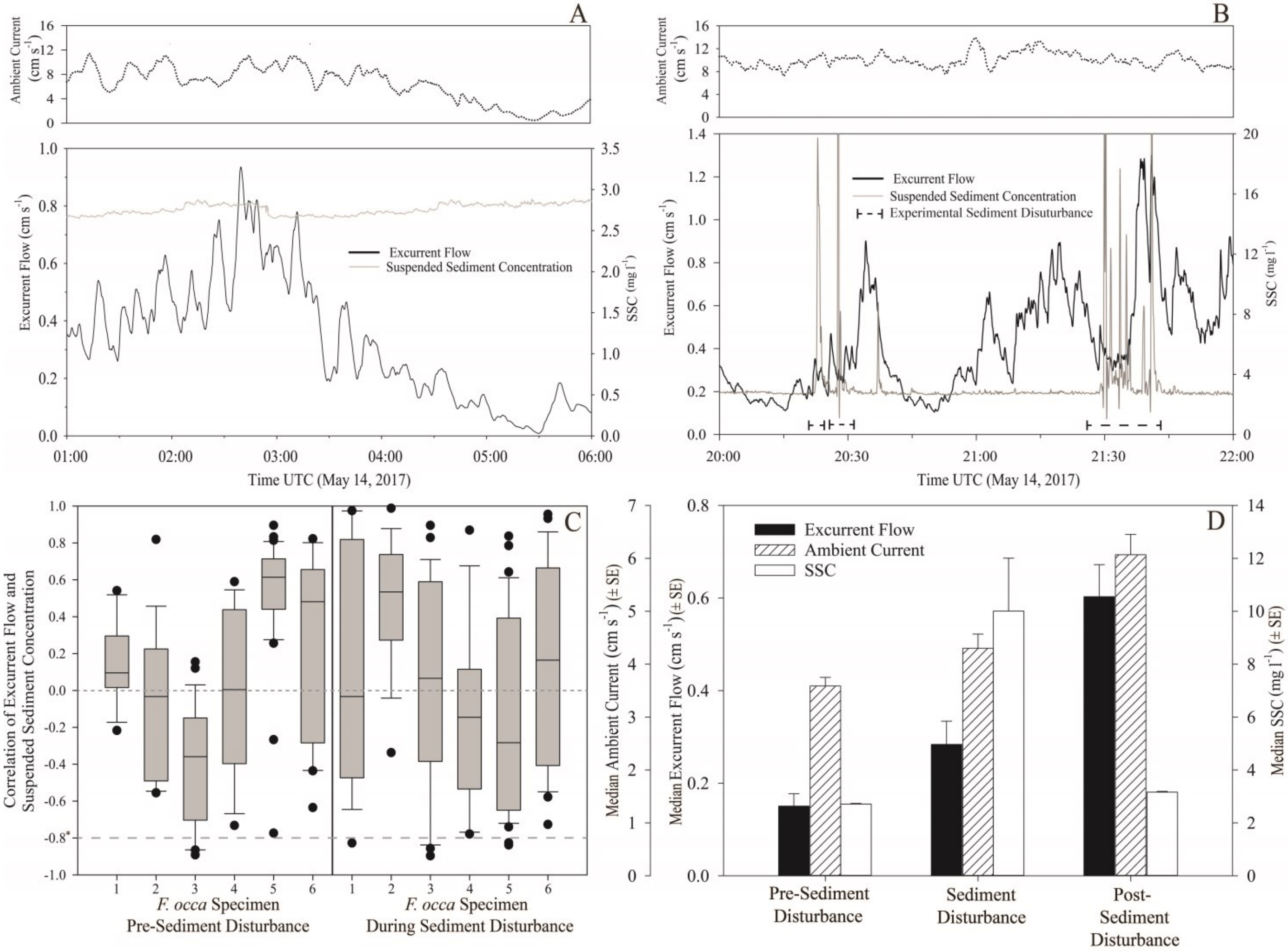

Figure 3-6: *Farrea occa* flow record. Excurrent and ambient flow recordings during undisturbed conditions and during experimental sediment disturbances. (A) Excurrent velocity follows the pattern of ambient flow during undisturbed conditions. (B) Excurrent flow increases in response to the scooping action but returns to pre-disturbance conditions without showing any clear arrest of filtration. (C) No correlation of pre-disturbance and disturbance flow with suspended sediment concentrations (SSCs) was found. (D) Median recordings of excurrent and ambient current velocity and of SSC before, during and after a sediment disturbance around a *F. occa* bush.

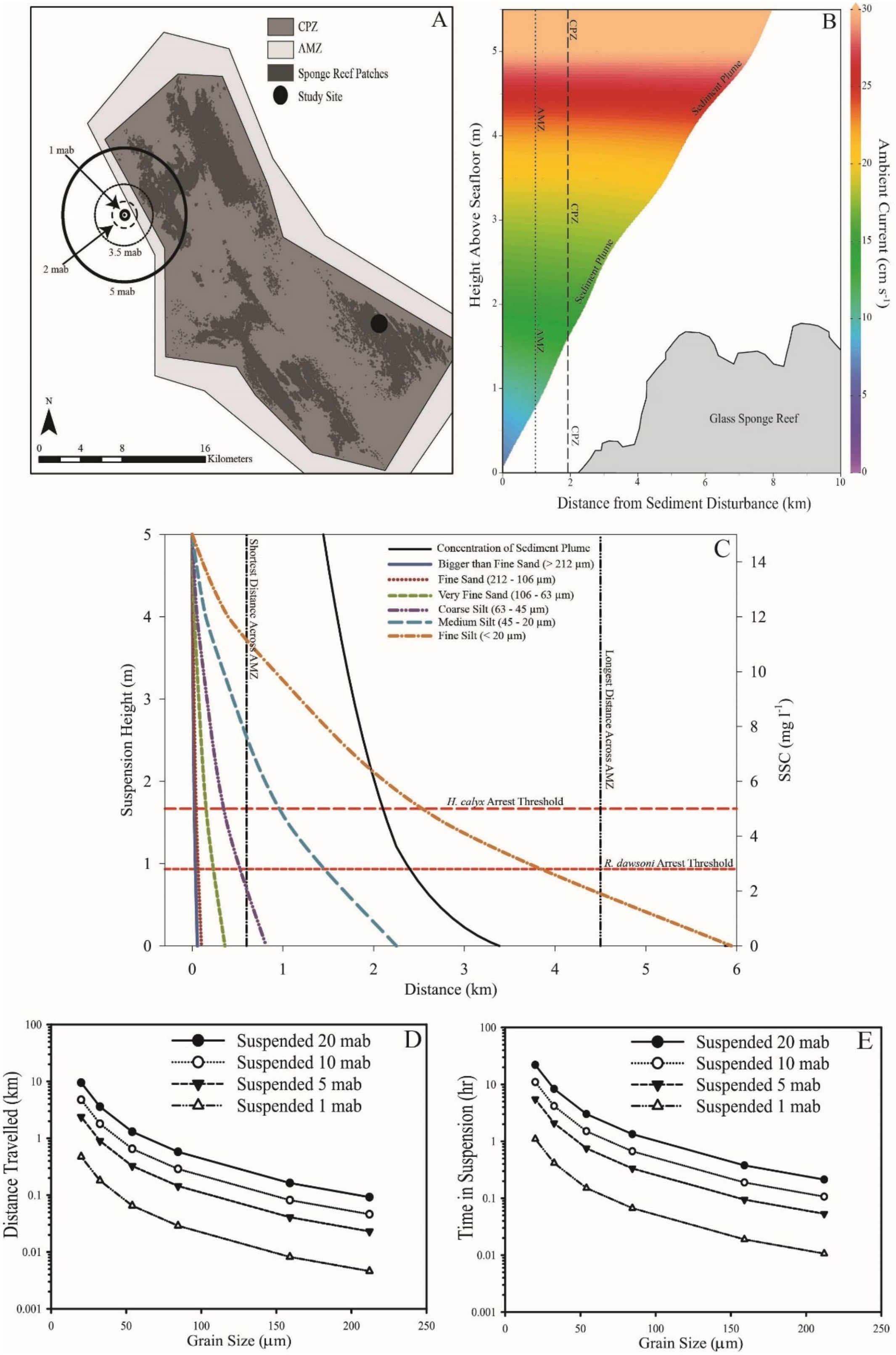

Figure 3-7: Model of the exposure potential of the northern reef complex within the Hecate Strait Marine Protected Area (MPA) sediment grains resuspended by bottom-contact trawling activity. (A) A top-down view of the maximum distance sediments would travel after

being suspended by a trawl. Each ring corresponds to a specific height of suspension and ambient current velocity. (B) A cross section showing the range of a plume of < 20 µm sediment grains (using the same model as A). Suspension heights of only a few meters are enough to allow particles to travel further than some of the current adaptive management zones. (C) The distance each grain size found at Hecate Strait will travel and the change in concentration of the sediment plume across that distance. Values are based on an initial 500 mg l^{-1} sediment plume suspended 5 mab. Threshold concentration for eliciting responses in *H. calyx* and *R. dawsoni* are drawn for reference along with maximum and minimum distances of the adaptive management zone (AMZ). (D) The maximum distance that a particle will travel in a single tidal cycle (6.15 hr) when suspended at various heights above the bottom (mab = meters above bottom). (E) Total time a particle or various grain sizes will remain in suspension when disturbed to a given height above the seafloor.

