



## Suspended sediment causes feeding current arrests *in situ* in the glass sponge *Aphrocallistes vastus*



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### ARTICLE INFO

#### Keywords:

Trawling  
*Aphrocallistes vastus*  
 Glass sponges  
 Reefs  
 Filter feeding  
 Suspended sediments  
 Porifera

### ABSTRACT

Bottom-contact trawling generates large, moving clouds of suspended sediments that can alter the behaviour of organisms adjacent to trawl paths. While increased suspended sediment concentrations (SSCs) are known to cause glass sponges to arrest filtration in lab studies, the response of sponges to sediment *in situ* is not yet known. Here we describe arrest behaviours in response to increased SSCs recorded from the glass sponge *Aphrocallistes vastus* at the Fraser Ridge sponge reef in the Strait of Georgia, British Columbia, Canada. We identified 23 arrests of the sponges' feeding current during experimental disturbances that raised SSC to between 10 and 80 mg l<sup>-1</sup>. Single arrests lasted 4.25 ± 1.3 min (± SD) and were characterized by a 2 cm s<sup>-1</sup> reduction in feeding current lasting 0.5–3 min (mean 1.91 ± 0.97 min, n = 19). In comparison, coughing arrests varied in length (31 ± 22.89 min) with arrest phases lasting 4–15 min (10.46 ± 5.26 min, n = 4). Coughing arrests showed a distinctive on/off pattern as sponge filtration returned to normal excurrent velocities, distinguishing them from single arrests. The onset of both arrest types was correlated with elevated SSCs (r = -0.83 to -0.92). Natural SSCs at the reef averaged 4.4 mg l<sup>-1</sup> and were correlated with tidal flow (r = 0.86 to 0.89). The combined data provide evidence that suspended sediments can stop glass sponge feeding *in situ* even at SSCs below those known to be generated by trawling.

### 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 that 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., 2015).

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, 1971; 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 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*

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*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 *Coscino-derma* 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, 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<sup>2</sup> 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, 2017a). 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. Methods

### 2.1. Study site

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* (Fig. 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 in order 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. 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 h 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 (Fig. 1b) such that the probe was completely in the osculum and did not touch the wall of the sponge (Fig. 1c). An 'Aquadopp' acoustic Doppler current profiler (ADCP, Nortek, Rud, Norway) was placed 17 m upstream of the thermistors (Fig. 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 (Fig. 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.

### 2.3. Data analysis

Thermistors recorded onto Omega data loggers (Laval, Canada) as voltage, which was converted to cm s<sup>-1</sup> using the calibrations made with the Vector ADV. Both the Vector and ADCP recorded velocity in m s<sup>-1</sup>, 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<sup>-1</sup> 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

