Effect of suspended sediments on the pumping rates of three species of glass sponge *in situ*

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ABSTRACT: The largest known glass sponge reefs in Canada are within the Hecate Strait and Queen Charlotte Sound Glass Sponge Reefs Marine Protected Area (HSQCS-MPA) in British Columbia. However, human activities outside the core MPA boundaries, such as trawling, can create plumes of suspended sediments capable of travelling large distances. We studied the response of 3 glass sponge species to changes in suspended sediment concentrations (SSCs) at 170 m depth inside the HSQCS-MPA. Two species reduced excurrent flow rate in response to natural and experimentally induced increases in suspended sediment. Background suspended sediment levels were low and showed little variation (2.71 ± 0.09 mg l^{-1}, mean ± SD). Species varied in the threshold of SSCs that triggered arrests. Sediment concentrations of 2.8–6.4 mg l^{-1} caused arrests in *Rhabdocalyptus dawsoni*, while *Heterochone calyx* did not arrest until concentrations reached 5–10 mg l^{-1}. Very small, but prolonged increases of suspended sediments (<1 mg l^{-1} for *R. dawsoni* and 3.2 mg l^{-1} for *H. calyx*) caused arrests of several hours in *R. dawsoni* and prolonged periods of reduced flow in *H. calyx*. No arrests were observed in *Farrea occa*, even after repeated exposures up to 57 mg l^{-1}. A sediment transport model showed that sediment concentrations can remain high enough to affect sponge behaviour as far as 2.39 km from the source of the plume. The results highlight the importance of understanding the biology of different species for establishment of adequate boundaries in MPAs.

KEY WORDS: Glass sponges · Reefs · Pumping Rate · Suspended sediments · Porifera · Trawling · Marine protected areas

1. INTRODUCTION

Globally, marine ecosystems are challenged by multiple human-caused stressors. In response, the United Nations has set targets to protect 10% of the oceans 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 2017). This MPA was established to protect the globally unique ecosystems formed by glass sponges, but as suspension feeders, sponges are sensitive to any activity that changes the water properties around them, including those that occur outside the MPA boundaries.

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Glass sponge reefs occur in depths of 30–200 m on the continental shelf of British Columbia, Canada, and Alaska, USA (Conway et al. 1991, 2001, Krautter et al. 2001). The reefs are built by 3 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 & 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, 2001, Jamieson & 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 4 glass sponge reef complexes in Hecate Strait and Queen Charlotte Sound (Fisheries and Oceans Canada 2017). The MPA consists of a core protection zone (CPZ), which excludes all human activities, and an adaptive management zone (AMZ) or buffer zone bordering the reef complexes, which is currently closed to fishing activity but may be opened in the future. However, it is 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 filterers capable of processing up to 900 times their body volume in 1 h (reviewed by Yahel et al. 2003, their Table 3). Generally, they filter constantly and take in both organic and inorganic particles alike. While they can excrete inedible detritus (Wolfrath & Barthel 1989, Yahel et al. 2007, Kahn et al. 2018), too much of it can be detrimental (reviewed by Bell et al. 2015). Sponges are sensitive to minute changes in water quality and respond to changes in seasonal characteristics of the water column (Reiswig 1971), food availability (Reiswig 1975, Kahn et al. 2012), ocean acidification (Bates & Bell 2018) and suspended sediments (Gerrodette & Flechsig 1979, Carballo 2006, Tompkins-MacDonald & Leys 2008). Sediments may smother and clog a sponge (Airoldi 2003, Tompkins-MacDonald & Leys 2008, Strehlow et al. 2017), and smaller grain sizes can fit through the incurrent pores on the sponge surface (<20 µm) (Kilian 1952, Reiswig 1974) potentially damaging their aquiferous system. To deal with sediments, most demosponges contract to prevent entry of sediment or to expel already ingested sediments (Prosser et al. 1962, Elliott 2004, Elliott & Leys 2007); others secrete mucus to slough sediments off their surface (Kowalke 2000). Of all sponges, however, glass sponges (Class Hexactinel-

lida) are the only group that instantly arrest pumping activity, using an action potential, in response to sediments (Leys et al. 1999, Tompkins-MacDonald & Leys 2008, Grant et al. 2018).

Arrests of pumping are triggered by action potentials travelling throughout the glass sponge's syncytial tissues (Mackie et al. 1983, Leys et al. 1999). These action potentials, and the ensuing arrests of pumping behaviour, have been recorded in *Rhabdocalyptus dawsoni* in laboratory experiments (Leys & Mackie 1997, Leys et al. 1999). Tompkins-MacDonald & Leys (2008) later found similar arrests of excurrent flow in *Aphrocallistes vastus* in response to suspended sediments added to the water. More recently, the arrest response of *A. vastus* was studied in the naturally turbid waters of the Strait of Georgia, British Columbia. That study found that *A. vastus* stopped pumping in response to suspended sediment concentrations that were far lower than those generated by trawling (Grant et al. 2018).

Reefs in the northern complex of the Hecate Strait MPA are made by different glass sponge species and are in a less turbid environment than reefs in the Strait of Georgia (reviewed by Leys 2013). To determine how other reef-building glass sponge species are affected by suspended sediments, and how effective the MPA might be in terms of protecting the sponges from resuspended sediments, we conducted experiments *in situ* at the northern sponge reef complex in the Hecate Strait and Queen Charlotte Sound Glass Sponge Reefs MPA (HSQCS-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, to 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 by arresting pumping activity.

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 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 adequate protective buffer zones around the conservation targets within MPAs.

2. MATERIALS AND METHODS

2.1. Study site and study species

Experiments were carried out on a sponge reef at approximately 170 m depth in the HSQCS-MPA during 2 cruises of the Canadian Coast Guard Ship (CCGS) 'JP Tully' in October 2015 and May 2017 (2015: 53° 11′ 37.2″ N, 130° 28′ 27.7″ W; 2017: 53° 11′ 38.0″ N, 130° 28′ 29.4″ W; Fig. 1). Dives were conducted using a remotely operated vehicle (ROV) (Remotely Operated Platform for Ocean Sciences, 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*. Goblet-shaped *Heterochone calyx* sponges were found growing between and out of *F. occa* bushes, while small chalice-shaped *Aphrocallistes vastus* and tube-shaped *Rhabdocalyptus dawsoni* were found adjacent to and between *F. occa* bushes.
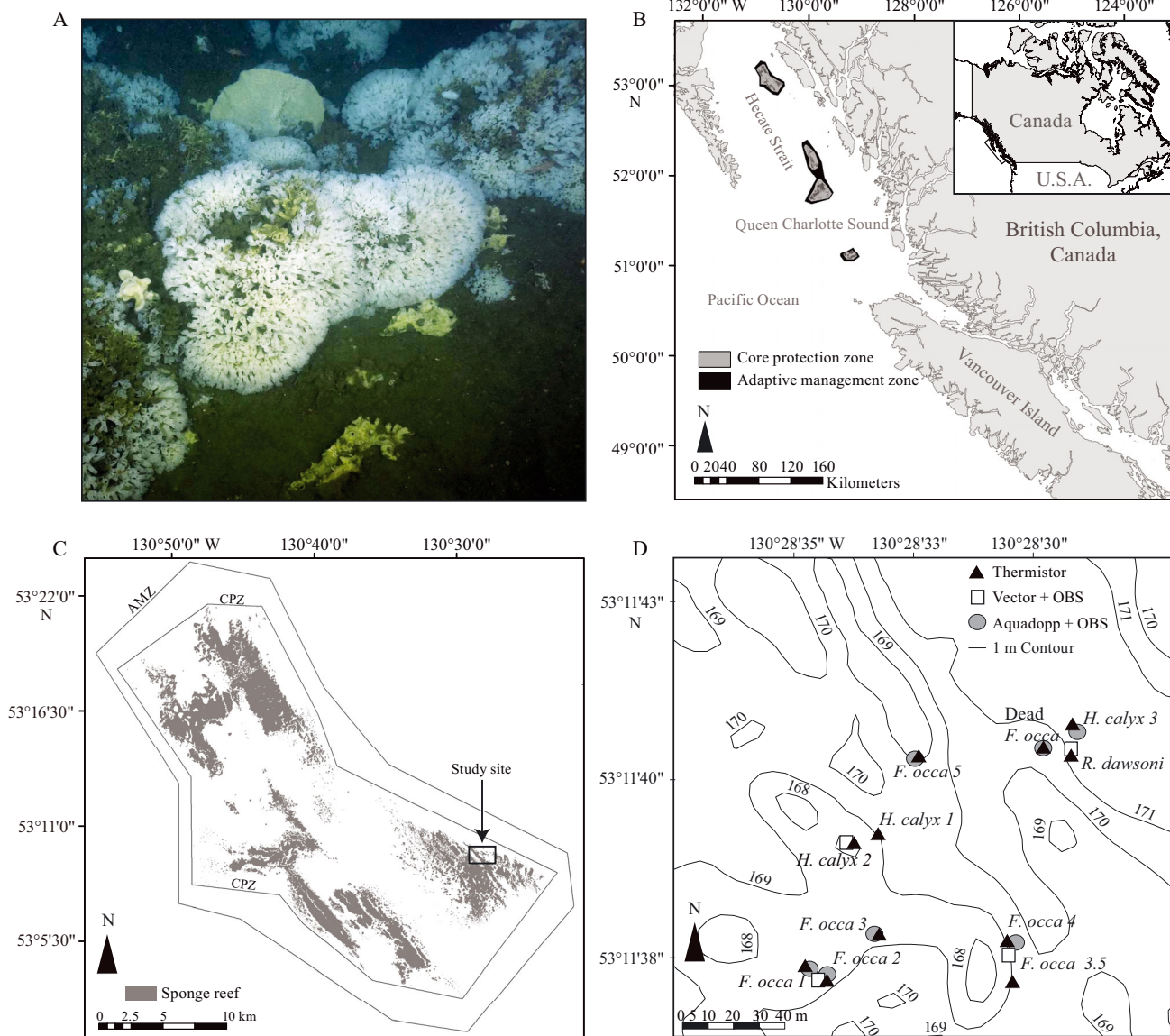

