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Canadian Science Advisory Secretariat (CSAS)

Research Document 2013/074

Pacific Region

Effects of Sediment on Glass Sponges (*Porifera*, *Hexactinellida*) and projected effects on Glass Sponge Reefs

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November 2013

Canada

Foreword

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Published by:

Fisheries and Oceans Canada
Canadian Science Advisory Secretariat
200 Kent Street
Ottawa ON K1A 0E6

http://www.dfo-mpo.gc.ca/csas-sccs/
csas-sccs@dfo-mpo.gc.ca

ISSN 1919-5044

Correct citation for this publication:

Leys, S.P. 2013. Effects of Sediment on Glass Sponges (*Porifera,Hexactinellida*) and projected effects on Glass Sponge Reefs. DFO Can. Sci. Advis. Sec. Res. Doc. 2013/074. vi + 23 p.

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ABSTRACT

Sponges are dependent on the environment for flow and therefore food. They lack nerves and muscle and are unable to rapidly relocate in response to changing environments. Glass sponges are particularly immobile due to their heavy silica skeleton. They are nevertheless animals which, like other animals, have tissues and sensory systems that allow them to sense changes to their environment and attempt to avoid detrimental effects. They do this either via sensory cilia and contractions of the filtration system (in demosponges) or sensory tissues and electrical signalling to arrest the feeding current (in hexactinellids = glass sponges).

Sponges are suspension feeders: they draw water through pores in their surface tissues, into canals to chambers of choanocytes where food is captured. They extract bacteria (0.2-1µm) and picoplankton (0.2-10µm) (e.g. unicellular algae). Clearance studies show sponges preferentially take up smaller particles (0-8µm), but are selective feeders – they eat the more nutritious items, and expel inedible particles. Sediment >10-11 mg/L irritates and eventually clogs the filtration system of demosponges. Clogging triggers an expulsion behaviour which causes the incurrent canals to inflate and then contract, pushing the sediment out of the sponge; several contractions in a row (about 10-40 min each) effectively expel small amounts of sediment waste.

Smothering by sediment causes increased respiration, decreases in oxygen consumption, and reduced reproductive ability and body weight. Death occurs in 3-6 months.

Glass sponges live in deep water (>30m) and usually on raised topography with accelerated flow. Reef sponges live in turbid water (high suspended solids, 7-8 mg/L) and are efficient bacteriovores. They take up nearly 99% of bacteria and 94% of unicellular eukaryotes from the water they filter. Sediment – clay/silt – is expelled as wastes. Sediment at reefs consists of 44-58% clays, and 75% of reef sediment is less than 3 microns in size. Whereas demosponges contract to expel debris and unwanted particles, Glass sponges if irritated by mechanical stimuli such as sediment use electrical signals to arrest feeding. No experiments have tested long-term effects of smothering of glass sponges by sediment but continued presence of >15-35 mg/L of sediment (grain size <25µm) causes complete and continued arrest of glass sponge pumping and filtration. Longer than 40 minutes exposure to 15-35 mg/L sediment causes clogging of sponge feeding tissues. Clogging by sediment reduces filtration in the glass reef sponge by 50-80% of normal levels.

Glass reef sponges rely on induced current to reduce the energetic cost of filtration. An estimated 2/3 of the sponge's daily food intake occurs during the maximum flood tides which occur approximately 20% of the time. Trawl activities cause temporary resuspension of bottom sediment (40-120 mg/L – a combination of inedible and edible particulates) during increased ambient current flows. Reef sponges take 6 hours or longer to recover normal filtration levels, which would reduce the daily time to feed by a minimum of 6 hours. Reduced feeding during maximum ambient current would deprive the reef sponges of 2/3 of their daily food intake, compromising growth and future reproductive ability.

RÉSUMÉ

Les éponges dépendent de leur environnement en ce qui concerne le débit de l'eau, et donc la nourriture. Elles sont dépourvues de nerfs et de muscles et ne peuvent pas changer rapidement de place en réponse à l'évolution de leur environnement. Les éponges siliceuses sont immobiles principalement en raison de leur lourd squelette composé de silice. Ce sont tout de même des animaux, car elles ont aussi des tissus et des systèmes sensoriels qui leur permettent de détecter les changements survenant dans leur milieu et de tenter d'en éviter les effets négatifs. Pour ce faire, elles utilisent leurs cils sensoriels et contractent leur système de filtration (chez les démosponges) ou leurs tissus sensoriels et des signaux électriques pour interrompre le courant d'alimentation (chez les hexactinellides [éponges siliceuses]).

Les éponges sont des organismes suspensivores : elles attirent l'eau par les pores de leurs tissus superficiels dans les canaux qui transportent l'eau jusque dans les cavités des choanocytes, où la nourriture est capturée. Elles extraient les bactéries (0,2-1 µm) et le picoplancton (0,2-10 µm) (p. ex., algues unicellulaires). Les études de clairance démontrent que les éponges absorbent surtout de petites particules (0-8 µm), mais leur alimentation est sélective : elles mangent les particules les plus nutritives, puis expulsent le reste. Une proportion de sédiments de plus de 10-11 mg/L irrite le système de filtration des démosponges, puis finit par le boucher. L'obstruction déclenche un réflexe d'expulsion, ce qui fait enfler puis se contracter les canaux internes, expulsant ainsi les sédiments de l'éponge; plusieurs contractions l'une à la suite de l'autre (environ 10 à 40 minutes chacune) permettent d'expulser avec succès de petites quantités de sédiments.

L'étouffement par les sédiments entraîne une respiration plus rapide et une plus petite consommation d'oxygène, tout en diminuant la capacité de reproduction et le poids corporel de l'animal. La mort s'en suit, de trois à six mois plus tard.