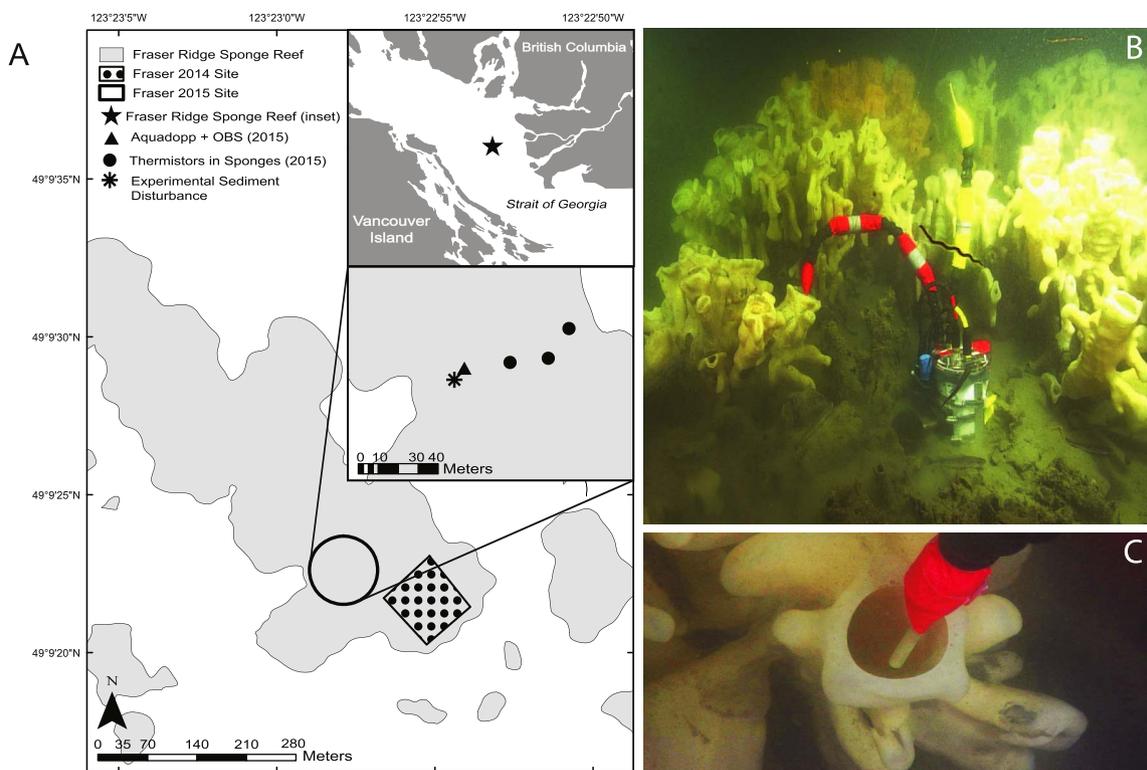


Fig. 1. A) Map of the 2014 and 2015 research sites located on Fraser Ridge reef, Strait of Georgia, B.C. B) A thermistor-flowmeter positioned in the osculum of *Aphrocallistes vastus*. C) View of the tip of the thermistor probe inserted into osculum of *A. vastus*.

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  $SSC = 0.0358 \cdot OBS \text{ counts} + 0.1542$  ( $R^2 = 0.99$ ). 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) (Fig. 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  $1.0 \text{ cm s}^{-1}$  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  $> 1.0 \text{ cm s}^{-1}$  in excurrent velocity with no concurrent reduction in ambient flow; an arrest phase lasting  $> 30 \text{ s}$ , 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