Fig. 1. Location of the glass sponge reefs and marine protected area (MPA) in northern British Columbia, Canada. (A) Sponges at the north-eastern portion of the northern reef complex. (B) Hecate Strait and Queen Charlotte Sound Glass Sponge Reefs MPA. (C) Precise location of the northern sponge reef complex as delineated by multibeam bathymetry. Borders around the reef complex define the core protection zone (CPZ) and adaptive management zone (AMZ) boundaries. (D) Locations of individual sponges that were studied and instrumentation placement (OBS: optical backscatter sensor). Species are *Heterochone calyx*, *Farrea occa* and *Rhabdocalyptus dawsoni*

We targeted *F. occa* and *H. calyx* because they formed the major component of the north-eastern Hecate Strait reefs, and no previous field experiments or recordings have been conducted on these 2 species. Due to the short time available on the cruise, the time involved in deploying instrumentation by ROVs, and the need to obtain replicate recordings, we did not carry out experiments on *A. vastus. A. vastus* has been the focus of our previous work and is accessible in waters much closer to the ship's home port. We also chose to place instruments around one specimen of *R. dawsoni*, because although it is not a reef-forming species, we have a good understanding of its pumping arrest behaviour from previous laboratory and field work (Leys et al. 1999, Yahel et al. 2007, Tompkins-MacDonald & Leys 2008).

F. occa and *H. calyx* were described in the late 1800s (Bowerbank 1862, Schulze 1886), but beyond these initial descriptions, little is known about their ecology, physiology and cell biology. *F. occa* forms leaf-like flutes, and up to 400–600 of these are fused to one another to make up the bush. Each flute is in essence a separate filtration unit, and its body wall is less than 1 mm thick. In contrast, *H. calyx* has a robust body wall, often over 1 cm thick, which forms large funnels that vary in breadth but can readily reach 1 m in diameter. Funnels are pock-marked by finger-like projections that are extensions of the incurrent surface area. *R. dawsoni* is a barrel-shaped sponge that often bends at the lower end where it is attached to the substrate, giving it a characteristic 'boot' shape. This sponge is hairy with long spicules protruding from the outer surface of the barrel, and some specimens can be coated with debris, giving the sponge a dirty appearance.

2.2. Instrumentation

We used both an acoustic Doppler velocimeter ('Vector' ADV, Nortek) and an acoustic Doppler current profiler ('Aquadopp' ADCP, Nortek) mounted on a flat frame to measure changes in ambient current velocity either at a single point (Vector) or for a 5 m profile above the bottom (Aquadopp) (Fig. 2A,C). The Aquadopp and the Vector were each paired with optical backscatter sensors (OBS, Campbell Scientific) to record suspended sediment concentrations (SSCs) (Fig. 2C). The Aquadopp was compass-calibrated prior to the expedition. The OBS instruments were calibrated following the calibration process outlined by Grant et al. (2018). The calibration process resulted in an equation to convert 'counts' to mg l^{-1} for each instrument: SSC = 0.0113 × OBS counts + 1.3021 (Aqua-

dopp-paired OBS, R^2 = 0.92) and SSC = 0.0103 × OBS counts + 1.9302 (Vector-paired OBS, R^2 = 0.99).

Custom-built thermistor-flowmeters (hereafter referred to as 'thermistors') with paired probes simultaneously recorded constant point flow rates out of the osculum (excurrent flow) of sponges and adjacent to the sponges (ambient flow) (Fig. 2A,C,E). Although the thermistors are non-directional, their position inside the osculum recorded the main direction of flow out of the osculum. Thermistors were calibrated *in situ* using the Vector for at least 8 h in an area of undisturbed ambient current. Thermistors were then placed beside a sponge with a probe positioned by the manipulator arm of the ROV into the sponge osculum, the chimney-shaped opening from which all filtered water exits; care was taken to prevent the probe from contacting the body wall of the sponge (Fig. 2B,D,F). The probe was 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 turbidity around the sponge during experiments.

Volumetric flow was calculated for each sponge by multiplying the area of the osculum by the excurrent flow rate recorded for that species. The diameter of the osculum was measured in ImageJ from ROV images looking down over the osculum. Oscula in these glass sponges are not contractile, and because flow rates are low and the oscula are wide, drag created by the edge of the osculum was considered to be minimal, and therefore a profile correction factor was not used.

2.3. *In situ* experiments

We positioned instruments over a total of 10 sponges to obtain recordings for the previously unstudied species of *F. occa* (n = 6) and *H. calyx* (n = 3). The single recording from *R. dawsoni* (n = 1) was used to verify the method of our *in situ* experiments because the sponge is known to arrest pumping in response to suspended sediments in lab experiments (Leys et al. 1999, Tompkins-MacDonald & Leys 2008), and its arrests in the field provided support of the method. Additionally, to assess the contribution of ambient flow to excurrent flow from the osculum, we recorded flow from one osculum of a dead *F. occa* specimen. Previous work *in situ* and in tanks has illustrated that excurrent flow rate from each sponge varies greatly depending on the size of the sponge and of the sponge's osculum (e.g. Mackie et al. 1983, Tompkins-MacDonald & Leys 2008, Leys et al. 2011), but follows a species-specific pattern
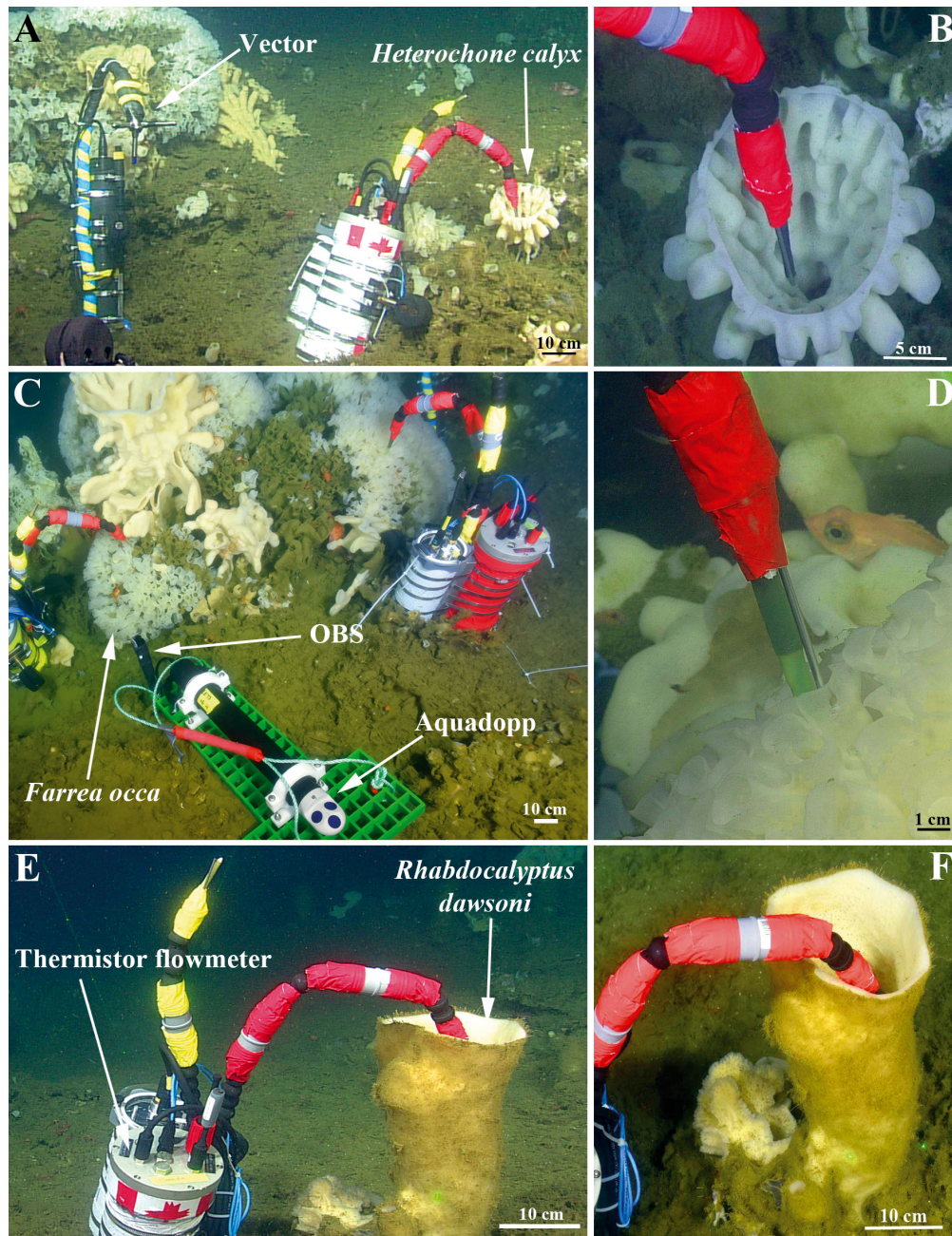
Fig. 2. (A,C,E) Overview of all sponge species and instrumentation used *in situ*. (B,D,F) Excurrent probes of the thermistor-flowmeters and oxygen sensors (red) were positioned into the centre of the osculum without touching the body wall. Ambient current sensors (yellow) were placed above the sponge oscula to record surrounding ambient current. OBS: optical backscatter sensor

which depends upon density of choanocyte chambers and design of the aquiferous system. Consequently, as is typical in studies of physiological data, a recording from a single sponge was treated as an experiment, with different individuals confirming the general physiological pattern for that species. We studied as many different individuals as time allowed within the different needs of the science team on the cruise.