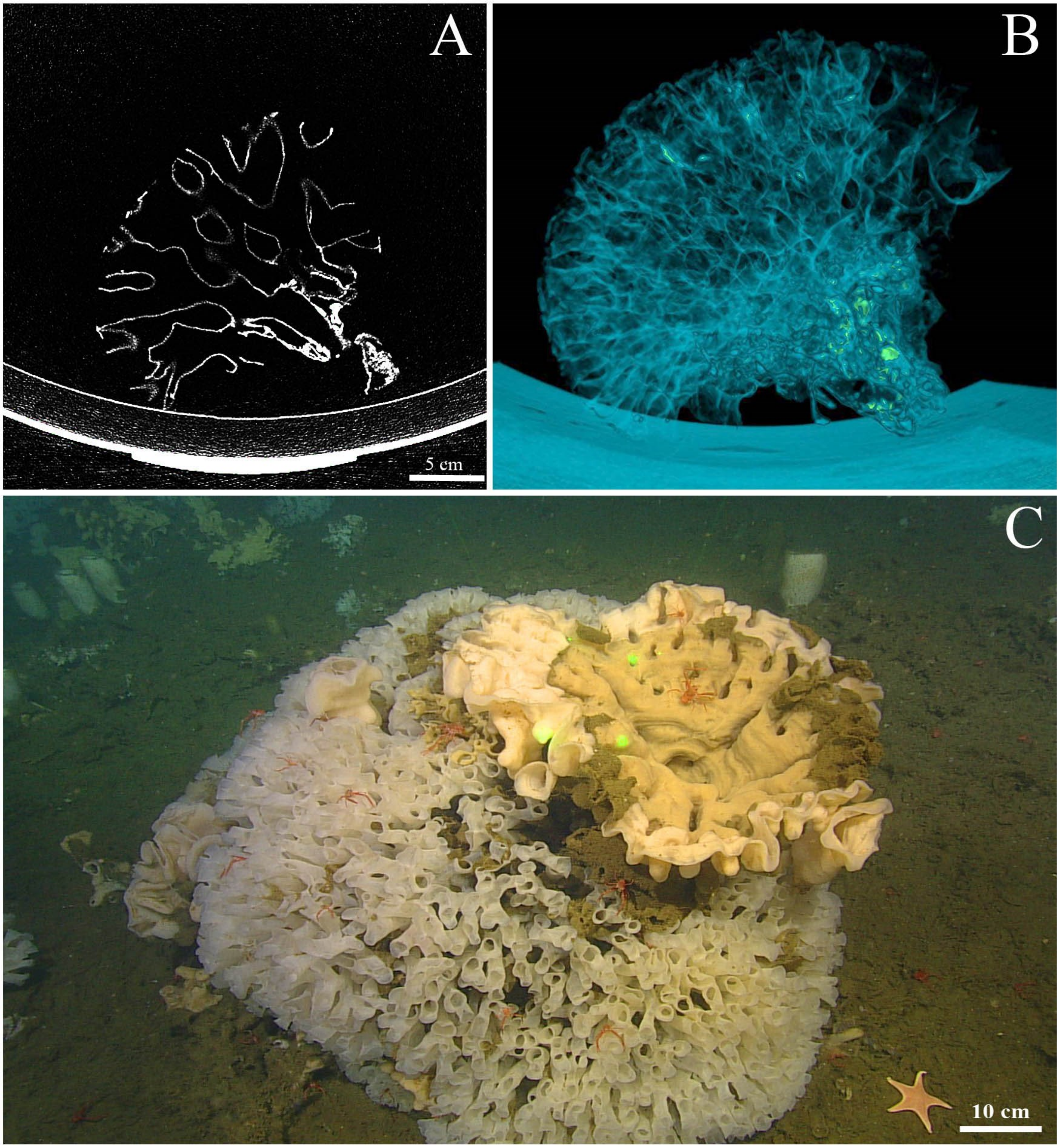

Figure 3-8: Views of the bush sponge *Farrea occa*. (A) CT side scan showing a cross section through a small sponge; (B) A 3-D model built by the CT scan sections; (C) An image of a *F. occa* bush with a *H. calyx* growing out of the top at the northern reef complex in Hecate Strait.