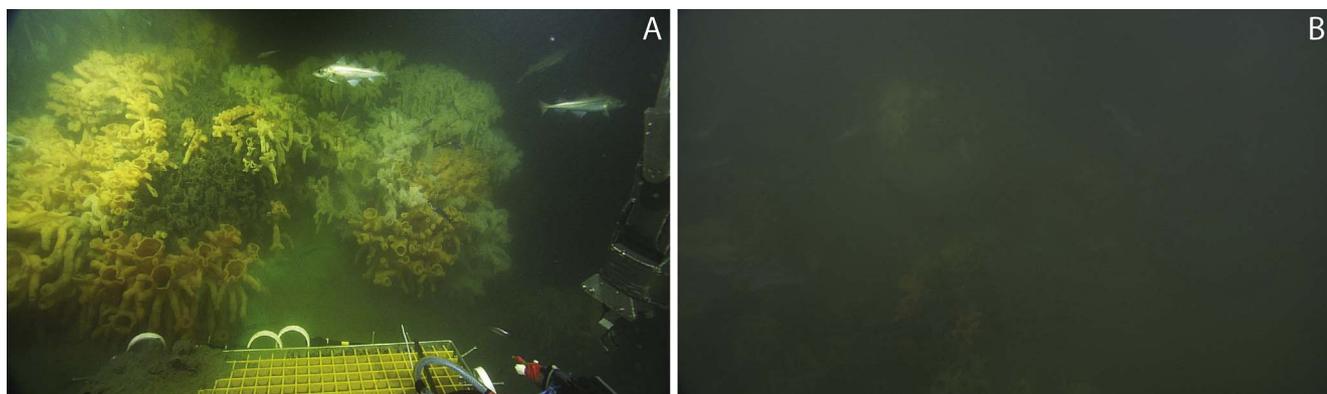
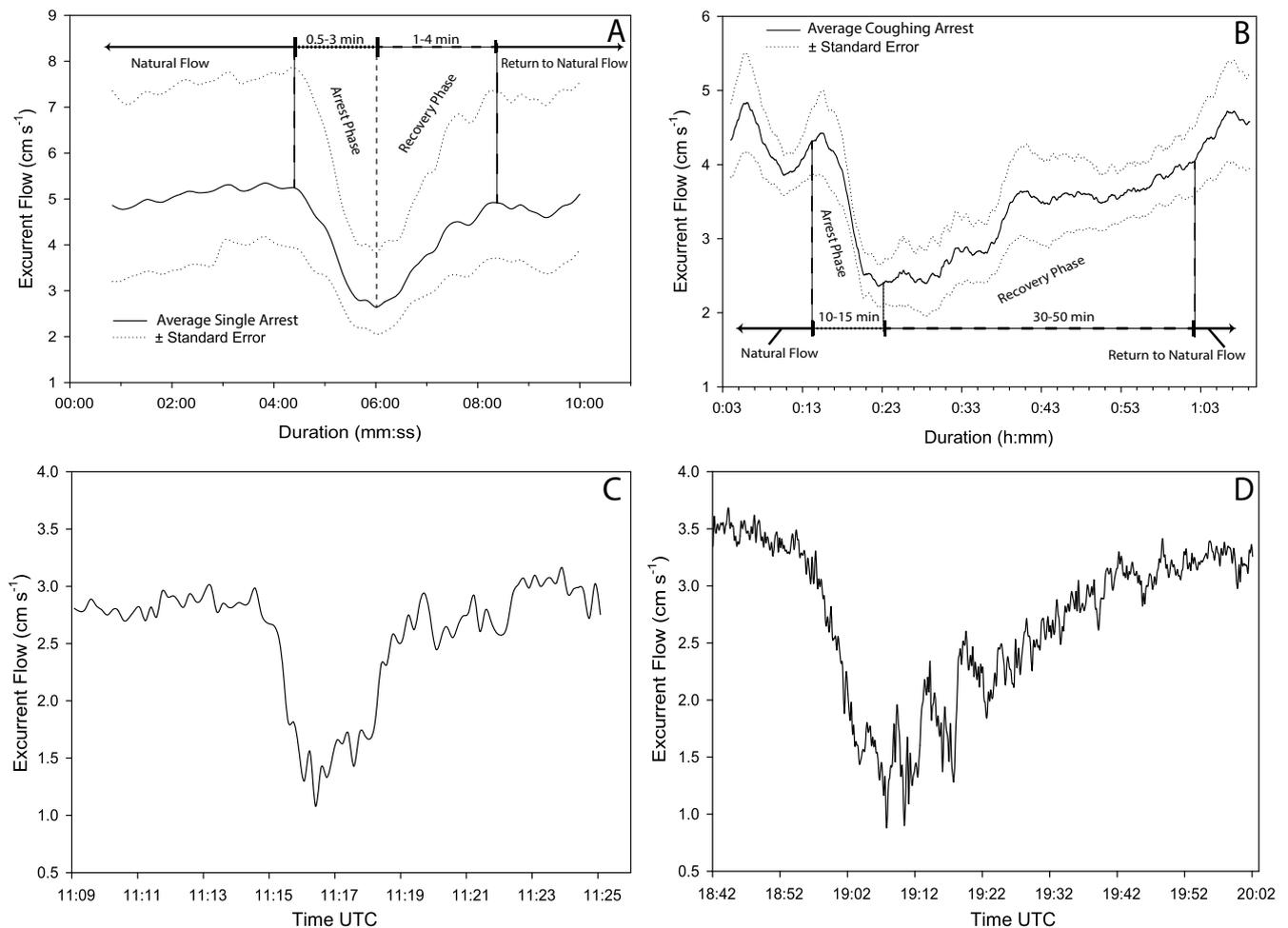


Fig. 2. View of sponge reef before (A) and after (B) an experimental sediment resuspension event created using ROPOS.



**Fig. 3.** Descriptive characteristics of a single and coughing arrest of the feeding current of *Aphrocallistes vastus*. (A) The average profile of a typical arrest of the feeding current (mean  $\pm$  SD, n = 19), and (C) a single arrest from the flow record. (B) The average profile of a typical coughing arrest (n = 4) and (D) a coughing arrest from the flow record. The kinetics of each arrest type is provided in Table 1.