Les éponges siliceuses vivent en eaux profondes (plus de 30 m), généralement sur les fonds à topographie élevée où le courant est plus rapide. Les récifs d'éponges vivent en eaux turbides (concentration élevée de solides en suspension [7-8 mg/L]) et sont d'efficaces bactérivores. Ces éponges absorbent près de 99 % des bactéries et 94 % des eucaryotes unicellulaires dans l'eau qu'elles filtrent. Les sédiments (argile, limon) sont expulsés en tant que déchets. Sur les récifs, les sédiments sont composés à 44-58 % d'argile, et 75 % des sédiments mesurent moins de 3 microns. Chaque fois que les démosponges se contractent pour expulser des débris et des particules indésirables, les éponges siliceuses sont irritées par des stimuli comme les signaux électriques arrêtant l'alimentation à cause des sédiments. On n'a encore jamais étudié les effets à long terme de l'étouffement des éponges siliceuses par les sédiments, mais la présence continue de plus de 15 à 35 mg/L de sédiments (taille des grains < 25 µm) entraîne l'arrêt complet et continu des processus de pompage et de filtration chez les éponges siliceuses. Une exposition de plus de 40 minutes à 15 à 35 mg/L de sédiments entraîne l'obstruction des tissus d'alimentation des éponges. L'obstruction par les sédiments réduit le processus de filtration des récifs d'éponges siliceuses de 50 à 80 % par rapport aux niveaux normaux.

Les récifs d'éponges siliceuses dépendent des courants, qui réduisent les coûts énergétiques de la filtration. On estime que les deux tiers de l'absorption quotidienne de nourriture d'une éponge ont lieu lors du flux maximal de la marée, qui lui se produit environ 20 % du temps. Les activités de pêche au chalut peuvent occasionner une remise en suspension temporaire des sédiments des fonds marins (de 40 à 120 mg/L; une combinaison de particules comestibles et indésirables) durant les périodes de vitesse accrue du courant de marée. Les récifs d'éponges prennent au moins six heures pour retrouver leurs niveaux de filtration normaux, ce qui réduit chaque jour d'au moins six heures le temps passé à s'alimenter. Une diminution de l'alimentation lorsque le courant atteint sa vitesse maximale empêche les récifs d'éponges d'absorber les deux tiers de leur nourriture chaque jour, ce qui compromet leur croissance et leur capacité de reproduction.

1. INTRODUCTION

Sponges are grouped into 4 Classes, three of which have a skeleton of glass (Demospongiae, Homoscleromorpha, and Hexactinellida) and one of calcium carbonate (Calcarea). Hexactinellids alone are referred to as 'glass' sponges however, because their skeleton forms more than 80% of the sponge biomass, and in this regard is more substantial that the glass skeleton of most other sponges. Demosponges make up 95% of sponges, and the other three classes including Hexactinellida make up less than 5% each. Demosponges are not only more abundant than other sponge types, but many live in easily accessible habitats. Correspondingly, knowledge of sponge function is highly biased to demosponges, and although many details can be generalized to all sponges, in some important aspects hexactinellids differ. It is important to know how both sorts of sponges function under sediment stress in order to have a proper understanding of the effects of sediment on glass sponge reefs. Therefore, section 2 describes sponge function and the effects of sediment on filtration focusing on the situation in non-hexactinellids.

Hexactinellids are unusual among sponges because of their heavily silicified skeleton, but a main feature which distinguishes them from all other sponges is their syncytial tissues (the whole animal is joined as a seemingly continuous giant cell) which allows electrical signalling. Furthermore, of all the hexactinellids, the reef forming glass sponges are unique in being able to fuse their glass skeleton into a scaffold of glass, which allows them alone among all sponges to form reefs. Sections 3 and 4 refer to the specific characteristics of glass sponges. In section 3 glass sponge habitats are described, as is the peculiar physiology of glass sponges and knowledge of their feeding and filtration capacity. Section 4 focuses specifically on the effects of sediment on reef-forming glass sponges. Terminology for sponge body parts requires some explanation, and a glossary is given in Appendix 1.

2. HOW SPONGES FUNCTION

2.1. The Sponge Filter

2.1.1. Sponges filter water by pumping

Sponges have no gut. They instead have cells called choanocytes which are small round or squat cells with a flagellum and a collar of microvilli. The flagellum is a whip-like organelle that beats in sinusoidal waves generating a flow of water along its length, away from the cell body. The collar surrounds the flagellum like fence posts. The collar microvilli are linked by a fine mesh of protein strands and these form the smallest dimension filter in the sponge. As the flagellum beats, water is drawn through the pores of the surface of the sponge, through canals to 'chambers' of choanocytes (= flagellated chambers). The flagella 'pump' draws the water through the microvilli and protein mesh and from there it goes out of the chamber and out of the sponge via canals and a large opening called the osculum.

The entire fluid-filled canal system from inhalant to exhalent surface of the sponge is called the aquiferous sytem. Experimental evidence indicates that there are no routes bypassing the filter system, and therefore any inedible particles must be consumed and ejected as wastes.

2.1.2. Sponge feeding

Sponges are largely bacteriovores but can take up pico-plankton (small unicellular eukaryotes) and capture particles of different size at different places in their filtration system. The largest

particles (>20 microns) are excluded from the aquiferous system (Kilian, 1952; Reiswig, 1974; Willenz, 1980; Pile et al., 1996). Particles 8-20 microns may be taken up by phagocytosis by cells in the walls of the canals. The smallest particles <8 microns are thought to be phagocytosed by cells that form the entrances to the flagellated chambers. Bacteria (≤ 1 micron) are thought to be phagocytosed by the choanocytes which have the collar filter.

The exception to feeding on bacteria occurs in sponges that actually contain large numbers of symbiotic bacteria in their tissues *(e.g., Theonella swinhoei, Yahel et al., 2003)*. These sponges have been found to take up dissolved organic carbon; this is thought to 'feed' the symbionts, which in turn must provide nutrients to the sponge.