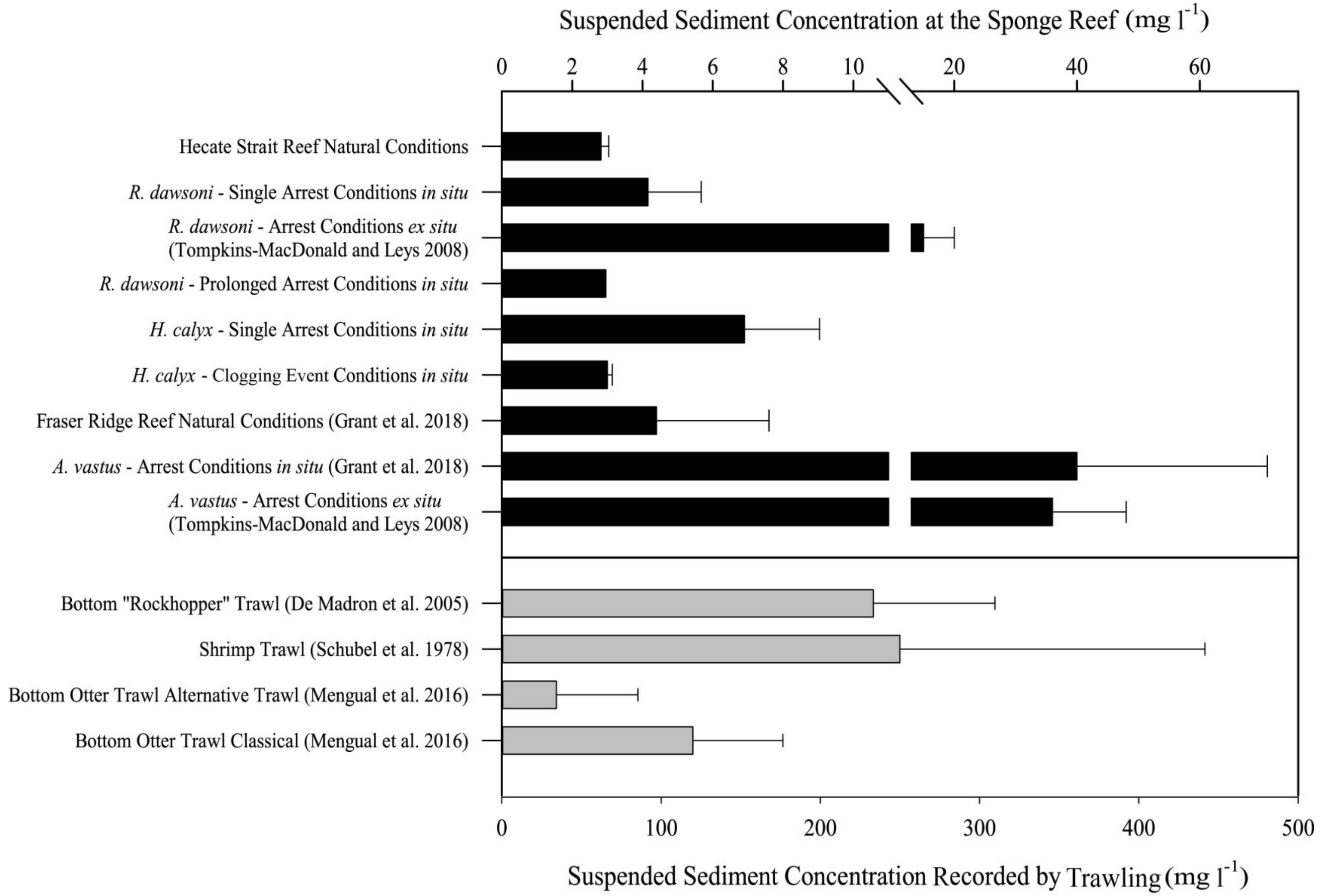

Figure 3-9: Suspended sediment concentrations (SSCs) associated with arrests in glass sponge species. Both *in situ* and in tank recordings are shown and are contrasted with SSCs known to be generated by different trawling gear. All thresholds of response by the glass sponges are below levels of SSC known to be generated by trawling activity.

Chapter 4. Discussion

4.1 Overview

The Hecate Strait and Queen Charlotte Sound Glass Sponge Reef Marine Protected Area (MPA), off the coast of British Columbia, Canada, was established in 2017 to protect a globally unique glass sponge reef habitat (Fisheries and Oceans Canada 2017c). This federal protection came to fruition 30 years after the initial discovery of the reefs, in 1987 (Conway et al. 1991). Since that time, researchers have steadily been filling in the remaining knowledge gaps through both laboratory and *in situ* studies. This thesis offers some of the first experimental, field-based results on the responsiveness of reef-building sponge species to suspended sediments. Here in Chapter Four, I will discuss the implications of these findings as they pertain to the wider relationships sponges have with sediment, additional factors that may impact the reefs, the future directions this work can take in regards to *Farrea occa*, the importance of field-based studies and how this work can be applied in the future conservation of sponge-based ecosystems.

4.2 Sponges and Sediment

Connections between sponges and sediments are not uncommon. In a review, Schönberg (2016) found 57 species and 10 genera of marine demosponges included some reference to sediments. Schönberg (2016) suggests that if one were to include all species names and genera that previously included references to sediments and those species with well-studied relationships with sediments, the proportion sponges whose ecology is directly connected to and influenced by sediment could be as high as 10% of all known sponge species. These relationships between sponges and sediments range from advantageous to detrimental depending on the habitat and species of sponge in question (Bell et al. 2015a). Some sponges reside in naturally sediment-rich habitats and have evolved strategies to take advantage of sediments. Incorporation of sediments into internal tissues (Cerrano et al. 2007, Giovine et al. 2013), forming crusts on external tissues (Cerrano et al. 2007, Schönberg 2016), cementing attachment points (Conway et al. 1991, Krautter et al. 2006) and even psammobiosis (living within sediments) (Rützler 1997, Ruetzler 2004, Cerrano et al. 2007) are all examples of positive sponge-sediment relationships.

In contrast to these interactions, and often more concerning, are the negative effects that sediments can have on many sponge species. As explored in this thesis, at glass sponge reefs, sediments induce filtration arrests in glass sponges that reduce feeding and respiration. Smothering and clogging by sediments is a concern for all sponges as sediment gains can block canals, cover and suffocate tissues and plug ostia, preventing sponges from filtering water (reviewed in Bell et al. 2015a). There is also evidence that suggests distributions of some species are limited, in part, by their response threshold to suspended sediments (Wilkinson and Cheshire 1989, Alvarez et al. 1990). To reduce the damaging effects of sediments, sponges respond by contracting ostia and canals to prevent entry of sediment, reducing pumping rate (possibly by contractions) and by producing mucus. These changes occur in response to SSCs at comparable threshold concentrations to those that elicit responses from reef-building glass sponges.

4.2.1 Physiological Sponge Responses to Sediments

Glass sponge arrests are coordinated cessations of filtration activity in response to a stimulus, which in this thesis is suspended sediment. These responses can be short 'on-off' responses termed 'single arrests', longer responses with a staggered return to undisturbed pumping activity which are termed 'coughing arrests' or the 'prolonged arrests' which are characterized by a delayed onset of the recovery phase of the response. Arrests, as described in Chapters 2 and 3, are only possible in glass sponges due to their syncytial tissues which allow electrical signals to propagate. In cellular sponges (classes Demospongiae, Calcarea and Homoscleromorpha), different responses have been observed.

Contraction of sponge tissues can control feeding and water movement in cellular sponges (Leys and Meech 2006). Contractions force water, sediment and any unwanted particles out and away from the sponge (Storr 1976, Elliott and Leys 2007). The entire sponge or individual portions of the animal (i.e., ostia, osculum and canals) have been observed contracting in response to mechanical stimuli across multiple studies (e.g., Prosser et al. 1962, Emson 1966, Prosser 1967, Nickel 2004b, Elliott and Leys 2007). These coordinated responses are not accomplished through electrical signalling, as is done for arrests in hexactinellids, but are instead thought to involve a combination of signalling molecules and mechanical cellular actions, as suggested by Leys and Meech (2006). Whole-body 'inflation-contraction' responses are possibly one of the most descriptively similar responses demosponges have to glass sponge arrests. They are actively triggered in response to the mechanical stimuli, are highly repeatable and are the result of the propagation of a response throughout the animal (Elliott 2004, Elliott and Leys 2007).

One of the more well-studied responses many sponges have to unwanted sediments is changes in pumping activity. Filtration arrests in glass sponges are often compared to reduction in pumping, which have been recorded in demosponges in various habitats across the globe (e.g., Reiswig 1971a, Gerrodette and Flechsig 1979, Ilan and Abelson 1995, Tompkins-MacDonald and Leys 2008). However, this is not the same as the instant filtration arrests seen in glass sponges as it does not occur via electrical signalling nor does it result in the complete cessation of pumping activity. As demosponges are the largest class of sponges, representing ~ 90% of known sponge species (Van Soest et al. 2018), they have been the subject of much of the work done on the relationship between sponges and sediments. Demosponges tend to reduce their pumping activity and undergo periods of physiological shutdown following exposure to increased SSC (Reiswig 1971a, Gerrodette and Flechsig 1979). This places a metabolic strain on the animal but prevents the ingestion of sediments (Reiswig 1971a, Bannister 2008, Tjensvoll et al. 2013).

This response to sediments was first experimentally studied in the Caribbean demosponge *Aplysina lacunosa* (formerly *Verongia lacunosa*). Gerrodette and Flechsig (1979) found a 7.5 - 41.1% reduction in pumping rate when exposed to sediment concentrations of 11 mg l^{-1} or higher. In contrast, exposure to 3 mg l^{-1}, the natural turbidity of its habitat, elicited no response. Large-scale experimental trials by Lohrer et al. (2006a) found that demosponges (genus *Aaptos*) in northern New Zealand had a 17% reduction in oxygen consumption and 50% reduction in filtering activity three weeks after being exposed to higher than natural sediment conditions. Natural SSCs at the site were 5 to 10 mg l^{-1}, and the experimental addition of a ‘thick’ layer of ‘sediment-seawater slurry’ (20 mm deposit of 1:3 sediment to seawater mixture) was designed to exceed this (Lohrer et al. 2006b). Similar results were later found in the deep-water sponge *Geodia barretti* in the north Atlantic. *G. barretti* had an 86% reduction in respiration following exposure to 100 mg l^{-1} of sediment with thresholds for a response coming at 10 mg l^{-1} (Tjensvoll et al. 2013). The findings of Tjensvoll et al. (2013) showed that filtration reduction responses to suspended sediments occurred in deeper-dwelling, cold-water sponge species in addition to tropical species and that the thresholds for response are similar across some sponge species. These thresholds are seen on the glass sponge reefs as *Heterochone calyx* and *Aphrocallistes vastus* do not respond until sediment concentrations exceeded 5 and 10 mg l^{-1} respectively. These concentrations are above those caused by tidal resuspension (the natural turbidity) of each sponge's habitat.