Once a sponge was paired with a set of thermistors, ROPOS left the area to allow recordings of undisturbed pumping activity; these recordings ranged from 6 to 24 h (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 (Fig. 3). Sediments were sus-

pended 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 arm to swing an empty scoop in the direction of the sponge (Fig. 3B). Between 2 and 6 control scoops were conducted depending on the time available during a dive. Following the control scoops, sediment was scooped up from the seafloor and shaken into the water column in the direction of the target sponge (Fig. 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 (Fig. 3D). A total of 13 experimental sediment disturbances were conducted (Table S1 in the Supplement at www.int-res.com/articles/suppl/m615p079_supp.pdf). All in-

strument placements, experimental disturbances and ROPOS activity near the sponges were recorded in the integrated real-time logging system of ROPOS to allow for quality control checking of the data during the analysis process.

2.4. Arrest response analysis

Arrests of pumping were identified in sponge excurrent recordings using the criteria outlined by Grant et al. (2018) with a modification based on descriptions of arrests in *R. dawsoni* by Tompkins-Mac-Donald & Leys (2008). We used excurrent flow rate as a proxy for pumping activity and filtration. Briefly, an arrest was defined as a decrease from the average excurrent flow (the arrest phase) followed by the gradual return to average excurrent flow (the recovery phase); the minimum recovery phase length was 20 s. As *R. dawsoni* has shorter arrests than *A. vastus*, these criteria ensured arrests could be identified from all species.
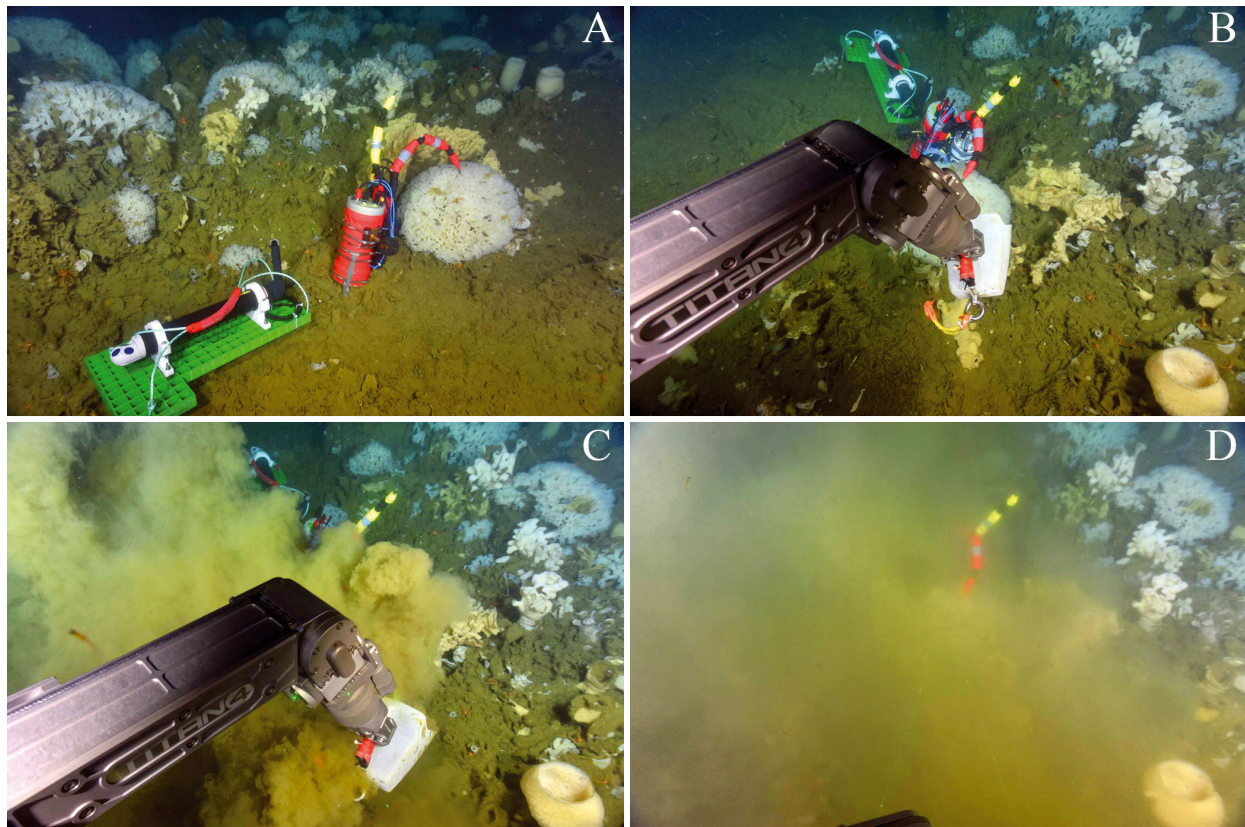

Fig. 3. Experimental sediment disturbances were used to expose each species to elevated concentrations of suspended sediment. (A) Instruments were positioned adjacent to a sponge such that the optical backscatter sensor (OBS) would be downstream from the sponge. (B) Example of the manipulator arm carrying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

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). Single arrests of pumping are short (2–5.5 min), off-and-on events, with little variation in recovery phase slope. Coughing arrests are slightly longer (11–54 min) and have a staggered recovery phase involving several attempts to increase pumping rate (interpreted in previous laboratory work as the pump switching on and off; Tompkins-MacDonald & Leys 2008) prior to reaching the full pumping rate. The duration of single and coughing arrests differs for different species: for *A. vastus*, the 2 arrest types have a characteristic 'V'-shape (see Grant et al. 2018) and the same was expected for *H. calyx* and *F. occa*; for *R. dawsoni*, both arrest types show a more 'U-shaped' pattern (see Mackie et al. 1983, Tompkins-MacDonald & Leys 2008). Prolonged arrests are distinguished by the length of the arrest, with flow completely arrested for over 40 min. 'Clogging events' are points in the record where excurrent flow rates were reduced for more than 50 min but excurrent flow did not completely stop. We do not assume that the sponge tissue was entirely clogged but that some level of sediment entered the sponge, causing a longer response than one of the previously described arrest responses.

For analysis, each excurrent flow record was first visually assessed to identify arrests. After this, a moving average of the variance was carried out on the time series at 10 s intervals to detect any additional potential arrest points. These were defined as periods during which the variance in excurrent flow decreased by more than 0.25 over a 10 s interval. This was followed by 2 additional manual inspections of each record to ensure that no arrests were missed. 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 pumping' consisted of only those records in which the decrease in excurrent flow was independent of the ambient current. To determine whether increases in SSC were correlated with decreases in excurrent flow, Spearman's rank correlation was used to account for any non-linearity seen in the data due to noise or irregularity of field data. Changes in SSC caused either by experimental disturbances immediately preceding an arrest or by natural events within the 2 min preceding the arrest were compared to the excurrent flow rate during the arrest phase using Spearman's rank correlation. These analyses were carried out using STATISTICA 13 (Statsoft).

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 and 60 cm long, were pressed into the sea floor to the maximum depth possible. In some areas, the core was filled, and in others the rock rubble prevented the core reaching the full 60 cm depth length. Cores were frozen on board 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 (from the seafloor to approximately 1 m above the seafloor) in 2011. Placement, collection and storage of those traps was described previously (Kahn et al. 2016).

2.6. Grain size analysis and modelling of transport

Sediment cores (n = 4) and 2 sediment traps were thawed and dried in a 60°C oven for 3 d prior to analysis. We did not retain distinct depth fractions. Dried sediments were placed in a W.S. Tyler 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 S2 in the Supplement). The mass of dried sediment samples was taken before and after entering the sieve shaker to calculate the proportion of each grain size by mass. Each core was analysed separately, and the mean of all 4 was calculated. *Z*-tests were used to test for differences in the proportion of different grain sizes between the 2 reefs.

Settling rates, time spent suspended, maximum distance travelled and the height of suspension needed to maximize the distance travelled in a single phase of a tidal cycle were calculated using the grain sizes in Table S2 and variables defined in Table 1. Settling rate was calculated using the Stokes settling equation:

$$V_t = \frac{g d^2 (\rho_p - \rho_m)}{18 \mu} \tag{1}$$

The maximum distance that could be travelled by a particle in a single ~6 h phase of the tidal cycle was modelled by:

$$X_{D\,\text{Max}} = U_{T_0} \frac{1}{\omega_T} [-\cos[\omega_T (T_{\text{Fall Max}} - t_0)] + \cos(\omega_T t_0)] \tag{2}$$

The maximum travel distance of a particle was modelled at different heights above the seafloor. The

total settling time of a particle suspended at a given height above the seafloor was calculated for each grain size using:

$$T_{\text{Fall}} = \frac{H_0}{V_t} \qquad (3)$$

Sediments were analysed and modelling was completed for all sediment collected from the northern Hecate Strait reef complex in May 2017 using the above equations in MS Excel 2016. This model assumes that all particles are spheres and does not account for particle flocking, turbulence or stratification of the water column.

3. RESULTS

3.1. Ambient conditions of the study site

Ambient currents at 1 m above bottom (mab) averaged 12.01 ± 6.39 cm s^{-1} (4 h average ± SD) during flood tides and 6.31 ± 3.63 cm s^{-1} during slack tides (Table 2; Fig. S1 in the Supplement). The ambient velocity increased with increasing height above the seafloor. At 5 mab, current during flood tides averaged 27.4 ± 12.12 cm s^{-1}, and 19.3 ± 9.37 cm s^{-1} during slack tides. The ambient current over the reef alternated in a west–east direction during flood tides, while during the slack tide we recorded a short duration of north–south movement. Background levels of SSCs showed little variation over the 6 to 24 h (20 ± 6.5 h) duration of our recordings, averaging 2.71 ± 0.09 mg l^{-1} at all instrument placements (Fig. S1).