**Table 1**

Kinetics of single and coughing arrests of filtration from 2015 recordings showing the length and rates of arrest and recovery phases. Fig. 3 shows examples of behaviour types and phases of the arrest behaviour.

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

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 (Fig. 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).

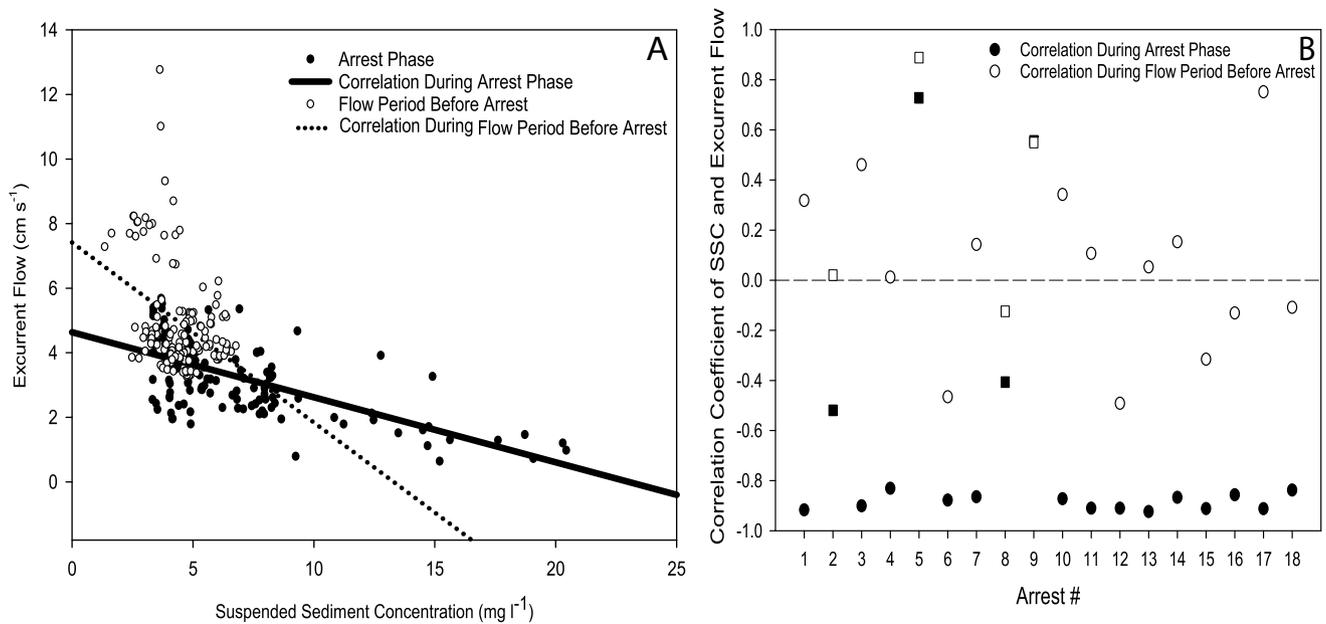
Recordings of arrest behaviours were paired with the Aquadopp current profiler and OBS records. Changes in SSCs and excurrent flow were compared using Pearson’s correlation coefficients during each

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.

### 3. Results

#### 3.1. Arrests of sponge filtration

A total of 23 arrests of filtration (19 single and 4 coughing, Fig. 3, Table 1) were identified in 29 h of excurrent recordings from a single sponge. The single arrests identified during this study lasted 2–5.5 min



**Fig. 4.** The correlation between the onset of the arrest behaviour 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.

( $4.25 \pm 1.3$  min (mean  $\pm$  SD),  $n = 19$ ) with arrest phases measuring 0.5–3 min ( $1.91 \pm 0.96$  min,  $n = 19$ ) and recovery phases of length 1–4 min ( $2.34 \pm 0.62$  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 ( $31 \pm 22.89$  min,  $n = 4$ ). Arrest phases averaged 4–15 min ( $10.46 \pm 5.26$  min,  $n = 4$ ) while recovery phases lasted 6–40 min ( $20.54 \pm 18$  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  $-0.0002$   $s^{-1}$ .