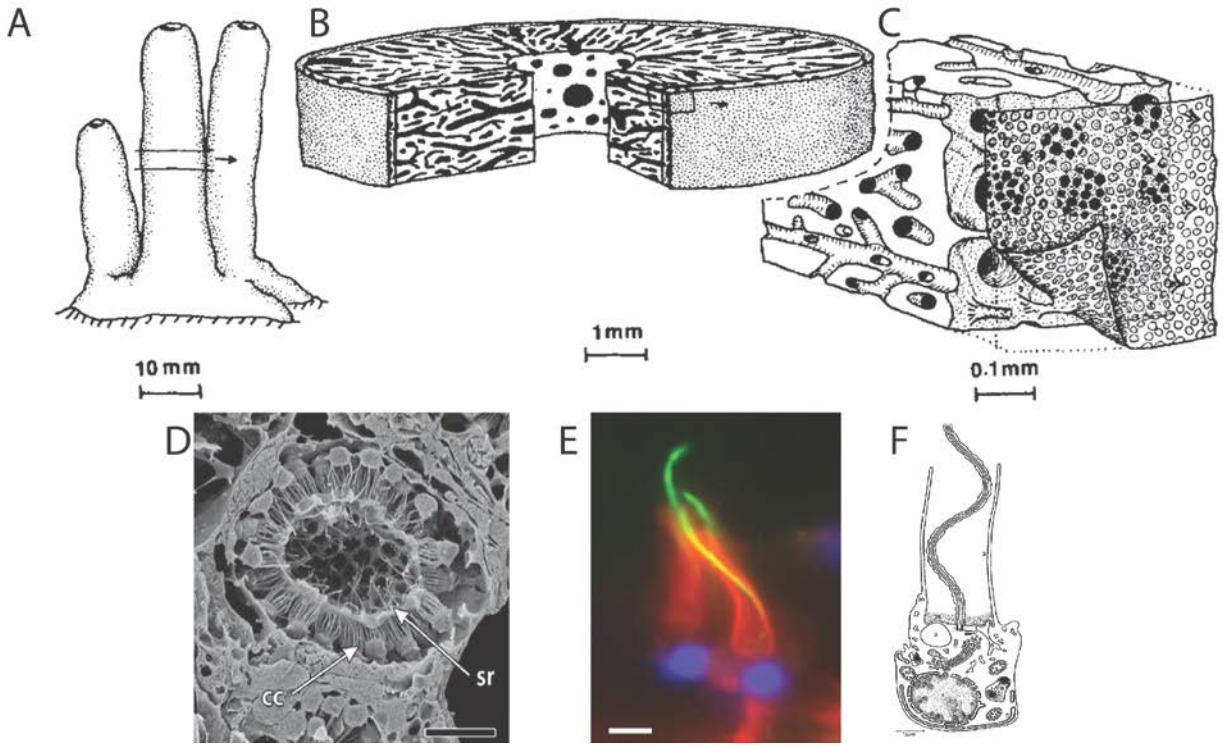

Figure 1. Structure of the filtration system in a demosponge. A-C Haliclona permollis (from Reiswig, 1975). A, whole sponge with a slice of the body wall, shown in B; C, portion of the outer wall showing the dermal membrane (skin) with ostia (holes) through which water enters to the canals below. D. Choanocyte chamber (cc, choanocyte, sr, secondary reticulum around collars) of Haliclona mollis (from Adams,2010); E,F, Structure of the choanocyte – with flagellum (green central whip-like projection) between collar microvilli (red), arising from the cell body which contains a nucleus (blue), (from Leys and Hill, 2012).

2.1.3. Sponge behaviour

Whereas most of the sponge's activity involves pumping water through the body to feed, sponges can react to non-edible irritants in the water they filter. The response is slow, and non-nervous, but nevertheless involves a coordinated wave of contraction that propagates across the body. Because there are no conventional muscles, sponge contractions are slow (10-40 minutes, depending on the species) but these can effectively reduce the body size by up to 50%.

It has been shown that many irritants can trigger contraction by sponges, including pin pricks and knocks, but also chemical stimulants such as glycine, glutamate, nor-epinephrine, caffeine, and nitric oxide (Parker, 1910; Emson, 1966; Prosser, 1967; Ellwanger and Nickel, 2006). In

recent years it has been shown that demosponges respond to a threshold level of sediment in the water by inflating and then contracting their bodies to eject unwanted material, much like a cough (Elliott and Leys, 2007). A series of coughs removes most inedible particles. The response can be triggered by glutamate and inhibited by GABA (Elliott and Leys, 2010), which indicates that glutaminergic signalling – like that used by conventional neurons – is involved in coordinating the cough response in sponges.

2.2. THE EFFECTS OF SEDIMENT ON SPONGES:

A review of the literature covering all aspects of the effects of sediment on sponges can be informative in understanding the potential effect of sediment on glass sponges. Sediment is a general term that may refer to solely inorganic particles, or include edible organic and inedible inorganic components, the former can contain mucus, fecal matter and bacteria – the matter of marine snow – and the latter often consists of silts and clays but may have other mineral particles. There are three types of studies which provide information about the effects that sediment has on sponges: a) distribution of sponges and correlation with sediment accumulation; b) manipulative (*in situ*) studies of recruitment or survival under different natural sediment conditions; c) direct sediment treatment to sponges and monitoring physiology (metabolism via respiration; pumping rates and oxygen consumption), and condition (growth/reproduction). The results of the best examples of these studies are summarized below.

2.2.1. Distribution of sponges in relation to sediment/turbidity

Two correlative studies clearly illustrate the relationship between sediment type/size and sponge distribution. On the Pacific coast of Central America, it was found that during periods of higher sediment deposition (winter/storms) the diversity of sponges in rocky shores was low. Some species retained similar numbers through all seasons, but massive, branching and cushion-shaped species were only present prior to sediment deposition events, during which vast amounts of sediment – up to 13 kg m^{-2} d^{-1} – can be deposited on the bottom (Carballo, 2006).