3.2. *Heterochone calyx*

We recorded excurrent flow from 3 *H. calyx.* Two bowl-shaped sponges were each exposed to a single experimental sediment disturbance *in situ.* Both sponges showed single arrests in response to increased sediment concentrations. They also showed reductions in flow rate that lasted longer than single arrests; we considered these to most likely be clogging events (Fig. 4A,B). In the third *H. calyx*, there were no spontaneous arrests over a 24 h recording, and no experimental disturbance was carried out, leaving one sponge as a completely undisturbed control since no *in situ H. calyx* pumping records had been collected prior to this. No coughing events were observed in *H. calyx.*

The single arrests (n = 5) recorded from both sponges ranged in duration from 1.2–7 min (mean: 3.76 ± 2.5 min). Arrest phases lasted 0.47–2.97 min (1.30 ± 1.03

min) and recovery phases took 0.75–4.03 min (2.46 ± 1.56 min) (Table 3, Fig. 4A). In all 5 single arrests, the decrease in excurrent flow was correlated with increased SSC in the 2 min prior to the arrest (Fig. 4C). The first sponge exhibited 3 single arrests that occurred after a single experimental sediment disturbance event, and the second sponge had 2 single arrests following an experimental sediment disturbance. In the single arrests of both sponges, the decreased excurrent flow rates were correlated with

Table 1. Variables used for modelling sediment transportation and settlement across all grain sizes recorded at the northern Hecate Strait glass sponge reef complex

Variable	Description
V_t	Calculated settling velocity of the particle
g	Gravitational constant
d	Particle diameter, assuming a sphere
ρ_p	Particle density for a given grain size
ρ_m	Density of seawater at depth
μ	Dynamic viscosity
$X_{d\,\text{Max}}$	Maximum distance travelled by a particle in one direction during one phase of the tidal cycle
U_{T_0}	Average ambient current recorded by instruments
ω_T	Tidal phase during suspension event
T_{Fall}	Time a particle spends falling in the water column from a given height of suspension
$T_{\text{Fall Max}}$	Maximum time a particle can spend falling in one phase of the tidal cycle
t_0	Initial time when particles are suspended into the water column
H_0	Height of particle suspension above the seafloor

Table 2. Mean excurrent and volumetric flow rates for each species recorded in this study. Records were taken from undisturbed flow periods during each tidal phase listed

|	Tidal phase	Mean	SD
H. calyx excurrent flow (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 flow (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
R. dawsoni excurrent flow (cm s^{-1}) (n = 1)	Flood	2.56	0.88
	Slack	0.42	0.06
R. dawsoni excurrent volumetric flow (l s^{-1}) (n = 1)	Flood	1.03	0.00034
	Slack	0.17	0.00006
Overall reef ambient current (cm s^{-1})	Flood	12.01	6.39
	Slack	6.31	3.63
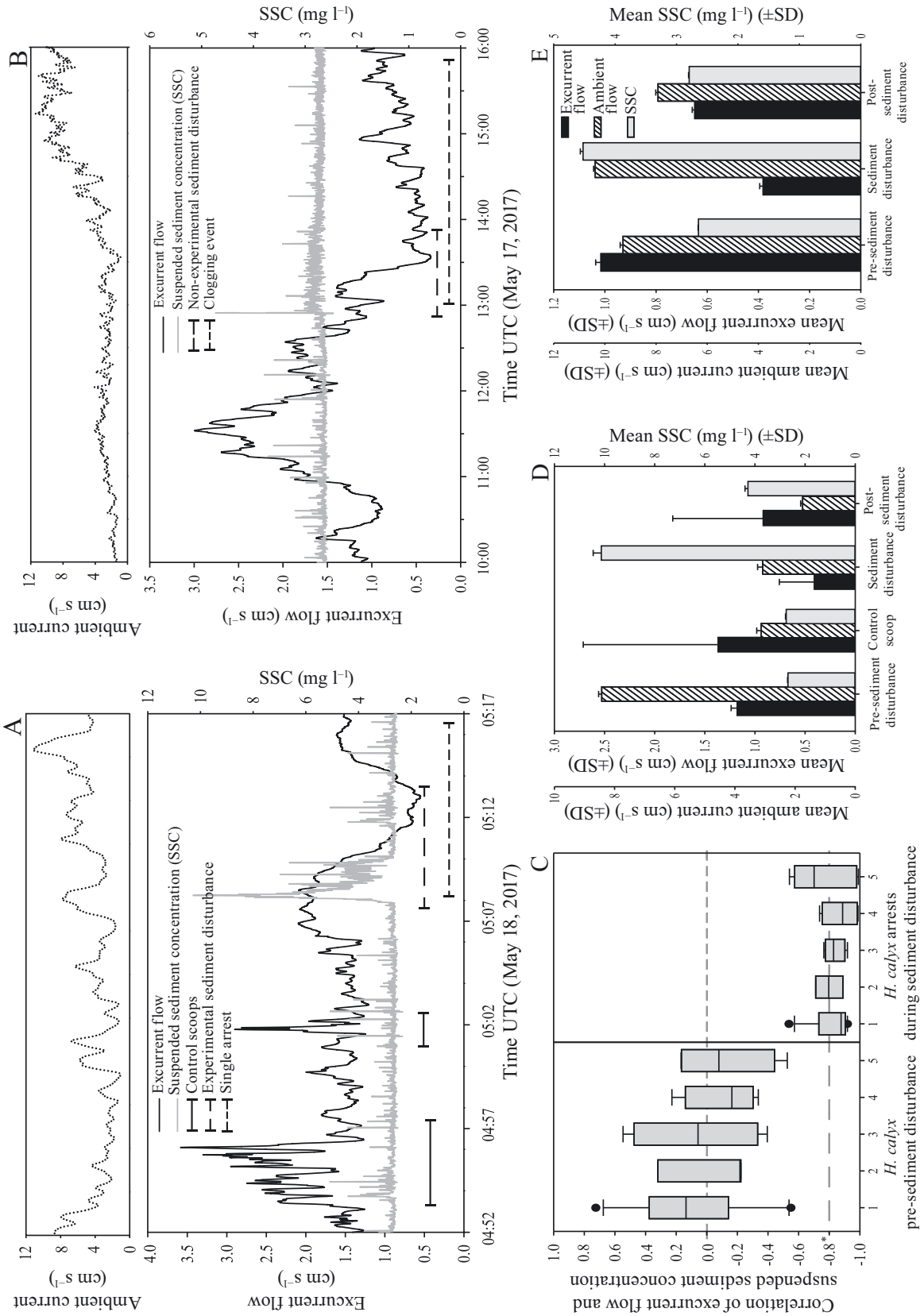
Fig. 4. Arrests by *Heterochone calyx*. (A) Two control scoops followed by an experimental sediment disturbance generated by the remotely operated vehicle that induced a single arrest. (B) Clogging event associated with prolonged exposure (~0.8 h) to elevated suspended sediment concentrations (SSCs). (C) Correlation of SSCs and sponge pumping activity prior to and during arrests of pumping. Dotted line indicates 0. Dashed line and * indicates significance (p < 0.05). Boxes are 25th and 75th percentiles, whiskers are 10th and 90th percentiles, midline is the mean, dots are outliers. (D) Measurements of mean excurrent and ambient current and of SSC prior to and during the control scoop and single arrest and following the experimental sediment disturbance. The large standard deviation seen during the control scoop is representative of the scoop pushing additional water over the probe, affecting the reading. This was accounted for in all other measurements but has been left visible here to depict the necessity of the control scoops in this methodology. (E) Recordings of mean excurrent and ambient flow and of SSC before, during and after a clogging event

increased SSC prior to the arrests (r = −0.89 to −0.92, p < 0.05; and r = −0.81 to −0.97, p < 0.05 for the first and second sponge, respectively).

When sponges were neither disturbed nor arrested, the mean excurrent flow rate from all 3 *H. calyx* was 1.75 ± 0.44 cm s^{-1} during flood tide and 0.48 ± 0.15 cm s^{-1} at slack tide (Fig. 4D, Table 2). The SSCs around the *H. calyx* individuals when the ROV was not in the area was on average 2.75 ± 0.03 mg l^{-1}. 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*. Twice during slack tides, the excurrent flow rate dropped to between 0.2 and 0.73 cm s^{-1} (Fig. 4B) 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 *Rhabdocalyptus dawsoni* (see Section 3.4) because they did not result in the complete cessation of excurrent flow from the sponge, but instead the record showed an extended reduction in excurrent flow rate, much as seen for *Aphrocallistes vastus* by Tompkins-MacDonald & Leys (2008). The first clogging event lasted 3.41 h and came after an extended period of increased SSC lasting 2.53 h, with a peak concentration of 4.53 mg l^{-1} and average of 2.98 ± 0.08 mg l^{-1} following this initial peak (Fig. 4E). The second clogging event lasted 0.79 h 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, manipulation of instruments by the ROV nearby and activity of fish are possible explanations. Decreases in excurrent

flow from the sponge were correlated with the increases in SSC prior to the clogging events (r = −0.86, p < 0.05).

3.3. *Farrea occa*

The excurrent flow from bush-shaped *F. occa* did not decrease 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 flow rate were not distinguishable from this natural variation. There was no correlation between changes in excurrent flow and experimental increases in SSC (Fig. 5C).