Contractions and reductions in pumping activity are not the only response sponges have to increased SSCs. Bannister et al. (2012) observed increased mucus production by the demosponge *Rhopaleoides odorabile* on the Great Barrier Reef following exposure to SSCs > 35 mg l^{-1}. Increased mucus production to remove sediments from the body wall of a sponge has been observed in other species as well (e.g., Gerrodette and Flechsig 1979, Turon et al. 1999, Kowalke 2000), even though it can be energetically costly to produce (reviewed in Bell et al. 2015a). Mucus production has yet to be documented on any reef-building glass sponges despite observations that some fjord-dwelling individuals were 'dripping with mud' (Leys et al. 2004).

4.2.2 Sponge Distributions are Releated to the Sediment or Turbidity of their Natural Environment

In 1963, Backus carried out an experiment to transplant sponges from clear water habitats to sandy lagoons in the central Pacific (Bakus 1968). He found that the species unaccustomed to the more turbid environment showed adverse effects to their health due to burial and clogging from the higher sedimentation rates (Bakus 1968). While negative relationships between filter feeders and suspended sediments had been known for many decades, this study by Bakus (1968) was one of the first experimental trials to explore how changes in turbidity and sedimentation levels can limit sponge distributions. Similar findings were concluded by Gerrodette and Flechsig (1979) after studying the effects of sediments on demosponge *A. lacunosa* in the Caribbean. Gerrodette and Flechsig (1979) suggested that its 11 mg l^{-1} SSC threshold was a limiting factor for the distribution of *A. lacunosa* in the area. This relationship was later examined extensively by Zea (2001), who, after studying distribution patterns of 96 Caribbean demosponges, found that tolerance to sediments was an important factor in determining the distribution and abundance of species in that area.

More recently Bannister et al. (2007) studied two demosponge species on the Great Barrier Reef that are adapted to differing levels of suspended sediments. *Coscinoderma* sp. was found to be fairly tolerant of sediment and *R. odorabile* was more sensitive to sediment.

Bannister (2008) suggested that exposure beyond the sponge's native sediment regime would result in reduced survival and thus limit the distribution of these species to habitats where sedimentation does not naturally exceed those thresholds. Because of the variable concentrations of suspended sediment across the Great Barrier Reef, *Coscinoderma* sp. and *R. odorabile* were determined to have become adapted to habitat ranges that are, in part, limited by the sediment concentration in the water (Bannister et al. 2007, Bannister 2008). This relationship between sedimentation and sponge distribution has also been observed in over 100 demosponge species throughout Indonesia, Venezuela, the Great Barrier Reef and other reefs along eastern Australia (e.g., Wilkinson and Cheshire 1989, Wilkinson and Evans 1989, Alvarez et al. 1990, Hooper and Kennedy 2002, de Voogd et al. 2006). These results are paralleled at the glass sponge reefs by the absence of *Farrea occa* and *Rhabdocalyptus dawsoni* from our more sediment-laden reef study site, Fraser Ridge reef. This suggests that while the responses to sediment may be distinct among sponges (i.e., arrests of filtration in glass sponges or pumping reductions and contractions in demosponges), SSC thresholds still play a role in the distribution of sponges across both shallow-water, tropical environments and deep-water, colder environments.

4.2.3 The Influence of Sediment Grain Size on Sponge Pumping and Distrubution

Sediment grain size is a common thread among studies of this nature, with fine silts and clays (< 20 μm) being the most common grain size to cause problems for the sponges. This is because these grain sizes can be filtered into the aquiferous system of sponges (Bergquist 1978) while they are also the most likely to flock together and land on the body wall of a sponge. This would cause particles to build-up over the sponge's incurrent pores and lead to the eventual smothering or clogging the sponge (Nafe and Drake 1961, Bergquist 1978). Bannister (2008) found that fine, easily suspended clay grains increased *R. odorabile* respiration rates by up to 43 % while decreasing pumping activity, indicating metabolic stress. Bannister et al. (2012) showed that this species' distribution was negatively correlated with the presence of fine, easily suspended clay grains in the environment; 3.5 times more *R. odorabile* individuals were found on offshore reefs where there was lower clay content in the sediments. As sponges are obligate filterers with little selective control over the their initial particle intake (Reiswig 1971b), these smaller grains increase the metabolic cost of pumping in environments where they are present, possibly explaining the limited distribution of *R. odorabile* (Bannister 2008, Bannister et al.

2012). We see a similar trend at glass sponge reefs as our sediment samples from Fraser Ridge reef contained a larger proportion of silts and clays than those from Hecate Strait, 30.59 % to 9.76% respectively. Fraser Ridge reef was also the site where we observed the absence of *F. occa* and *R. dawsoni*. *R. dawsoni* was the study species with the lowest sediment threshold and the threshold for *F. occa* has yet to be determined but could be quite low (see section 4.4.2). Their absences could be partially explained by the higher proportion of silts and clays in the water as these sizes are more easily resuspended.

4.3 Cumulative Impacts on Sponge Reefs

The stress associated with responding to bottom-contract trawling, and the suspended sediments it can generate, takes a toll on glass sponges. For example, *Aphrocallistes vastus* is known to have a balanced daily energy budget (Kahn et al. 2015) during its natural, undisturbed pumping activity. This means the food and nutrient consumption of a single specimen meets its daily energy usage during daily, uninterrupted filtering. Repeated single and coughing arrests can reduce the sponges ability to take up nutrients by up to 70%, which could be fatal for animals that live with such a tight energy budget (Grant et al. 2018; Chapter 2, this thesis). Arrests can be compensated for when food is highly abundant and the sponge is given ample time to recover, as is known from the survival of specimens exposed to repeated sediment exposures in laboratory studies (Tompkins-MacDonald and Leys 2008). However, in their natural habitat sponges will likely be exposed to repeated bouts of sediments from fishing activity in addition to other stressors not found in the laboratory. It is clear that the effects of fishing-induced suspended sediments on glass sponges can be detrimental on their own, but these can be compounded by number of additional stressors that reef-building glass sponges may experience such as changing ocean temperatures, oxygen and salinity due to climate change, El Niño-induced increases in coastal run-off and recovery strain and even fish farming.

4.3.1 Changing Water Properties

A common stressor associated with many marine ecosystems is climate change and this is no different for Canada's glass sponge reefs. The effects of global warming are not likely to cause large, fast or drastic changes to the sponges' environments, but additional stressors like changing water temperature, salinity and oxygen levels should still be accounted for when addressing sponge conservation legislation.

The most common factor associated with climate change is often rising global temperatures, such as the continued increase in ocean sea surface temperature. This rise in temperature, ~ 0.2 ºC per decade, may cause variability in surface currents and productivity which could be stressful for glass sponges as they rely on these avenues for feeding (Royer 1989, Hansen et al. 2006). However, changes in continental and ocean temperatures could alter how sponges react to sediments as well. Glass sponges on the Pacific coast of British Columbia are known to have an optimum temperature associated with their filtration and arrest responses, between 7 and 12 ºC (Leys and Meech 2006). Changes in ocean temperature of just a few degrees could exceed the glass sponge optimal environmental zone, preventing arrests when above 12 ºC. This is predominately a concern for those reefs found at shallower depths, 30 m, but evidence suggests that deep water temperatures are also increasing with climate change (Purkey and Johnson 2010). This warming has been recorded as deep as 1000 m, well below the deepest sponge reefs, which are found between 170 and 200 m.

As global temperatures rise, the rate at which glacial and sea ice melt also increases, primarily in polar regions (Hansen et al. 2006, Larsen et al. 2007). At first this may not seem like a concern for glass sponge reefs but both Alaska and B.C. have glaciers that are melting similarly to those elsewhere in the world (Larsen et al. 2007). Melting glacial ice can cause an influx of freshwater into the fjords and surrounding areas, decreasing the salinity. While this may not be a primary concern for sponges with the MPA, those found in shallower waters will likely be affected by this. Leys et al. (2004) found that fjord sponges were more abundant towards the oceanic end of Pacific Canada's fjords. Sponges appeared to preferentially settle and grow away from the freshwater input of the inland portion of the habitat (Farrow et al. 1983, Leys et al. 2004). The results of this thesis indicate that glass sponge species like *R. dawsoni* and *H. calyx* prefer stable environments and shifts in salinity could possibly add yet another stressor on to these sponges.