On the Great Barrier Reef, Australia, the abundance of a sponge of interest for commercial aquaculture (*Rhopaloeides*) increased significantly further from coastal habitats with 3.5 times more found on offshore reefs than in coastal regions (Bannister et al., 2012). This gradient of distribution correlates with the type and grain size of sediment found across that region. Sediment collected at inner reefs (near coastal habitats) consisted mostly of clays, while sediment at outer reefs consisted mostly of carbonates. The particle size at inner reefs was <45 microns, at mid-coast reefs was 90-150 microns, and sediments from the outer reefs had the largest sizes of particles with grain sizes of 180-250 microns.

2.2.2. Recruitment and survival with sediment

Five studies have examined recruitment/survival of sponges under different sediment conditions. An early experiment (Bakus, 1968) in Fanning Island, Central Pacific, found that sponges on the undersides of coral slabs died when the slabs were either turned over to expose sponges, or transplanted to a region where sedimentation was higher. Sponges became smothered in the new location: from 1-5 mm of silt was found to cover the sponges in the high sediment area even if they were on the underside of the coral slabs.

In a more recent experiment, panels placed in different light and sediment conditions with and without covers over the substrate showed less recruitment of sponges on panels that were

exposed to sediment deposition. Transparent covers allowing light to penetrate but no sediment to accumulate had the most recruitment (Maughan, 2001).

There is evidence that some sponges do better in areas of higher sediment, but only if sediment doesn't accumulate on the sponge. For example, sponges that live on scallops seem to do better (grow and reproduce well) if the scallop is in higher sediment areas, but the sponges die if the scallop is dead and cannot 'clap' (its normal movement), even if sediment was cleared manually. Scallops normally clap or swim up off the bottom 2-3 times per hour, and this seems to keep the sediment from settling on the sponge (Burns and Bingham, 2002).

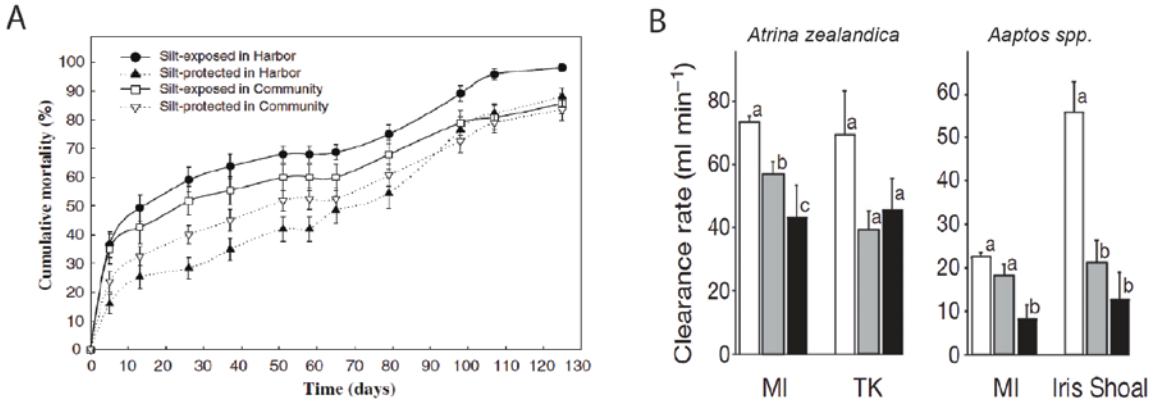

Figure 2. Effect of silt on (A) sponge survival and (B) clearance rate. A, Rates of mortality of sponge explants (Scopalina) in a harbor (dark symbols) and away from the harbor (open symbols); not protected from silt (circles) and protected from silt (triangles) (From Maldonado et al., 2008). B. Clearance rates (ability to remove particles from the water) of two species of sponge (Atrina zelandica and Aaptos spp.) at different locations MI, TK and Iris Shoal, when treated with no sediment (clear bars) and thin (10 mm deposition on the substrate; grey bars) and thick sediment (20mm deposition on the substrate, black bars)(From Lohrer et al., 2006).

The effects of shading, silt, nutrients, and salinity on sponge condition (growth, reproductive status and amount of symbiotic algae) were studied in the phototrophic sponge *Cymbastela concentrica*. The sponges were transplanted to different sites *in situ* which replicated these conditions. It was found that both shade and silt had a negative impact on sponge condition but nutrients and salinity had no significant effect. Silt (5g added once a week to the top of the sponge) caused reduced weight and reduced reproductive activity and also altered the relationship with the symbiotic algae (Roberts et al., 2006).

Perhaps the most comprehensive study examining survival of sponges under sediment and natural conditions is by Maldonado and colleagues (2008). The survival of the Mediterranean sponge *Scopalina* was compared for pieces transplanted into a harbor compared to those placed in a natural area; the harbor had 4 timesthe amount of fine grained sediment (0-30 micron size) than in the natural area. Some explants were protected from sediment by 'shields', others not. Only 11% of all explants survived in both conditions, but survival was significantly shorter in theharbor compared to under natural conditions (Figure 2A). Importantly, even in the natural habitat sponge survival increased significantly if protected from sediment by shields, so sediment was considered to play a large role in the mortality of sponge explants. Mortality was found to be dependent on both amount of sediment and genetics of the individual (i.e. what individual the explant came from – made a difference to sediment tolerance). The authors

concluded that small grain size is harmful, because it both clogs the aquiferous system and adsorbs toxicants (Maldonado et al. 2008).

2.2.3. Application of sediment to sponges, and assessment of their physiology

The most informative study is that which experimentally changes the amount of sediment to which sponges are exposed and records changes in their pumping rates, filtration efficiency, respiration, and overall condition. These sorts of experiments have been carried out on both demosponges and hexactinellids (glass sponges) in vastly different parts of the world, and have had very similar results. Here, studies on demosponges are described.