Nine experimental sediment disturbances were carried out on 6 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 flow rate increased with increased ambient current (r = 0.83, p < 0.05), independent of changes in SSC (Fig. 5D). Undisturbed flow out of the sponge bushes averaged 1.54 ± 1.81 cm s^{-1} during flood tide and 0.32 ± 0.22 cm s^{-1} at slack tides (Table 2). Recordings from a dead bush gave comparable excurrent velocities to the live bushes: 2.58 ± 1.02 cm s^{-1} during flood tide and 0.49 ± 0.39 cm s^{-1} at slack tides. The comparable excurrent flow rates between live and dead sponge bushes may be an indication that pumping rates are too small to be detected. To determine how much flow was generated by *F. occa* and how much might be caused by ambient currents disturbing the water around the flow probes in the sponge oscula, we collected 2 individuals, and immediately after the ROV arrived on

Table 3. Numerical description of single and prolonged arrests, as well as clogging events, recorded from *Heterochone calyx* and *Rhabdocalyptus dawsoni*. Duration refers to the overall duration of the phase or response, while rate equates to the average slope of each phase of the response. NA: not applicable

| Sponge species	Type of response	Total no.	Duration (min) (mean ± SD)			Rate (s^{-1})	
			Arrest phase	Recovery phase	Total	Arrest phase	Recovery phase
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 to −0.03	<0.01–0.02
	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 to −0.06	<0.01–0.04
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 to 0.03	<0.01–0.2
	Prolonged arrest	1	61.5	NA	>360	0.03	NA
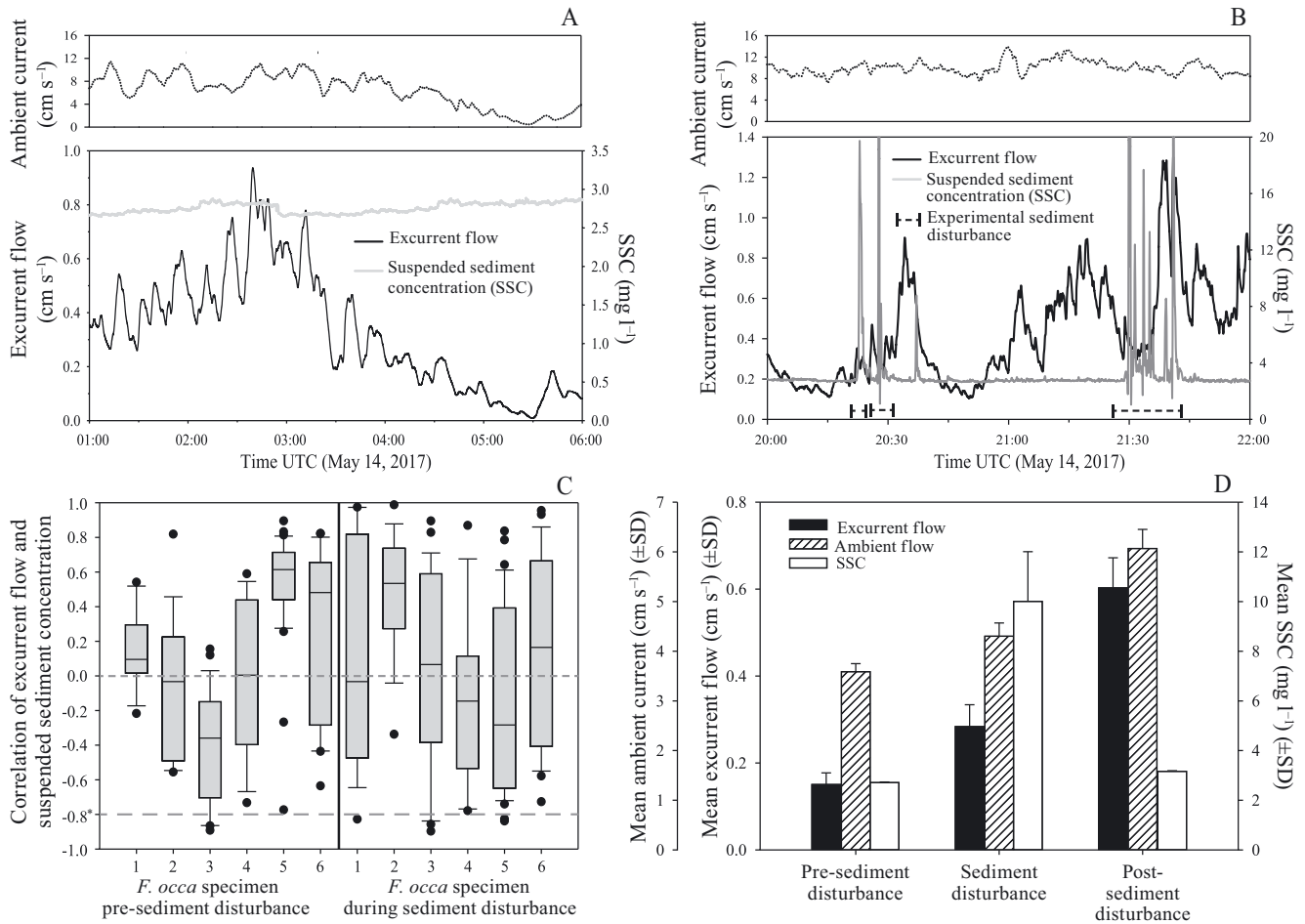
Fig. 5. *Farrea occa* flow record. Excurrent and ambient flow recordings during undisturbed conditions and during experimental sediment disturbances. (A) Excurrent flow rate follows the pattern of ambient flow during undisturbed conditions. (B) Excurrent flow increases in response to the scooping action but returns to pre-disturbance conditions without showing any clear arrest of pumping. (C) No correlation of pre-disturbance and disturbance flow with suspended sediment concentrations (SSCs) was found. Dotted line indicates 0. Dashed line and * indicates significance (p < 0.05). (D) Recordings of mean excurrent flow and ambient current and of SSC before, during and after a sediment disturbance around an *F. occa* bush

deck, we put fluorescein dye beside the wall of the sponge. In one case, the sponge did not appear to take in any dye, but the second sponge moved dye through the body wall extremely slowly prior to stopping, potentially because 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 behaviour in *F. occa*.

3.4. *Rhabdocalyptus dawsoni*

R. dawsoni (n = 1) showed the highest number of arrests in response to increased SSCs. A total of 8 single and 1 prolonged arrest were identified throughout the 21.5 h recording. Single arrests matched previous descriptions of arrests in *R. dawsoni* (Tompkins-

MacDonald & Leys 2008) and lasted 0.65–9 min (mean: 2.12 ± 2.64 min) in total duration, with arrest phases lasting 0.32–3.55 min (0.91 ± 1.01 min), and recovery phases 0.33–5.5 min (1.21 ± 1.64 min) (Table 3, Fig. 6A). In 7 of the 8 single arrests, the decrease in excurrent flow rate was correlated with increases in SSC of <1.7 mg l^{-1} (r = −0.81 to −0.87, p < 0.05) that occurred in the 2 min prior to the onset of the arrest phase (Fig. 6C). The sediment suspension events linked to these arrests corresponded with ROPOS movement at or near the sponge, which generated plumes that remained around the sponge for between 9 and 307 s (65 ± 92). The ambient SSCs before arrests of pumping 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 flow from the sponge before arrests was 2.56 ± 0.88 cm s^{-1} during flood tides and 0.42 ± 0.06 cm s^{-1} at slack tides (Fig. 6D).

A single prolonged arrest was shown by *R. dawsoni* following a long sediment disturbance caused by ROPOS moving in the area. The prolonged arrest was recorded for more than 5 h (Fig. 6A,B), but instruments were collected before the sponge began pumping again, and so the full duration of the arrest was undetermined. The reduction in excurrent flow was correlated with increases in suspended sediments ($r = -0.85$, $p < 0.05$) (Fig. 6B,E) that remained elevated around the sponge for 2.45 h, with a peak concentration of 3.20 mg l^{-1} (mean 2.74 mg l^{-1}). Prior to this disturbance, the SSC averaged 2.64 ± 0.17 mg l^{-1}. The thermistor flowmeter was collected before the sponge began pumping again, so it is not known exactly how long the sponge remained without filtering. No coughing events were observed in *R. dawsoni.*

3.5. Sediment grain size

Four push cores of sediment from the Hecate Strait and 4 sediment traps from Fraser Ridge reef were analysed for grain size, for a total of 1150 g and 432 g (dry weight) respectively. Only 2 grain size categories differed significantly between the 2 reefs (Table 4). First, Hecate Strait samples contained significantly more grains larger than fine sand (>212 µm; 69% in Hecate Strait compared 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 2 locations for the remaining grain sizes.

3.6. Sediment transport

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 h 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 in 3.8 h before settling out of suspension (Fig. 7A,B). As the ambient current flow rate increases with increasing height above the sponges, 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 AMZ (4.5 km). As larger particles settle out of suspension, the concentration of the plume will decrease as well (Fig. 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 found for *H. calyx* and *R. dawsoni* even when the sponges are 2.11 and 2.39 km away from the initial disturbance, respectively (Fig. 7C).

As seen in Fig. 7C,D, each grain size has a maximum range, with larger sand grains settling out of suspension within a few metres 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 (Fig. 7C,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 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 h (Fig. 7E). Therefore, smaller particles (<20 µm) would remain in suspension for longer than 6 h of the tidal cycle and could be transported in multiple directions as they experience changes in tidal cycles.

While sediment grains may be continuously settling as represented by the model shown in Fig. 7, it is also possible that turbulent bottom currents could cause continued suspension of the smaller grain sizes throughout the 6 h tidal period.