The distribution of many organisms is determined by the concentration of dissolved oxygen in the oceans deep waters (e.g., Wishner et al. 1990, Rogers 2000, Domke et al. 2017) and glass sponges are no exception. The habitat at which the sponges are currently found is balanced to meet these requirements but as the oceans change due to climate change, this may not be the case forever. A study by Leys et al. (2004) found that glass sponges require a steady income of water oxygenated to around ~ 2 ml l^{-1}. Whitney et al. (2005) estimated that if the steady flow of new water over a sponge reef were to cease, all the remaining dissolved oxygen would be used up by the ecosystem in less than two months indicating the necessity for a continuous influx of oxygenated water. Previous prolonged low-oxygen events in the region were also believed to be the cause of the numerous lifeless sponge skeletons observed at the lower depths of some fjords. This indicates that glass sponge reefs will be in danger if oxygen concentrations in the ambient water were to decline over time or if the hypoxic zones off the continental shelf were to rise (Leys et al. 2004, Stramma et al. 2010). Unfortunately, over recent decades, a negative trend in oxygen levels has been reported throughout the ocean (Matear et al. 2000, Matear and Hirst 2003), and the northeastern Pacific is no exception (Whitney et al. 2007, Kouketsu et al. 2010). Whitney et al. (2007) found that the dissolved oxygen concentration in this area was declining at a rate of 0.39 – 0.70 µmol O_2 kg^{-1} y^{-1}, marking a decline of 22% over the past 50 years. In some areas off the coast of British Columbia, Canada and Alaska, U.S.A., boundaries of hypoxia have moved shallower, from 400 m to 300 m, and have the potential to continue to shift as the effects of climate change continue (Andreev and Watanabe 2002, Whitney et al. 2007, Stramma et al. 2010). If these changes continue, the oxygen available to the sponges that form the reefs could fall below what is necessary for them to survive.

4.3.2 Amplified Coastal Run-off

El Niño events are known to increase precipitation in the Pacific Northwest of North America, leading to higher run-off rates in the region's rivers (Shabbar et al. 1997, Tang et al. 2015). This adds yet another stressor on Canada's glass sponges as more sediment could cause more frequent and longer arrests of filtration. Sediment run-off through the Fraser, Squamish and Campbell rivers is the primary source of sedimentation in much of the Strait of Georgia (Thomson 1981b, Hill et al. 2008). Increased precipitation in the winter and spring causes an influx of sediments into these rivers, which will then spread throughout the Strait of Georgia (Church et al. 1989, Shabbar et al. 1997, Hill et al. 2008). However, run-off is not limited to the Strait of Georgia and can occur in the fjords of British Columbia and northward along the coast of Hecate Strait (Thomson 1981b, Farrow et al. 1983, Whitney et al. 2005).

Leys et al. (2004) found that fjord sponges settle away from areas where run-off enters a fjord, increasing in abundance towards the oceanic end of the fjords (Farrow et al. 1983, Leys et al. 2004).

The distribution of all currently known glass sponge reefs and glass sponge-dominated ecosystems in the coastal waters of B.C. means that nearly every glass sponge-dominated habitat could be affected by increased sediment loads from climate change induced run-off. There are identified glass sponge reefs throughout the Strait of Georgia such as Fraser Ridge reef (Conway et al. 2007, Chu and Leys 2010, Fisheries and Oceans Canada 2017a) and Howe Sound reefs (Leys et al. 2004, Fisheries and Oceans Canada 2018) and more reefs continue to be discovered such as the reefs near Port Hardy, B.C. which reside only 30 m below the surface (Jameson 2018). Heading northward, sponge reefs exist within Queen Charlotte Sound and Hecate Strait (Conway et al. 1991, Krautter et al. 2001) and more glass sponges reside within numerous fjords throughout the western Canadian coast (Leys et al. 2004). Sponges and sponge reefs found in shallower waters and in the fjords will likely be affected first but the affected area could increase as sediments continue to spread out from the rivers and fjords.

4.3.3 Variations in Recovery Strain during El Niño / La Niña

There is evidence to suggest that some reef sponges may grow faster during cooler La Niña periods and grow slower during warmer El Niño years. During El Niño years, the waters off the coast of British Columbia tend to warm and the influx of deep-water nutrients up to the surface decreases, resulting in less primary production and lower amounts of marine snow (Mysak 1986, Philander et al. 1989). The opposite is true for La Niña events, which cool the coastal waters off British Columbia, bringing more nutrients up from the depths and likely increasing the food availability for reef sponges as glass sponges feed on the bacteria and marine snow that falls from the surface waters. Marliave (2016) found that *A. vastus* damaged by trawling gear had greater healing and resilience during the cooler La Niña events when more food is available compared to those measured during El Niño periods. Sponge recovery during a warmer El Niño year was slower and even unsuccessful in some instances (Marliave 2016, Marliave 2017), possibly because the energy available to a sponge for the repairing of damaged tissues is negatively influenced by warming El Niño events. Though this work is still in its infancy, the current evidence suggests that the effect of an El Niño period could be additive to the negative energetic effects that arrests of feeding currents caused by sediment have on sponges. Arresting filtration can greatly reduce the time available for the sponges to feed and respire, and so recovery following these behaviours is crucial to a glass sponge's well-being. Offsetting the lost feeding time might therefore be more difficult during El Niño periods.

4.3.4 Recent Observations from Fish Farms

The impact the fisheries industry can have on sponge reefs extends beyond suspended sediments and the numerous observations of barren trawling tracks occasionally littered with the fragments and stumps of glass sponges in the northern reefs (Conway et al. 1991, Conway 1999, Krautter et al. 2001, Malecha and Heifetz 2017). Observations near Port Hardy B.C. found that fish farming can also affect a reef. Recent footage of two shallow sponge reefs in the Broughton Archipelago, B.C. shows one vibrant, flourishing *A. vastus*-based reef contrasted with the second reef smothered and nearly completely dead (Jameson 2018). This second reef resides underneath an open net-pen salmon farm, resulting in the sponges being covered in a steady rain of feed waste and fish feces (Lavoie 2018). No formal research has been conducted on the effects of fish farming on the reefs, but the available footage gives a clear indication of the damage that can occur.

4.4 *Farrea occa*

4.4.1 A Unique Case Study Among Reef-building Glass Sponges

As presented in Chapter Three, *Farrea occa* was found to differ from the other two reef-building glass sponge species in not clearly arresting its filtration. The pumping rate of *F. occa* appeared to be so low that excurrent velocities could not reliably be distinguished by our flowmeters in the field; therefore we could not distinguish active pumping from the ambient flow. Specimens of *F. occa* were collected by the ROV (remotely operated vehicle), and when they were first on the deck of the ship we put fluorescein dye on the body wall inside the collection tank. We saw dye being drawn through the body very slowly before it stopped completely. Given that the ambient water inside the tank was stagnant this indicates that the movement of the dye was due to the sponge actively pumping water through its tissues. The reason the pumping ceased shortly after our observations is unclear. The sponge may have been irritated by the process of being brought to the surface and arrested pumping activity as a result. Another possibility is that *F. occa* cannot sustain continuous flow through its body wall on its own, requiring ambient flow to help draw water through its tissue to meet its energy requirements. Further investigation could lead to a better understanding of this reef-building species.

A closer look at collected whole specimens of *F. occa* showed that this sponge's body wall is less than ~ 1 mm thick, which is consistent with descriptions made by Reiswig and Mehl (1991) and Leys et al. (2004), and has the appearance of folded paper tubes (Reiswig 2002). These thin tissues could be an evolutionary trait that accompanies reducing pumping capacity in this species. The thinner tissues of *F. occa* could require less daily energy to draw water through than the thicker tissues found in sponges like *Aphrocallistes vastus*, *Heterochone calyx* and *Rhabdocalyptus dawsoni*. Additionally, large *F. occa* bushes (~ 2 m in diameter) initially appear to be towering masses of living tissue yet photographs and ROV footage from our 2017 expedition show it is likely that only the outer ~ 30 cm of each bush that is live, growing tissue. The internal sections of these large bushes appeared dead, possibly indicating that the species is not able to maintain large quantities of living tissue with its pumping rate.