The earliest work is that of Gerrodette and Flechsig (1979) who applied natural marine clay (sediment) to the tropical demosponge *Verongia* in a chamber with controlled water flow. The experiment was done *in situ* in the sponge's natural habitat in the Caribbean, and the effects were assessed by changes seen in the pumping rate over hours and days. The results were that pumping rate decreased as sediment concentration increased, with >11 mg/L causing reduced pumping. However it was longer term (5 days) exposure to higher concentrations (100 mg/L) that caused continued a decline in pumping rates. Given the response to concentrations as low as 11 mg/L, the authors concluded that sponges were "...more sensitive to sediment than other suspension feeding organisms".

Lohrer and colleagues (2006) took a large scale approach and tested the effect of a one-time application of sediment onto $2m^2$ plots that had sponges of the demosponge genus *Aaptos* in New Zealand. Three weeks later the condition of sponges (oxygen consumption, wet and dry weight, and reproductive output) was evaluated in comparison to that of sponges in control plots. The tissue weight of sponges in the sediment plots was reduced in comparison to controls, oxygen consumption was reduced by 17% and the clearance rates (ability to filter the water) was half (50%) that of the control sponges (Figure 2B).

In Australia, Bannister and colleagues (2012) tested effect of carbonates and clays on metabolism (via respiration) of *Rhopaloeides*. Whereas clays are more common in inner Great Barrier Reef (GBR) area, carbonates – from sand and corals – are more common in the outer GBR. Increased concentrations (35-65 mg/L) of clays – mean size 3.1 microns – in the water for more than 7 hours caused 35% increase in respiration, while respiration only increased 12% when sponges were exposed to carbonates (35-57mg/L; mean size 8.2 microns). Smaller particles remained suspended for longer and may have caused the difference in results. Treatment of the sponges with clays for 4 days caused respiration to increase by 43% (double that of control sponges). Sponges took 4 days to recover normal respiration rates after the treatments ceased. During treatment the sponges produced mucus, presumably to remove the sediment. In corals, mucus production is metabolically costly (Weber et al., 2006). It was concluded that clays (fine particles) have a high metabolic cost on sponge feeding.

2.2.4. Effects of sediment on demosponges - summary

I. Water column turbidity (opacity due to particulates in the water column) results from organic and inorganic matter. Generally the inorganic part is inedible some of which may accumulate on surfaces; the organic part may be consumed or removed by processes prior to settlement.
II. Sponges and other benthic suspension feeding invertebrates capture food from the water column and can live in areas of high particulates if there is little accumulation of silt. Where silt deposition is high, fewer sponges are found. In experimental manipulations in situ, sponges generally die from being covered by silt.

III. With respect to filtration, finer grained particles cause reduced pumping (and filtration) but increased respiration. The latter is thought to be due to increased mucus production and the need of the tissues to remove the sediment by feeding or otherwise.

3. GLASS SPONGES

3.1. WHERE GLASS SPONGES LIVE

3.1.1. Glass sponge habitats world-wide and oceanographic requirements

Glass sponges are found in deep-water world-wide. In many areas they occur in what are termed 'beds' (e.g., *Sericolophus hawaiicus*, *Pheronema carpenteri*), where large numbers of the same species live in close proximity to each other, but the densest communities are found on continental shelves in a depth range of 30m to around 250m (e.g., in Antarctica and on the Pacific coast of North America). In only four locations world-wide are there populations shallow enough to reach by SCUBA diving (e.g., Weddell Sea, the fjords of the north-east Pacific from Washington State up to Alaska, some submarine caves in the Mediterranean, and some fjords of New Zealand).

Glass sponges live in cold water. Temperatures in Hecate Strait British Columbia are 5.5 - 7.3ºC (Whitney et al., 2005). In Barkley Sound, temperatures at fjord wall habitats are 7.5 - 10ºC (Yahel et al., 2007). In the Strait of Georgia they are 9.4 - 10.5ºC (2004 - 2005) (Leys et al., 2011). In Arctic and Antarctic water, temperatures may be as low as 0 - 4ºC.

Species of glass sponges known from Hecate Strait attach to hard substrates (e.g., rock, cobble, other sponge skeletons), but because studies of larval metamorphosis are limited because of the deep sea habitat, it is possible that some larvae are able to settle on soft substrates

Studies of sponge distribution from shallow to deep water have shown that more sponges are found on steep or even vertical inclines, and fewer where the substrate shelves or is flat (Farrow et al., 1983; Maldonado and Young, 1996). Generally, sloped or flat areas accumulate sediment and the sediment is prone to slumping, which would dislodge new recruits as well as any established individuals. There are a few places where glass sponges occur in high densities, and in these instances there is a balance between high turbidity (suspended particulates in the water column some of which settle) and current which prevents accumulation of sediment.

In the Porcupine Sea Bight, west of Ireland, *Pheronema carpenteri* lives in densities of 1.5 per m^2 on slopes. Observations of resuspension of material from upper slopes suggest they may benefit from increased food, but by their location on the slopes they avoid burial (Lampitt, 1985; Rice et al., 1986). The relationship of macrofauna to sediment loading was studied in Knight Inlet, a fjord typical of many of the inlets in British Columbia (Farrow et al., 1983). The head of the inlet is described as having a 'continual rain of glacial silt' with summer sedimentation rates of 4 $kg/m^{-2}/d^{-1}$. Only two types of animal were common at the delta head (brachiopods and sabellid worms), while both encrusting demosponges and glass sponges increased in abundance towards the delta mouth and sill. The sill had the highest numbers of hexactinellids.

In Antarctica dense sponge communities and hexactinellids form a dominant component on hard substrates (rock) at depths of 99-225m off Kapp Norvegia in the Weddell Sea with up to 200 per m^2 (Barthel and Gutt, 1992). Substrate, rather than depth, was the main determinant of sponge type and abundance, and in particular, once hexactinellid communities were

established, their spicules formed a substrate for settlement of other sponges and thus formed a major structuring agent in those areas (Barthel, 1992).