4. DISCUSSION

Arrests of pumping in response to elevated concentrations of suspended sediment were recorded for the first time from a variety of glass sponges *in situ* in Hecate Strait, British Columbia, Canada. Our data showed that not only do different species of glass sponge have different responses to suspended sediment, but that the sensitivity of the glass sponge filtration system seems to be adapted to the relative turbidity of its habitat.
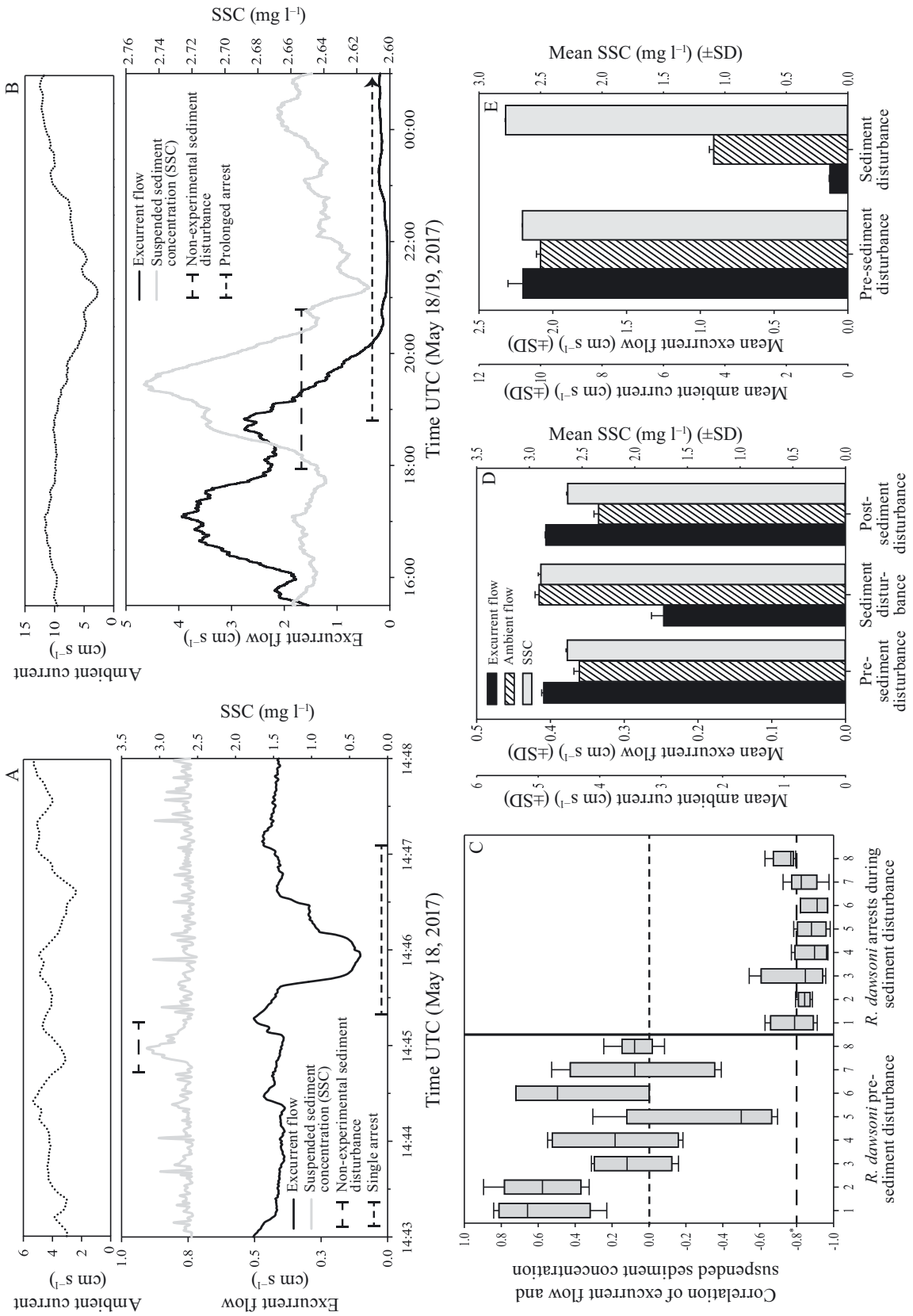
Fig. 6. Arrests by *Rhabdocalyptus dawsoni*. (A) Single arrest following a non-experimental sediment disturbance likely generated by the remotely operated vehicle. (B) Prolonged arrest associated with a 2.45 h exposure to elevated suspended sediment concentrations (SSCs). (C) Correlation of SSCs and sponge pumping activity prior to and during arrests of pumping. Dotted line indicates 0. Dashed line and *indicates significance (p < 0.05). (D) Measurements of mean excurrent and ambient flow and of SSC prior to, during and after single arrests by *R. dawsoni*. (E) Measurements of mean excurrent flow and ambient current and of SSC before and during the prolonged arrest shown in (B). No measurements were made following this arrest

Table 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 samples collected from a site. *Significant difference between the 2 locations (p < 0.05)

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 5. Time (h) spent in suspension (T_{Fall} in Table 1) of each grain size measured at Hecate Strait depending on the initial height of suspension (mab: metres above bottom)

Particle	Settling velocity (cm s^{-1})	Height of suspension (mab) 10	5	1
>Fine sand	2.607	0.11	0.05	0.01
Fine sand	1.47	0.19	0.09	0.02
Very fine sand	0.415	0.67	0.33	0.07
Coarse silt	0.184	1.51	0.75	0.15
Medium silt	0.067	4.17	2.08	0.42
Fine silt	0.025	11.00	5.50	1.10

## 4.1. Sensitivity of Hecate Strait sponges to suspended sediments

Our previous work in the Strait of Georgia showed that *Aphrocallistes vastus* arrests pumping activity 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). Strait of Georgia sponge 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% (higher transmissivity is associated with fewer particles in the water) (Conway et al. 2005). We hypothesized that glass sponges in Hecate Strait would either be sensitive to smaller increases in SSC than sponges in the Strait of Georgia because they are not naturally exposed to such high SSCs, or alternatively that Hecate Strait sponges would

be adapted to continual feeding without responding because they are unaccustomed to increased SSCs. Our results suggest that both may be correct.

At the northern Hecate Strait reef, *Rhabdocalyptus dawsoni* and *Heterochone 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 flow when concentrations of sediment reached 4–10 mg l^{-1}, a relatively small increase from the average turbidity of 2.71 ± 0.09 mg l^{-1} 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 ± 0.7 mg l^{-1}), arrested in response to SSC of 10–40 mg l^{-1} (Grant et al. 2018). 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 2 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 ± 0.9 mg l^{-1} (Grant et al. 2018) and seasonal increases up to 7 to 8 mg l^{-1} due to deposition from the Fraser River (Thomson 1981, Hill et al. 2008). Interestingly, *H. calyx* can be found at both

Fig. 7. Model of sediment transport at the northern reef complex in the Hecate Strait and Queen Charlotte Sound Sponge Reefs Marine Protected Area. (A) Top-down view of the maximum distance sediments (<20 µm) would travel after being suspended by a trawl. Each ring corresponds to a specific height (mab: metres above bottom) of suspension and ambient current velocity. (B) Cross-section showing the range of a plume of <20 µm sediment grains (using the same model as in A). When the sediment plume originates at the point indicated by '0', the distance it travels will increase with height suspended, as indicated by the coloured shape. Suspension heights of only a few metres are enough to allow particles to travel further than some of the present adaptive management zone (AMZ) widths. (C) 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 concentrations for eliciting responses in *Heterochone calyx* and *Rhabdocalyptus dawsoni* are drawn for reference along with maximum and minimum distances of the AMZ. (D) Maximum distance that a particle will travel in a single phase of the tidal cycle (~6 h) when suspended at various heights above the bottom. (E) Total time a particle of various grain sizes will remain in suspension when resuspended to a given height above the seafloor
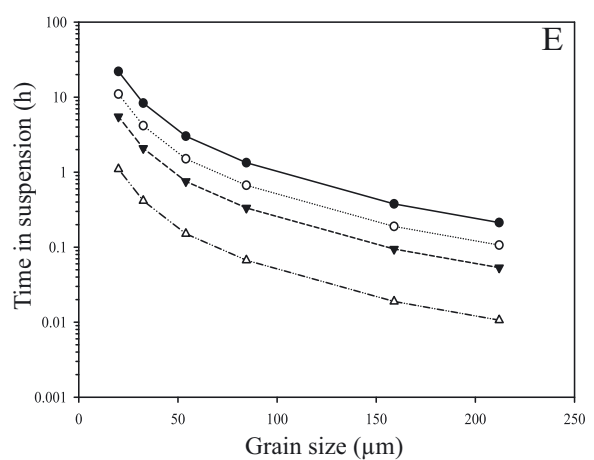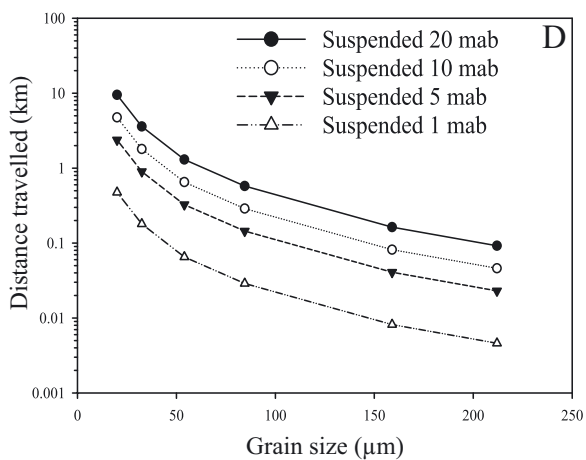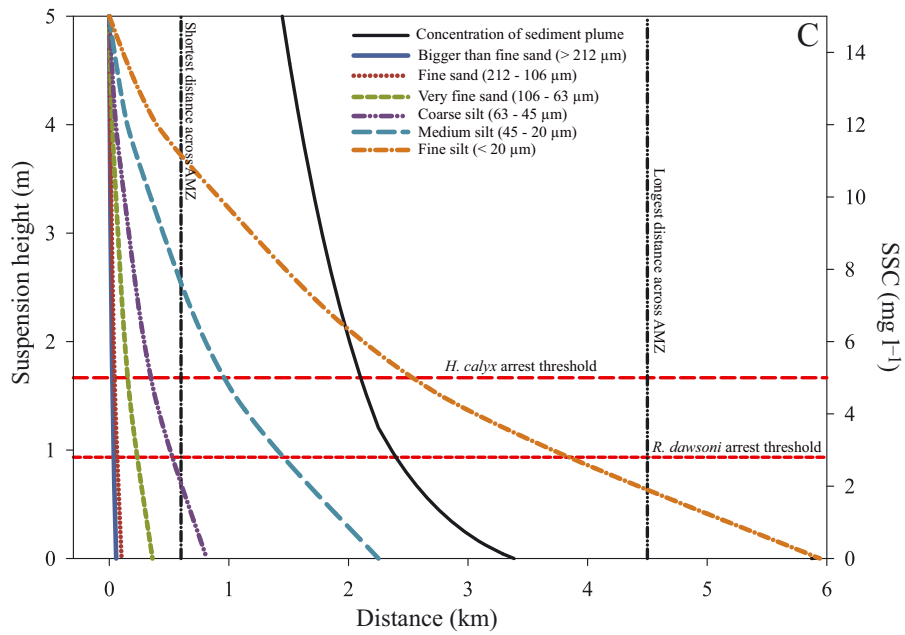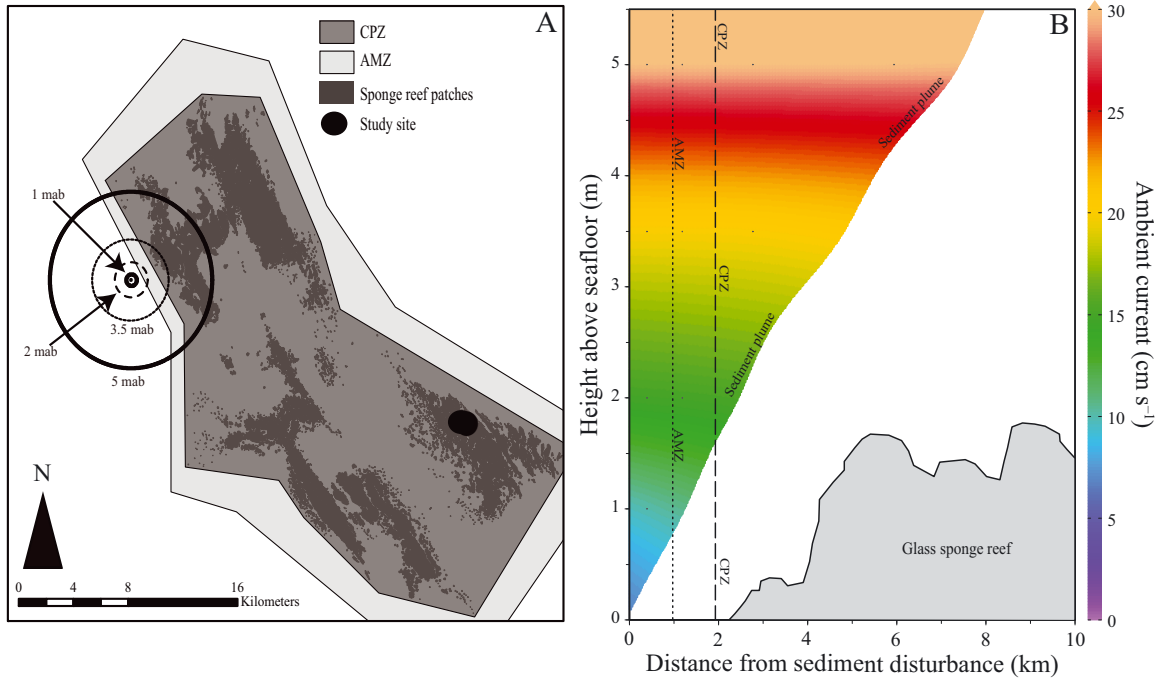
locations (Conway et al. 2001, Krautter et al. 2001), but imagery captured by the ROV indicates that this species may be more common in the northern reef complex of Hecate Strait.