A CT scan of a 30 cm diameter bush showed that *F. occa* consists of a series of interconnected tubes that are completely hollow from the top of each osculum to the base of the sponge. *F. occa*'s body form may facilitate the movement of ambient currents throughout the sponge to compensate for its limited pumping activity. Ambient water likely flows between and through the tubes naturally at the reefs with the bottom currents, in an "induced current"-like model, similar to what was described by Vogel (1974, 1977) and Leys et al. (2011). *F. occa* could take advantage of this to help draw water through its tissues instead of forming its own current in the way other sponge species do.

4.4.2 Species Distribution

Despite its high abundance at the northern sponge reef, our understanding of *F. occa* and why it is dominant in these areas is limited. Its distribution is limited amongst the known sponge reefs when compared to *Aphrocallistes vastus* and *Heterochone calyx*. At our 2017 study site at the northern reef complex of the MPA, *F. occa* was the dominant reef-builder yet is completely absent from other reefs in the Strait of Georgia. This limitation is particularly interesting as *F. occa* is considered a deep-water cosmopolitan species, with a depth distribution of 50 to 5218 m (Burton 1928, Reiswig 2002, Stone et al. 2011). Why this globally distributed species would be limited to individual reefs remains unclear but it could be due to the environmental conditions at these reefs.

F. occa is generally recorded at depths below 200 m in areas such as Portugal, New Zealand, Antarctica, California, U.S.A., Madagascar, Indonesia and the North Atlantic (Burton 1928, Reiswig and Kelly 2011, OBIS 2018). These deep-water environments are characterized by their long-term stable conditions such as low temperatures, low but consistent food supply and low turbidity and sedimentation rates (Krautter et al. 2001, Davies et al. 2007). Off the coast of B.C., Canada and Alaska, U.S.A., *F. occa* is only found in similar stable environments. This stability is consistent with observations made by Krautter et al. (2001) that the foraminifera present at the Hecate Strait reefs mirror those found in other stable deep-sea environments. Leys et al. (2004) found *F. occa* in northern channels, fjords and Hecate Strait. These northern areas all share a similar stability among them, with consistent temperature, salinity, dissolved oxygen and turbidity being recorded (Whitney et al. 2005, Stone et al. 2013). Leys et al. (2004) failed to find it in the waters between Vancouver Island and the mainland and reef mapping in the Strait of Georgia by Conway et al. (2007) later confirmed the species' absence from that area. The waters in the Strait of Georgia, Howe Sound and surrounding fjords are continuously changing due to sediment input from the surrounding land and rivers (Thomson 1981b). Variable levels of sedimentation in these areas could be the limiting factor for the *F. occa* distribution. The minimal pumping activity of *F. occa* may only be effective at lower, consistent levels of sediment in the water, such as that found in Hecate Strait.

4.4.3 A Model Specimen for Experimentation

By using the specimens of *Farrea occa* we collected, it is possible to test these hypotheses about *F. occa* in preparation for future research expeditions. Our observation that this species ceases to pump completely once collected would suggest that using it in experimental trials in laboratory conditions will be difficult, if not impossible. Instead, experimental trials would need to be designed in the laboratory and then applied to *in situ* specimens. A 3-D rendering of *F. occa*, using data from the CT scans of our dried specimen, would allow us to make a printed, plastic model of the sponge that could be repeatedly used in experiments. This reusable model would allow us to test some of our current theories about *F. occa* and its role at the reefs. The model could be repeatedly placed into a flow flume with either dyes or sediments to see how flow interacts with this sponge's bush-like body form. The hollow body of *F. occa* may be designed to facilitate induced flow through its body from multiple angles or be optimally designed to baffle sediment while allowing some to pass through the sponge body, preventing the smothering and clogging we observe in other species. With a plastic model, the bush could be cut in half and one side replaced with a pane of plastic or glass to allow observations of what occurs internally within the bush. The concepts of induced flow and sediment baffling at the reefs could be explored using this experimental set-up. As sponge reefs are built on the cemented skeletons of deceased glass sponges, baffling sediments is a primary role of the reef-building species. This would also allow us to determine if induced currents through the sponge would facilitate continuous water flow despite the presence of sediments.

4.5 Field Studies vs. Laboratory Studies

The motivation for the work carried out in this thesis came from the lack of *in situ*-based knowledge of how the glass sponge reef species respond to suspended sediments. Observations of extensive trawling damage at the Hecate Strait reefs (e.g., Conway et al. 1991, Conway et al. 2001) prompted a protection plan for the reefs to be set in place over the course of the 30 years following their discovery. After the implementation of fishing closures and proposal of the adaptive management zone (AMZ) to protect the sponge reefs from trawl-induced suspended sediments, members of the fishing industry cited the lack of field experiments these decisions were based on (Fisheries and Oceans Canada 2014b). Prior to this work, our understanding of these responses was limited to observations of *Rhabdocalyptus dawsoni* arresting filtration as divers approached (Lawn et al. 1981, Mackie et al. 1983, Leys and Mackie 1997) and the laboratory study on *R. dawsoni* and *Aphrocallistes vastus* by Tompkins-MacDonald and Leys (2008). Through the *in situ* recordings analyzed in Chapters 2 and 3, it was discovered that those *ex situ* results may have been underestimations of how sponges respond to sediments in the field. Tompkins-MacDonald and Leys (2008) reported that that *R. dawsoni* arrested filtration at suspended sediment concentrations (SSCs) of 15 mg l^{-1} and *A. vastus* arrests at 36 mg l^{-1}. However, field-based recordings place these thresholds lower, around 3 mg l^{-1} for *R. dawsoni* and 10 mg l^{-1} for *A. vastus*. These results emphasize the importance of studying sponges in the field and without them, any legislation and protection based solely on laboratory results may be overestimating the amount of sediment reef sponges can tolerate.

However, a purely field-based approach is not necessarily a viable or even positive approach. Studying glass sponges *in situ* is difficult and costly as they are primarily a deep-water animal, often found below 300 m (Leys et al. 2007) or below 80 m in the case of the sponge reefs (Conway et al. 1991, Conway 1999). Some glass sponge species can be reached by SCUBA from the fjords along the coast of B.C., Canada, such as *R. dawsoni* found at 30 m, but not all species are present at these depths. The three reef-building species are generally collected by ROV at depths beyond 100 m (Tompkins-MacDonald and Leys 2008). This process is expensive both monetarily and in terms of time. Procurement and operation of an ROV, such as ROPOS which was used for this thesis, costs upwards of $500,000 CAD (http://ropos.com) while the ship time and crew for an expedition to the reefs can cost an additional > $400,000 CAD. The high level of expertise required, limited ability to control external variables and necessary custom instrumentation make it difficult to accurately and consistently collect results. The thermistors used for this thesis had to be custom-made to collect the appropriate data accurately at depth, and has been an iterative process over many years (LaBarbera and Vogel 1976, Leys et al. 1999, Tompkins-MacDonald and Leys 2008). Additional recording equipment, such as the acoustic Doppler velocimeter (Vector ADV, Nortek, Rud, Norway), acoustic Doppler current profiler (ADCP, Nortek, Rud, Norway) and optical backscatter sensor (OBS, Campbell Scientific, Edmonton, Canada) can individually cost $10,000 CAD. All of these instruments require extensive calibration prior to deployment and expertise to both retrieve and understand the data output. Additionally, any adjustments to the experimental design or additional data and variables needed for analysis must be done and collected while in the field as otherwise they cannot be included in the analysis until another expedition is undertaken. During our time in the field, our team encountered many set backs such as interference from animals, changing currents, inconsistent ambient conditions and continual recovery and redeployment of the instruments due to battery life constraints.

If conservation and management were to rely solely on results from field-based research for the protection of glass sponge reefs, their progress would be extraordinarily slow due to the time and costs associated with collecting such data. Utilizing laboratory studies allows for science-based conservation plans to be set in place much more quickly. Laboratory studies can be used to determine what should be studied in the field before any extensive costs are incurred. The field-based results presented here were not likely to be finalized before the implementation of the marine protected area (MPA) was completed. Laboratory studies can garner lower-cost, faster results with a larger number of trials that can then be complimented by field studies that provide the detailed and highly representative results which can ultimately be used to 'fine-tune' the size of the AMZ post-establishment. This highlights the benefit of the utilizing both laboratory and field-based research for conservation of the glass sponge reefs.