A similar substrate/structuring role was found for stalks of the glass sponge *Hyalonema* which lives in beds of 2-3 per 10 m^2 (a stalk approx. every 5m) (Beaulieu, 2001a; Beaulieu, 2001b). Here the sponge lives high on the end of a stem of glass spicules and though the sponge can live up in the water column the tissue on the stalk dies and the stalk is colonized by other filter feeders including zooanthids, tunicates, bryozoans and ophiuroids.

In deep waters (360-430m) near Kona Hawaii *Sericolophus hawaiicus* forms beds of up to 4.7 per m^2. This sponge, like *Hyalonema*, forms a cushion-like body at the end of a stalk of glass spicules. The sponges' exhalent openings (oscula) all face the same direction – downstream – and the inhalant surface forms an umbrella-like bell facing the current (Pile and Young, 2006).

3.1.2. Glass sponge populations in British Columbia, Canada

Between 1980 and 1986 some 60 submersible dives were carried out in BC fjords to study the distribution of benthic animals. Glass sponges were present in all inlets; the shallowest observation was at 18 m and deepest, in Jervis Inlet, at 590 m, but the greatest abundance occurred between 90 and 200 m depths with up to 240 individuals per 10 m^2 (Leys et al., 2004). Of three inlets – Jervis, Howe and Saanich – in which multiple dives were carried out and which could therefore be compared more equally, Howe Sound had the most dead sponges. That inlet has the most anthropogenic influence with, in the past, 2 pulp and paper mills and a copper mine, and more recently, municipal development. The submersible records note sponge graveyards at the base of the sill, but it is unknown whether mortality was related to smothering by sediment, low oxygen, chemicals, or a combination of these factors.

It should be noted that Rossellid, non-reef forming, glass sponges can trap particulate material in their outer spicule scaffold which then appears brown. This scaffold houses a whole community of invertebrates (Boyd, BSc Thesis, University of Victoria, 1981), and is sloughed during winter months (Leys and Lauzon, 1998).

3.1.3. Sponge Reefs

Sponge reefs are found on ridges and raised topography scoured by retreating glaciers and icebergs (Conway et al., 2001; Conway et al., 2005a; Conway et al., 2005b). The northern reefs in British Columbia occur at 165-240m depths on substrates formed by Quarternary geologic history, namely glacial troughs – which reach to 450 m deep – that are covered with 50m of diamicton (mud of terrestrial origin) (Conway et al., 1991; Krautter et al., 2001). Because sea levels were much lower (150m lower) during the last glaciation, there was a heavy distribution of thick sediment deposited throughout the shelf region, except on the inner shelf where the iceberg scours exposed glaciomarine sediments.

The sponge bioherms were initiated on the rock debris on the shoulder of the furrows and then gradually, by trapping sediments, became structures of their own (Krautter et al., 2006). The structure and succession is similar to that of deep water coral beds (*Lophelia*) on the Norwegian continental shelf (Freiwald et al., 1999; Conway et al., 2005a). The northern sponge reefs occur in clusters in four locations in the troughs. In the Strait of Georgia and Johnstone Strait, smaller sponge reefs are found on ridges left by glacial scour, and which have flow regimes that kept rock surfaces free of sediment allowing original attachment of sponges (Conway et al., 2007).

3.1.4. Location of glass sponges - summary

Large numbers of glass sponges benefit from the advantage of increased flow over raised topography on the seafloor, around corners on fjord walls, over sills at fjord entrances, and

down valleys created by iceberg scours. From distribution of glass sponges in fjords, increased flow appears to be able to offset the otherwise negative effects of increased particulates in the water by preventing settlement of sediment.

3.2. PHYSIOLOGY OF GLASS SPONGES

3.2.1. Glass sponge tissues and electrical conduction

In their basics, glass sponges are like other Porifera – they have pores on their surface that lead via long channels to chambers of pumping units where water is filtered over a fine collar mesh. They filter water and extract bacteria (>95% efficiency) and excrete nitrogen as ammonia and carbon as carbon dioxide and fecal pellets. Wastes travel out through larger excurrent canals to a very large opening, the osculum (Leys, 1999).

Unlike all other sponge groups, however, glass sponges are not made of individual cells: one giant cell with many nuclei – called a syncytium – forms the body (Leys, 1995; Leys, 2003). The syncytial tissue is extremely thin and cobweb-like, and forms a thin veneer on the transparent glass skeleton. Glass sponges become syncytial by fusion of individual cells in the embryo. The common reason for any tissues to be syncytial is to allow rapid signalling among all parts of the animal. Whereas cells form membrane barriers to electrical signals, syncytial tissues have no insulating barriers and electrical signals can travel rapidly across the whole body, like a giant nerve.

Glass sponges are the only type of sponge known to use electrical signals to rapidly stop their feeding current (Leys and Mackie, 1997). Electrical signals are triggered in the sponge by any sharp mechanical stimulus (e.g. a knock by a fish) or by irritation of the tissue by sediment (Lawn et al., 1981; Leys et al., 1999). Sediment or mechanical stimuli both cause an immediate arrest of the feeding current by sending electrical signals through the whole body.

Cold temperatures are needed for the electrical signal to function. In laboratory experiments on *Rhabdocalyptus* and *Aphrocallistes* pumping stopped at temperatures below 7ºC, and electrical arrests of pumping were difficult to trigger at temperatures above 12ºC. The electrical signals are calcium-based action potentials (as opposed to the sodium/potassium action potentials of other animals) and cold temperatures are needed for the calcium channels to function normally (Leys et al., 2003; Tompkins-MacDonald and Leys, 2008). In British Columbia glass sponges live in waters that remain a constant 7-9ºC year round; those in Antarctic waters may have greater tolerance of even cooler waters (0-4ºC).

We might wonder why glass sponges use this rapid system to stop the feeding current, rather than contract to expel sediment like other sponges. Probably this has to do with the fact that the canal system is so wide that slow contractions would have less force – contracting a thin canal has more effect in moving the internal fluid than contracting much wider canal. The wide canals in glass sponges are needed to allow water to move through them with as little resistance as possible. Resistance through the canal system makes filtering more difficult, and therefore more energetically costly. Energy conservation seems to be the ultimate goal of the glass sponge design.