### 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  $-0.92$ ) (Fig. 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  $0.75$ ) (Fig. 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  $10$ – $80$   $mg\ l^{-1}$ , 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 h (Table 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 (Fig. 5b). The coughing events occurred during periods of higher tidal flow (Fig. 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.

### 3.3. Natural sediment resuspension

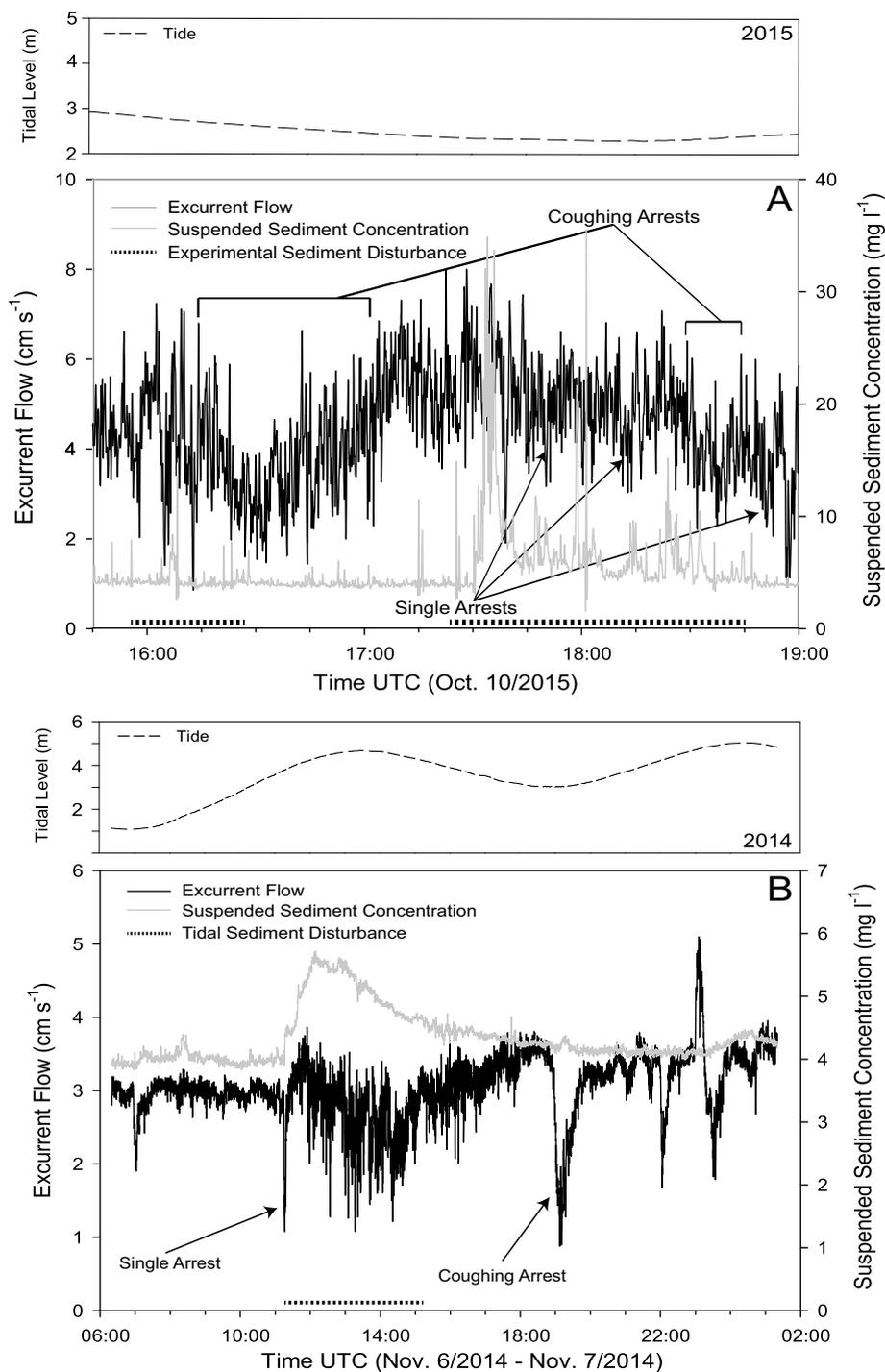
The changes in SSCs recorded during 2014 roughly corresponded to the tidal cycle, indicating that the tides can increase the suspended sediment at the sponge reefs (Fig. 6a). The concentration of suspended sediment at Fraser Ridge reef, between tides, was  $4.4$   $mg\ l^{-1}$  ( $\pm 0.7$   $mg\ l^{-1}$ ). Tidal resuspension in 2014 generated a slight increase in suspended sediments to  $5.3$   $mg\ l^{-1}$  ( $\pm 0.9$   $mg\ l^{-1}$ ), 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 (Fig. 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.