4.6 Global Conservation of Sponges

Only 20 of the ~ 8500 globally described sponge species appear on threatened species lists (Bell et al. 2015b) and as such, receive some level of protection. All listed species are marine sponges located in the northeastern Atlantic and Mediterranean, despite the wide distribution of both marine and freshwater sponges around the world. In a review by Bell et al. (2015b), the authors conclude that, on a global scale, most sponges may not appear threatened but this is likely due to how little information has been collected on the majority of sponge species the anthropogenic threats that may affect them. This is reflected in conservation practice as sponges often only receive protection when they reside within marine reserves and MPAs that are designated for other animals or ecosystems such as shallow- and deep-water coral reefs (Bell et al. 2015b). Some species are classified as forming vulnerable marine ecosystems and may receive some protection, but this only includes a select few of the most prominent species that form such ecosystems (Kenchington et al. 2015, Dinn 2018). Outside this, sponge-based protective legislation is limited to the Hecate Strait and Queen Charlotte Sound Glass Sponge Reef MPA.

Canada's glass sponge reefs are an example of a sponge-dominated ecosystem that is at the forefront of sponge conservation. Currently, not a single reef-building species is listed as threatened yet, in February of 2017, four glass sponge reefs were given protection within an MPA (Fisheries and Oceans Canada 2017c). Additional reefs throughout coastal B.C. had fishing closures implemented in their regions to offer some protection outside the MPA (Fisheries and Oceans Canada 2016, 2017d). This shows that conserving sponges based on their ecological importance, instead of their listed status, is possible. This MPA could be the catalyst for other sponge-dominated ecosystems to receive protection based on their communities and not the status of the present species.

Sponge grounds, “ostur”, sponge gardens and sponge fields are names given to the large assemblages of sponges found around the world, all of which are formed from combinations of calcareous, demosponge, homoscleromorph and hexactinellid sponges (Klitgaard 1995, Klitgaard and Tendal 2001, Marliave et al. 2009, Hogg et al. 2010). These habitats perform similar ecological functions to those of Canada’s glass sponge reefs (Maldonado et al. 2015). Large sponge grounds attract many species across a variety of taxa by providing microhabitats within their body forms and injecting habitat heterogeneity into areas that might otherwise be featureless (Bett and Rice 1992, Klitgaard 1995, Klitgaard and Tendal 2004). Vast sponge grounds in the northeastern Atlantic are threatened by bottom-contact trawling, drilling muds and mine tailings; similar habitats exist off Canada’s Arctic coastline (Kutti et al. 2015, Edge et al. 2016, Dinn 2018). When mining sediments and contaminants are released at high enough concentrations near the sponges, it can reduce their pumping activity and cause acute toxicity within sponge tissues, leading to sponge death. Kutti et al. (2015) found that *Geodia barretti*, one of the primary demosponge species in Atlantic sponge grounds, has a specific threshold for exposure time to and concentration of suspended stressors like mining contaminants and sediments. Knowledge of these impacts is crucial if this sponge-based ecosystem is to be appropriately protected. A well-informed protective plan, that parallels Canada’s glass sponge reef MPA, could be an ideal strategy for the future conservation of sponge grounds.

The results of Chapter Three represent how an understanding of present sponge species’ responses to suspended particles can inform the necessary sizing of MPA buffer zones. The initial establishment of the glass sponge MPA in Canada was based on the information available at the time. Trying to retroactively resize Canada’s current glass sponge MPA to completely accommodate newly uncovered sponge sediment thresholds will likely be difficult to achieve but should be attempted. As for other sponge reefs that have yet to be given a protective status, if responses and thresholds to stressors are known prior to the development of a sponge conservation plan, establishing properly sized MPAs that exclude a wide range of potentially harmful activities becomes easier. Designation of a larger AMZ, or even two levels of AMZs, would open up more options for changes to the conservation areas to be made once the science is available. Atlantic sponge grounds are but one example of an ecosystem where this could be implemented. Numerous other sponge-based ecosystems could benefit from MPAs that improve on the design and criteria of the Hecate Strait and Queen Charlotte Sound Glass Sponge Reef MPA.

4.7 Concluding Statements

Canada's glass sponge reefs are globally unique ecosystems that have remained a complex puzzle of questions and discoveries since they were found only 30 years ago. With this thesis I have provided a few more answers to the puzzle by focusing on the reef-building species themselves and their sensitivities to suspended sediments. Described here are three distinct classifications of filtration arrests in four glass sponge species along with their threshold sensitivity to sediment. I have provided information that can be used to improve current and future glass sponge reef MPA boundaries based on the reported responsiveness of each species. The preservation of Canada's unique glass sponge reefs is dependent on our ever-increasing understanding of the ecosystem and the resident sponge species themselves. Efforts should be made to fully understand the extent to which various stressors, like suspended sediments, will impact each reef-building species and how protective legislation and boundaries can be tailored to minimalize their impacts.

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Appendix 1. Supplemental Material for Chapter Two

Supplementary data related to the journal article:

Grant, N., Matveev, E., Kahn, A.S., Leys, S.P., 2018. Suspended sediment causes feeding current arrests in situ in the glass sponge *Aphrocallistes vastus*. *Marine Environmental Research*, **137**, 111-120.

has been published online and can be found at: http://dx.doi.org/10.7939/R3KS6JJ80 .

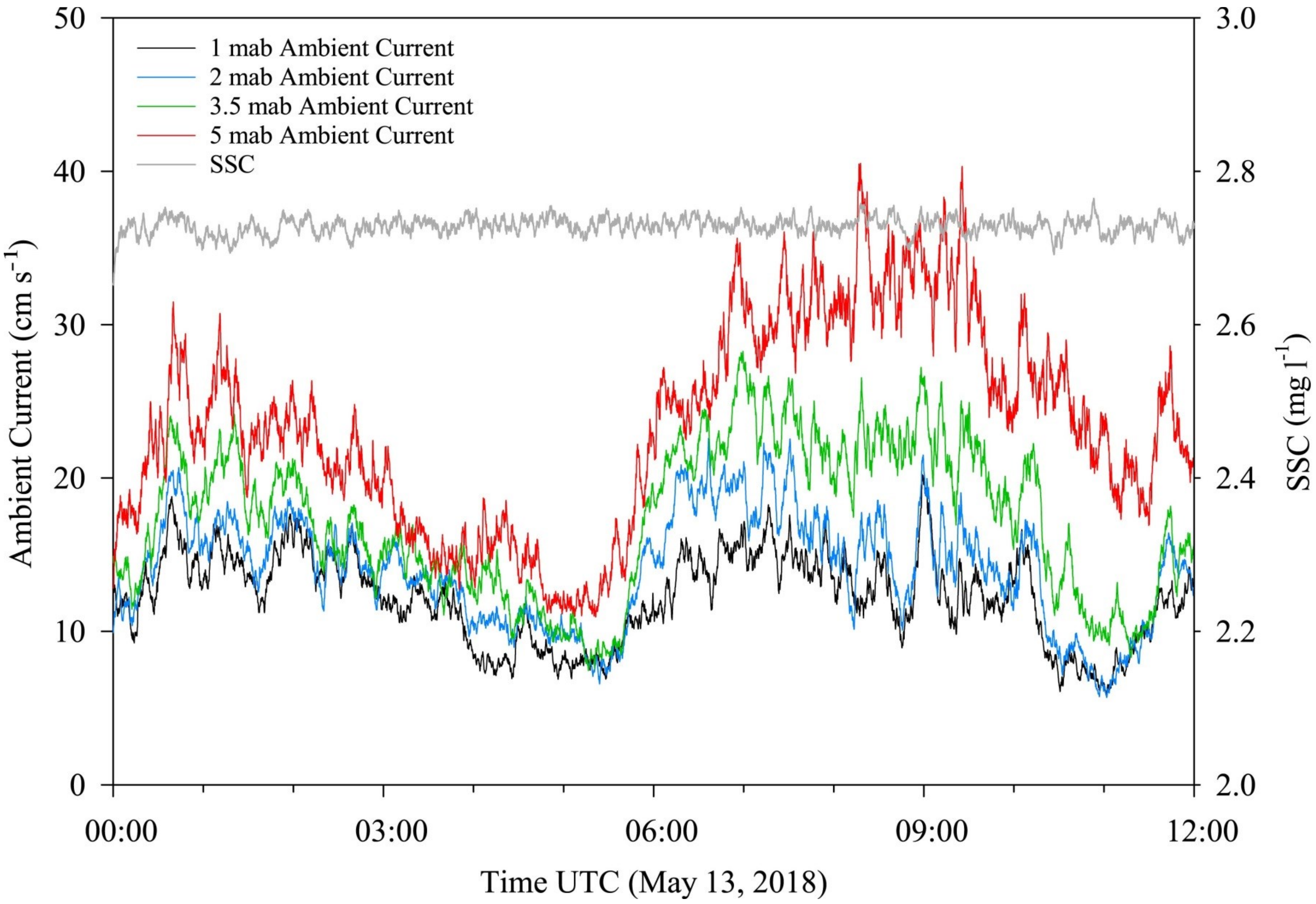
Appendix 2. Supplemental Material for Chapter Three