3.3. Feeding

3.3.1. What glass sponges eat

Deep water – whether deep sea or continental shelf – is low in particulate food such as plankton and bacteria (Taylor and Haigh, 1996; Ribalet et al., 2010). Most productivity occurs at

the surface 20m. Phytoplankton at the surface is digested by zooplankton whose fecal pellets mixed with mucus and bacteria fall, with some time-lag, in strands (called marine snow) to deeper waters below. The low food availability in deep water is the reason some filter feeders have turned to carnivory; several tunicate species (e.g., *Megalodicopia,* Ogawa et al., 2005) inhale larger crustaceans and one group of sponges (Cladorhizids) has lost the filter chambers and instead has Velcro®-like spicules that trap small shrimp, and bacteria-rich cells that allow the sponge to digest the muscle tissues without digestive enzymes (Vacelet and Boury-Esnault, 1995; Lee et al., 2012).

Glass sponges eat bacteria and single celled eukaryotes (protists). This food is in water drawn into their bodies by the flagella pumps. It passes through small pores (approximately 4-8 microns in diameter) on the surface of the animal, and from there into a series of canals of diminishing diameter until it reaches the flagellated chambers, where the pumps are (Figure 3). These 'chambers' are ovoid structures with 200-300 pores 2-4 microns in diameter which let the water pass through the sponge's collar filter. As the water moves through the collar filter the surface area increases causing a drop in pressure and a reduction in velocity allowing bacteria and protists to be phagocytosed by the tissues of the chamber walls (Figure 4).

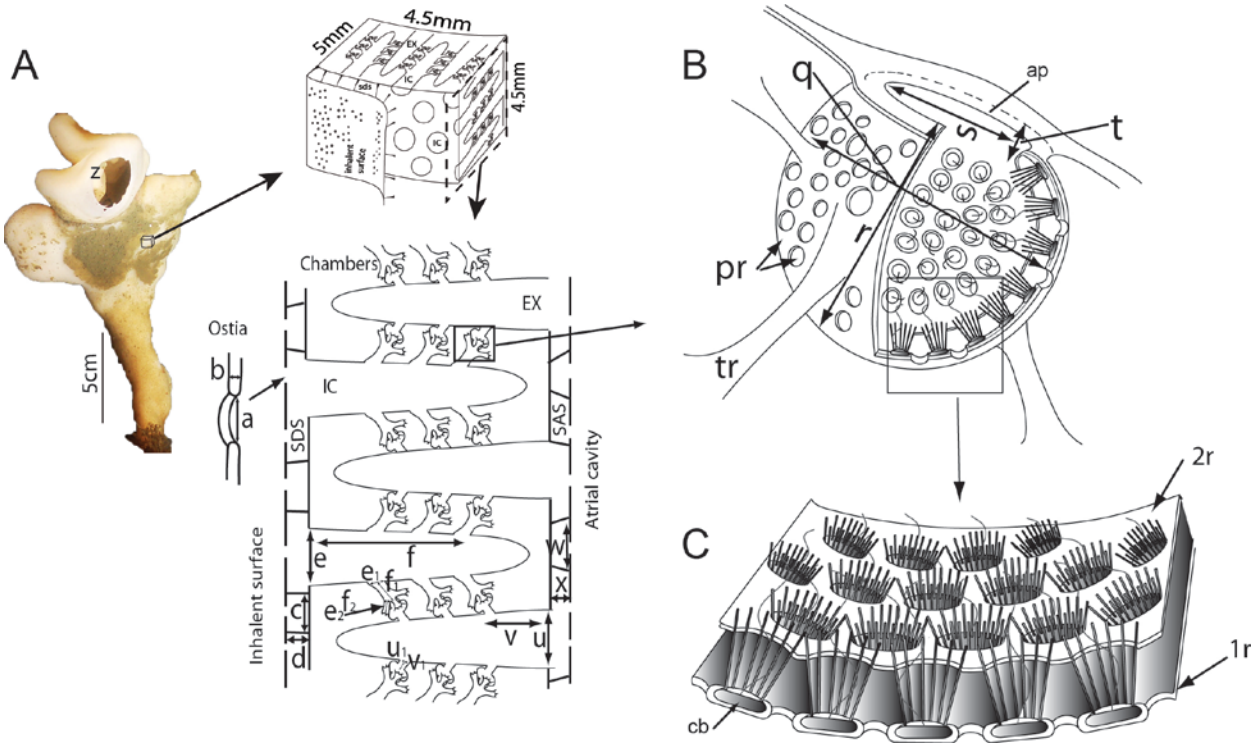

Figure 3. Structure of the filtration system in the reef glass sponge Aphrocallistes vastus (from Leys et al., 2011). A, whole sponge with a cube of the body wall, shown in cross section below; B, a flagellated (feeding) chamber; C, portion of the chamber wall showing the collar cells (cb). Letters refer to locations identified in (Leys et al., 2011).