## 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) (Fig. 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.

### 4.1. Arrest behaviours

In 2014 the sponges' excurrent flow was recorded for 39 h without disturbance; that period included a full tidal cycle. Higher tidal flows were found to increase SSCs to a limited degree: over 39 h, 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 (Fig. 5a). The frequency of arrests in 2014, five total over 39 h, indicates that they are

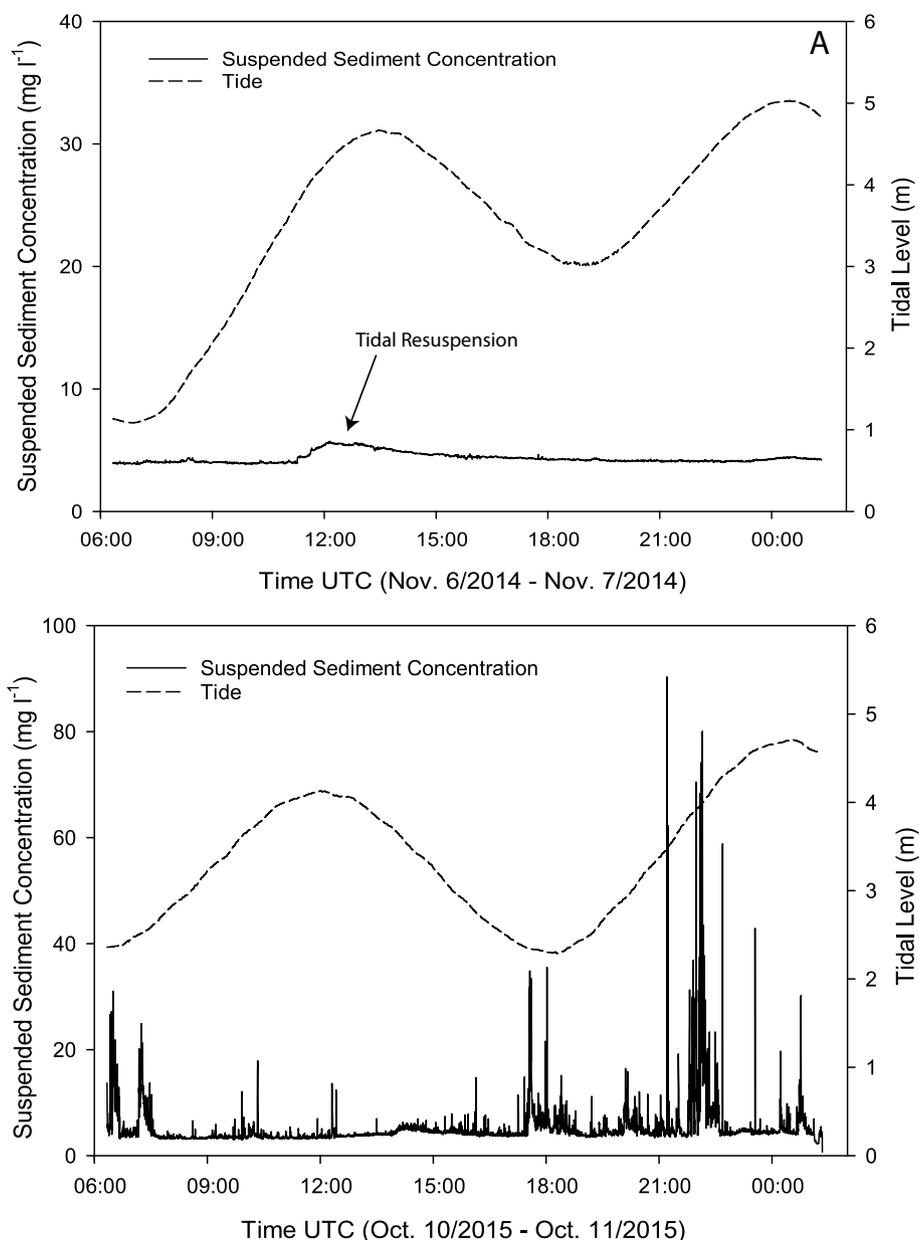


**Fig. 5.** A record of filtration behaviour and arrests of filtration. (A) Arrests in filtration seen in the excurrent flow recording from a single sponge in 2015 occurred across a range of SSCs (from 10 to 80 mg l<sup>-1</sup>). (B) A recording from a sponge in 2014 shows both single and coughing arrests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

not a common behaviour, often only being triggered when necessary to prevent potential harm from tidally suspended sediments (Fig. 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 of filtration are presumed to be protective behaviours that reduce the risk of damage caused by suspended sediments, but arrests 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



**Fig. 6.** Tidal flow and suspended sediment records for 2014 and 2015. 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).

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  $40 \text{ mg l}^{-1}$  during a disturbance (range  $10\text{--}80 \text{ mg l}^{-1}$ ). During a 1.5 h 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 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  $16.20 \mu\text{g}$  or  $1.34 \mu\text{mol}$  carbon per liter pumped (Table 2, Kahn et al., 2015;  $3.4 \text{ g C m}^{-2} \text{ d}^{-1}$  consumed from  $210 \text{ m}^3 \text{ m}^{-2} \text{ d}^{-1}$  of water filtered). Whereas a sponge osculum would normally filter  $763 \mu\text{mol}$  of carbon in 1.5 h (from Table 2, Kahn et al., 2015), a 1.5 h sediment disturbance would lead to a loss of 70%

or  $534 \mu\text{mol}$  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., 2015; McGrath et al., 2017). A study on phototrophic and heterotrophic demosponges has shown decreased survival and energy reserves and increased necrosis for sponges 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.