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 ± 0.09 mg l^{-1}. This small change in SSC was an order of magnitude lower than concentrations found to trigger arrests of pumping by *R. dawsoni* in previous tank experiments (Tompkins-MacDonald & Leys 2008). *R. dawsoni* may indeed be more sensitive to sediment, as suggested by Mackie et al. (1983) and Mackie & 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) or 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 sensitives 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 less responsive to sediment, like *A. vastus,* common both at the low turbidity site in Hecate Strait as well as 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*, was seen more often than *Farrea occa* (Law 2018). This indicates that sedimentation is likely not the only factor that determines which reef-building species are present at a given reef patch. 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.

4.2. Species-specific differences in glass sponge responses

In situ recordings from this study and Grant et al. (2018) show 3 classifications of arrest: simple 'off-on'

responses (single), arrests with intermittent attempts to restart ('coughing') and what we have termed 'prolonged arrests'. In addition to arrests of pumping, we observed reductions in flow rate associated with increased SSC which we termed 'clogging events'. Prolonged arrests may be a longer version of a simple arrest or may reflect clogging of the filter. As all species that we studied have syncytial tissues and are expected to share a similar physiology in terms of sensitivity to mechanical stimulation and mechanism by which they arrest pumping, we did not expect to find the inter-species variations seen in this study. Arrests are triggered by electrical signals that travel throughout the sponge at 0.3 cm s^{-1} (recorded in *R. dawsoni*) (Leys & Mackie 1997, Leys et al. 1999). Action potentials in *R. dawsoni* 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 & Mackie 1997, Leys et al. 1999). If a second action potential is triggered during this period, the arrest will be prolonged (Leys et al. 1999, Tompkins-MacDonald & 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. Another possibility is that the shape of the sponge and its osculum cause different lag periods for the arrest of flow through the sponge. This could fairly readily be tested using models.

H. calyx and *R. dawsoni* both had single arrests like those previously described for *A. vastus* (Tompkins-MacDonald & Leys 2008, Grant et al. 2018), but the concentrations of resuspended sediment that trigger the arrests are unique to each species. *R. dawsoni* arrested all excurrent flow for more than 5 h following a minimal increase of SSCs of 0.1–0.6 mg l^{-1}, in what is referred to here as a 'prolonged arrest'. It is unlikely that this concentration caused clogging. In *H. calyx*, in contrast, the sponges showed a reduction in excurrent flow lasting 0.79–3.41 h, 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 & Leys 2008), but if these do reflect clogging, then in *H. calyx* clogging occurred after sustained but very slight increases in SSC of only 1–2 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 to water-column sediments. 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 variation in responses to sediment concentrations between regions; environmental adaptations that result in differing responses to stressors by individuals that reside in different environments are seen in many animals (e.g. Levinton 1991, Somero 2002, Chiba et al. 2016, Stickle et al. 2017). Our finding of different SSC thresholds among glass sponge species living in different reefs suggests that variation in arrest response is partially driven by environmental factors. Comparing the responses of species that live 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 into whether the differences we see are species- or environment-driven.

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 6 recordings and 10 sediment experiments did we see a clear arrest of pumping. 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 see in *F. occa* is that it may take advantage of water being induced to flow through the tubes by ambient current moving over the bush. The body wall of *F. occa* is often less than 1 mm thick, and these wafer-thin walls form 'flutes' (Fig. 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 up from the base of the sponge. Krautter et al. (2001) suggested 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 to use ambient flow to assist feeding while still baffling sediments on the reefs. If the sponge does baffle sediments, then it would not be effective to easily arrest when continuously exposed to low levels of sediments. If that is the case, then a lower pumping rate would be less likely to draw sediment-laden water through the aquiferous system. Determining whether this is the case will help build a better understanding of this species.

4.4. Long-term effects of suspended sediments on sponges

Understanding the extent to which anthropogenic activities influence abiotic conditions like suspended sediments is crucial for management of reefs and species in the HSQCS-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 2017). The sediment concentrations known to be resuspended by trawl gear are above the levels that cause arrests in glass sponge reef species (Fig. 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 used in our study suggests that plumes of this size could easily pass over the present protective boundaries of the MPA. We calculated how far trawl-induced resuspended sediment could travel (Fig. 7). Our model indicates that within a 6.5 h phase of the tidal cycle, smaller-grained sediments in plumes generated by activities 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 for causing repeated or longer arrests of pumping. Multiple arrests were previously calculated to reduce the daily energy intake 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). 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. The long-term effects of repeated 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 conservation of the glass sponge reefs.
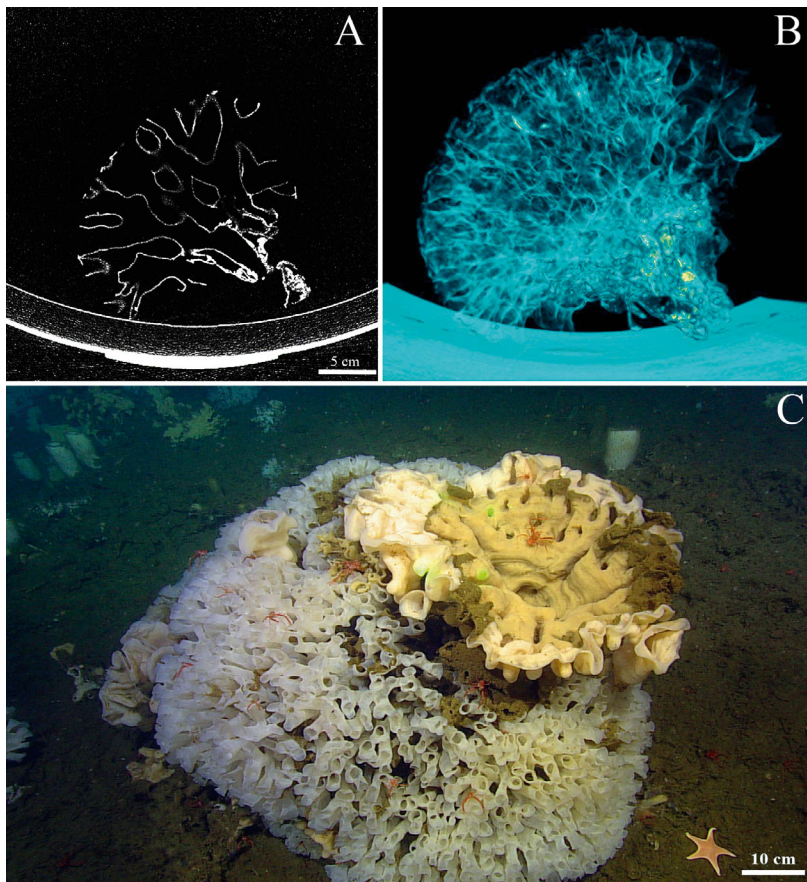
Fig. 8. Views of the bush sponge *Farrea occa*. (A) CT side scan showing a cross section through a small sponge. (B) 3-D model built by the CT scan sections. (C) Image of an *F. occa* bush with a *Heterochone calyx* growing out of the top at the northern reef complex in Hecate Strait