Supplemental Table 3-1. Mean, undisturbed measurements at the Hecate Strait reef recorded in May 2017. Overall ambient velocity is the mean flow recorded from the thermistors, Aquadopp and the Vector at 1 mab.

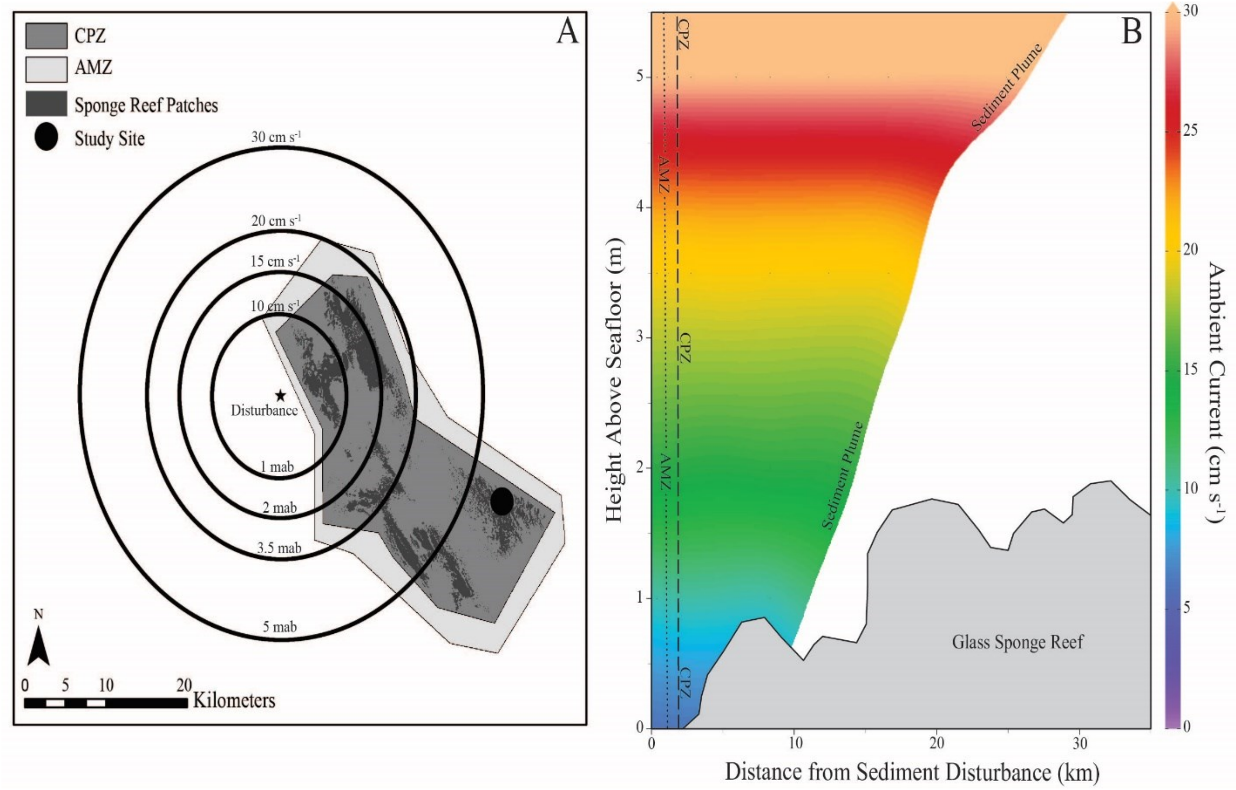
	Tidal Cycle	Mean	Standard Deviation
Suspended Sediment Concentration (mg l^{-1})		2.71	0.09
R. dawsoni Excurrent Velocity (cm s^{-1}) (n = 1)	Flood	2.56	0.88
	Slack	0.42	0.06
R. dawsoni Volumetric Flow (l s^{-1}) (n = 1)	Flood	1.03	0.00034
	Slack	0.17	0.00006
H. calyx Excurrent Velocity (cm s^{-1}) (n = 3)	Flood	1.75	0.44
	Slack	0.48	0.15
H. calyx Excurrent Volumetric Flow (l s^{-1}) (n = 3)	Flood	0.33	0.00027
	Slack	0.09	0.00007
F. occa Excurrent Velocity (cm s^{-1}) (n = 5)	Flood	1.54	1.18
	Slack	0.32	0.22
F. occa Excurrent Volumetric Flow (l s^{-1}) (n = 5)	Flood	0.00967	0.0001
	Slack	0.00201	0.00002
Overall Reef Ambient Velocity (cm s^{-1})	Flood	12.01	6.39
	Slack	6.31	3.63

Supplemental Table 3-2. Table of events that occurred at each sponge used in this study. Non-experimental disturbances can include resuspension due to fish activity and any suspended sediment not caused by the scooping action of ROPOS. *F. occa* 1 and 2 were side by side and experienced the same experimental disturbances.

Specimen	Length of recording (hr)	# of Total Single Arrests	# of Total Prolonged Arrests	# of Total Clogging Events	# of Sediment Disturbances Total	# of Arrests Due to Non-Experimental Disturbances	# of Arrests Due to Sediment Experiments	# of Control Scoops Done	Represented in:
Rhabdocalyptus dawsoni	21.5	8	1	-	1	9	-	1	Figure 3-4A-E
Heterochone calyx									
H. calyx 1	38.75	-	-	-	-	-	-	-	-
H. calyx 2	25.5	3	-	2	1	2 - Clogging	3	1	Figure 3-5A-E
H. calyx 3	20	2	-	-	1	-	2	-	Figure 3-5C
Farrea occa									
F. occa 1	37.5	-	-	-	4	-	-	-	Figure 3-6A-D
F. occa 2	4	-	-	-	4	-	-	-	Figure 3-6C
F. occa 3	38.5	-	-	-	3	-	-	-	Figure 3-6C
F. occa 4	21	-	-	-	1	-	-	-	Figure 3-6C
F. occa 5	27	-	-	-	1	-	-	1	Figure 3-6C
F. occa 6	27	-	-	-	1	-	-	-	Figure 3-6C
Dead *F. occa*	9.25	-	-	-	-	-	-	-	-



Supplemental Figure 3-1: The tidal cycle and ambient flow data at different heights above the bottom at the study site. There is no tidal resuspension of sediment despite fluctuations in ambient current velocity with tides. The heights above bottom (mab = meters above bottom) correspond to those shown in Figure 7A and B.



Supplemental Figure 3-2: A 'worst-case scenario' model of the exposure potential of the northern reef complex within the Hecate Strait Marine Protected Area (MPA) to < 20 µm sediment grains resuspended by bottom-contact trawling activity. This model represents what could happen if sediments were initially suspended by trawling activity, then transported by bottom currents but did not settle out of suspension. Turbulence and bottom currents keep particles in suspension in this model, allowing sediments to travel greater distances than those calculated in Figure 7. (A) A bird's eye view of the maximum distance sediments would travel. (B) A cross-section of the water column showing the range of the sediment plume following suspension.