#### 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  $200 \text{ mg l}^{-1}$  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  $20 \text{ mg l}^{-1}$  SSC but reached peaks of  $110 \text{ mg l}^{-1}$ . Shrimp trawls have generated SSCs of  $100\text{--}550 \text{ mg l}^{-1}$  (Schubel et al., 1978). Using a bottom trawl with “rockhopper” gear, Durrieu De Madron et al. (2005) recorded maximum SSCs between 150 and  $300 \text{ mg l}^{-1}$  behind the path of the trawl. The turbidity of  $10\text{--}80 \text{ mg l}^{-1}$  we recorded during arrest behaviour of the glass sponges was an order of magnitude higher than the normal conditions found at Fraser Ridge reef of  $4.4 \text{ mg l}^{-1}$ , 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 suggest that the sponges’ 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 (Pilska 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  $\sim 80$  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 happened 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 to 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 ( $< 20 \mu\text{m}$ ) 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 ( $2\text{--}2000 \mu\text{m}$ ) (Thomson, 1981; 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.

#### 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, 2017a). 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, 2017b). 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.

## 5. Conclusions

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.

## Funding sources

ROPOS was funded via an NSERC Ship Time grant to S.P.L. Funding for the CCGS JP Tully came from Fisheries and Oceans Canada to M.O. (2015) and for the CCGS Vector through an NSERC Ship Time grant to S.P.L. and R. Case (2014). Research costs and salaries of N.G., E.M. and A.S.K. were funded in part by NSERC Discovery and NSERC Strategic Network grant (CHONeII) grants, and DFO Canada ARCP grants to S.P.L., and by the University of Alberta.

## Acknowledgments

We thank the captain and crew of the Canadian Coast Guard Ship JP Tully and Vector and the pilots of ROPOS for their careful work. D. Eerkes-Medrano helped substantially with instrument deployments and provided comments on a draft of this manuscript. We gratefully acknowledge K. Ladell, M. O, S. Creighton and A. Mar of Fisheries and Oceans Canada for initiating the request for this information, which arose out of a CSAS meeting in Nanaimo in 2012.

## Appendix A. Supplementary data

Supplementary data related to this article can be found at <http://dx.doi.org/10.7939/R3KS6JJ80>.

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