tissue condition (Pineda et al. 2017, Scanes et al. 2018). However, because in some species choanocyte chambers could not be found in explants, and active filtration was not seen, it seems difficult to draw conclusions about whether a sponge is 'tolerant' or not of sediment treatment. A promising approach is to use video cameras to monitor the oscula diameters as a proxy of active filtration, and as a gauge of sensitivity to water conditions (Kumala et al. 2017, Strehlow et al. 2017, Goldstein et al. 2019). Again, there are caveats to this approach. Although contractility of the osculum in demosponges may be correlated with excurrent flow rates, and therefore the amount of water filtered, reduced excurrent flow rates do not necessarily mean that the sponge has reduced the pumping activity of its choanocytes. Demosponges can constrict sphincters in the canals throughout their bodies, thereby reducing excurrent flow rate (Parker 1910), something not known to be possible in glass sponges due to their syncytial tissues. Glass sponges, in contrast, stop filtering by arresting the choanocyte pumps; this is a fundamental difference in the physiology between demosponges and hexactinellids (Leys et al. 2007). Another consideration, not often addressed in interpreting demosponge filtration behaviour in response to sediments, is the effect of season on sponge filtration activity. Even warm-water species show a reduction in filtration rate with season (Reiswig 1975), so the time of the year in which experiments are carried out may strongly affect the interpretations.

Our estimates that extended periods of reduced excurrent flow rates could be fatal are supported by mesocosm experiments in demosponges (e.g. Pineda et al. 2017, Scanes et al. 2018). *Geodia barretti* held in tanks with suspended sediment was found to reduce respiration rate (Kutti et al. 2015), but for longer-term experiments, large sponges are difficult to keep in high enough numbers that they are not affected by other aspects of husbandry. More recently, explants of *G. atlantica* were cultivated for this explicit reason, generating sample sizes of 5 for the different treatments of sediments and temperature (Scanes et al. 2018). Under those conditions, the sponge explants did not die, but respiration rates were significantly lower after 40 d of increased temperature and suspended sediments.

A similar study on explants of warm-water species found that 'tolerance' to suspended sediment varied among species (Pineda et al. 2017). Most work has inferred sponge 'health' from respiration rates and

4.5. Suspended sediments influencing the Hecate Strait MPA

The threshold concentrations of suspended sediments that triggered arrests in this study were all below 10 mg l^{-1}. This level of SSC is much lower than that found previously at the Strait of Georgia (Grant et al. 2018), at 40 mg l^{-1}. Modern trawl equipment currently used near the reefs causes plumes of sediment well above these thresholds. The 2 most commonly
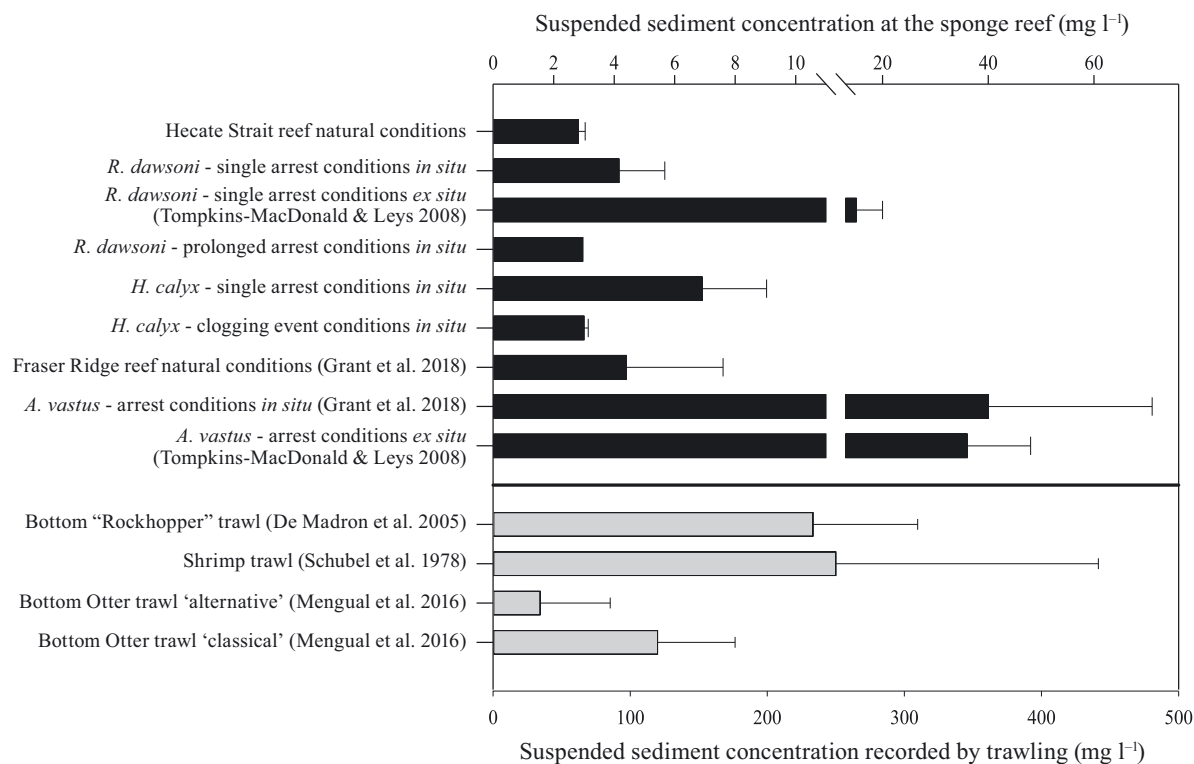
Fig. 9. Suspended sediment concentrations (SSCs) associated with arrests in glass sponge species. Both *in situ* and in tank recordings are shown (black bars, top axis) and are contrasted with SSCs known to be generated by different trawling gear (gray bars, bottom axis). Note the different scales on the 2 axes. All thresholds of response by the glass sponges are below levels of SSC known to be generated by trawling activity

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} (Fig. 9) (Schubel et al. 1978, Mengual et al. 2016). Trawls designed to reduce the impact on and contact time with the seafloor, such as those with Jumper doors (Morgère), can resuspend 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 above what is currently known to induce arrests in glass sponges and would take considerable time and distance to dissipate to concentrations below 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 to which the sediments are resuspended and the grain sizes within the sediment plume and the 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 (Fig. 7). Sediments suspended by fishing trawls have been reported to reach ~5–10 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 above the threshold of response for both *H. calyx* and *R. dawsoni* (Fig. 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 estimated model 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.

Increased suspension height and faster ambient currents mean small grain sizes travel farther, and if sediments remain in suspension for more than a single phase of a tidal cycle, there is increased risk of a sediment cloud reaching far from the initial disturbance (Nafe & Drake 1961, Jones 1992). Smaller particles, like silts and clays found at the sponge reefs

(~8% of sediments at Hecate Strait, Table 4), are more easily resuspended, are more likely to suspend higher in the water column and settle more slowly than larger sand grains, and they can be resuspended by bottom current turbulence before settlement occurs (Nafe & Drake 1961). Once in suspension, ambient currents move sediments away from the source. Some 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 may be affected by sediments to an even greater extent than once expected. To avoid detrimental sediment impacts, the AMZ would need adjustment to a width that would allow for the dissipation of sediment plumes to concentrations below noted species thresholds.

The estimates of sediment dispersal reported here are conservative, and in fact the problem could be beyond what has been calculated. Our model assumes that all particles are spheres and does not account for particle flocking, turbulence or stratification of the water column. These assumptions 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 assumed in our model, increasing their travel time. This may underestimate the total distance these smaller sediment grains would disperse. Additionally, our model assumes a constant ambient current velocity which may not reflect how currents move around the sponges. If the skeletons of sponges decrease local ambient currents (by effectively increasing the boundary layer), more sediment would settle out directly over or around the sponges themselves instead of continuing to move with the currents. These factors should be considered in future models of sediment dispersal around the reefs.

5. CONCLUSION

Two glass sponge species, *Heterochone calyx* and *Rhabdocalyptus dawsoni*, from Canada's HSQCS-MPA show arrests of pumping in response to changes in suspended sediments *in situ*. The thresh-

old concentrations of suspended sediments that induced these arrests are lower than those previously found for *Aphrocallistes vastus* at Fraser Ridge reef in the Strait of Georgia, and lower than previously reported for *R. dawsoni* in laboratory experiments. *R. dawsoni* appears so sensitive that several hours of reduced pumping 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 pumping activity or responses to sediment disturbances. The distance sediments are predicted to travel in Hecate Strait suggest that bottom contact activities outside the current AMZ could generate SSCs that would be damaging to sponges reefs within the CPZ. Additionally, our data also suggest a larger buffer (AMZ) of >2.39 km would be beneficial for preventing any anthropogenically resuspended sediment from reaching the concentration thresholds of sponges; this is substantially larger than has been considered so far by managers (Rubidge et al. 2018). A future study, running a numerical ocean model such as ROMS (Regional Ocean Modeling System) and using the results of this paper, would allow drawing sediment dispersion risk contours around the reefs (as in Boutillier et al. 2013, Fisheries and Oceans Canada 2018), to inform adjustments to the size and/or shape of the AMZ. Our study highlights the fact that understanding the range of effects of suspended sediments on different species of deep-water sponges is important for effective design of MPA boundaries and regulations.

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