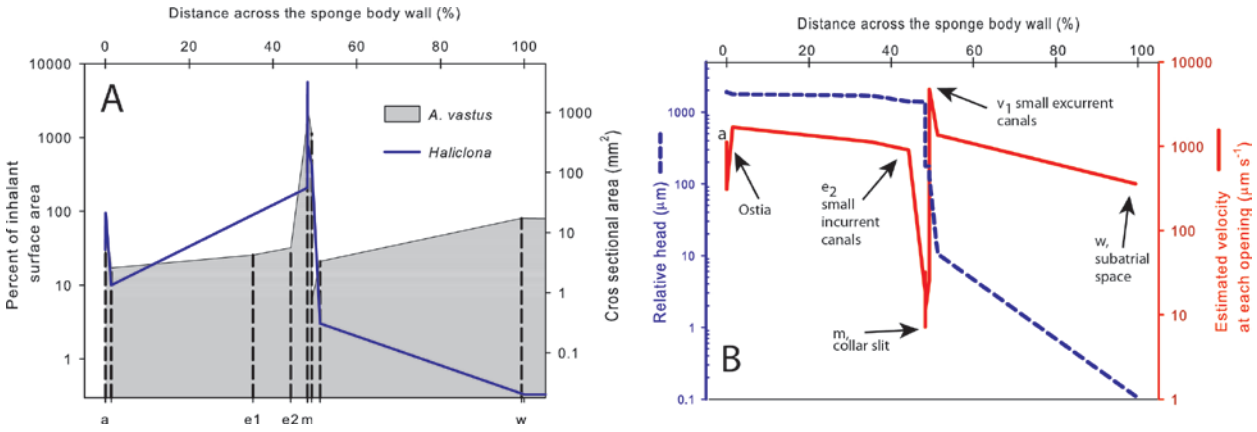

Figure 4. A, Cross sectional area across the body wall of Aphrocallistes (grey shaded) and Haliclona (blue line). B. Water velocity and relative head (pressure) across the body wall of Aphrocallistes. (From Leys et al. 2011).

Studies on NE Pacific fjord and reef sponges (*Aphrocallistes, Rhabdocalyptus*) which compared the water inhaled (taken in) with the water exhaled (excreted) show both species remove up to 99% of the smallest and most abundant bacteria, and also up to 94% of the larger more rare single celled eukaryotes (protists) (Reiswig, 1990; Yahel et al., 2006; Yahel et al., 2007). The sponges are selective filterers, taking up the more carbon-rich (nutritious) protists during the times of year they are available, and more bacteria when the protists are not so abundant. In the fjord studies, both in situ and in tanks, the diameter of the tubes used to collect water exhaled from the sponges was so small that the water was collected at a rate 1/10th of the rate the sponges' filtered, thereby preventing any contamination of the exhalent water.

Retention efficiencies of *Sericolophus hawaiicus* were much lower (47% of bacteria, and 54% of small eukaryotes) (Pile and Young, 2006). The difference in retention between these sponges and those in the fjords could be structure of the animal. Unlike *Aphrocallises* or *Rhabdocalyptus* which are roughly vase shaped, *Sericolophus* is shaped like a bowl and therefore in the latter study the mechanism of sampling inhalant and exhalent water was unlikely to be able to prevent uptake of ambient water on the exhalent side.

3.3.2. Ejection of inedible particles:

Neither *Aphrocallistes vastus* nor *Rhabdocalyptus dawsoni* retain inorganic debris. The identity of particles ingested by those species was determined by flow cytometry (Yahel et al., 2006). Single celled eukaryotes and different bacteria have characteristic fluorescent signals based on their size and content of DNA and chlorophyll. Samples are calibrated against standards. In the samples of water exhaled by the glass sponges there was an unidentified large particle (LDet) (Yahel et al., 2006) (Figure 5). These particles were collected and examined by scanning electron microscopy with Energy Dispersive X-ray (EDX) microanalysis and found to contain aluminum and silica, characteristic of clays (when less than 3.9 microns) and silt (>3.9 microns). It was concluded that the sponges could take up clays and silt but selectively excrete them into the exhalent water. This mechanism would be the only way in which unwanted material could be removed from the sponge.

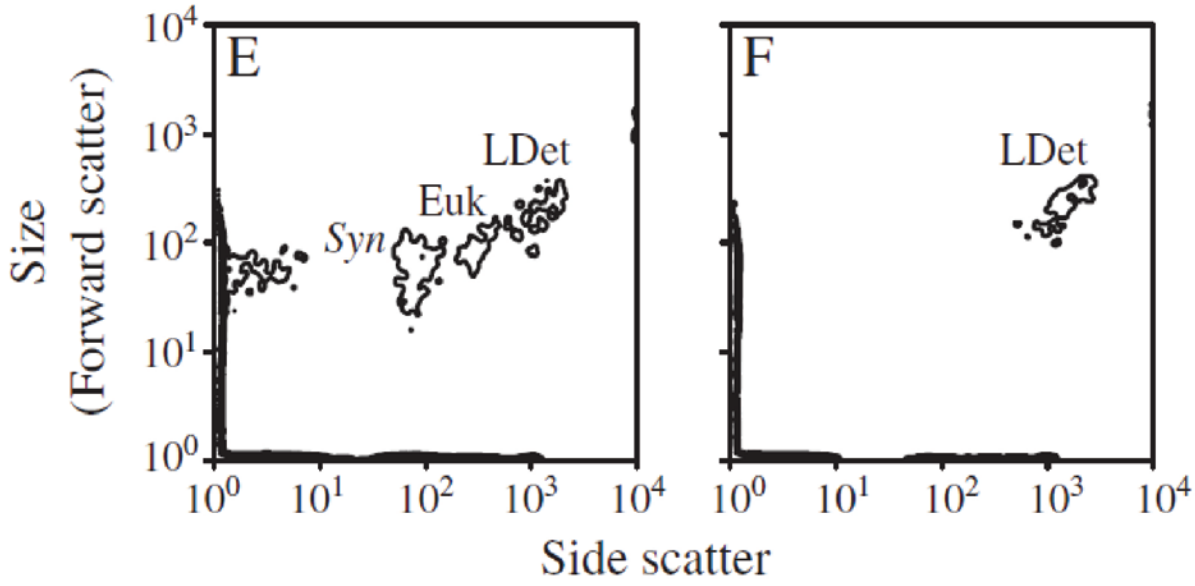

Figure 5. Flow cytometry of Inhaled water (E) and exhaled water (F) from the reef sponge Aphrocallistes vastus. Inhaled water contains populations of unicellular eukaryotes and bacteria (Syn), while exhaled water contains only large detrital (LDet) objects, considered to represent sediment (From Yahel et al., 2006).

3.4. HOW GLASS SPONGES FILTER

3.4.1. The structure of the filter

The glass sponge tissue is particularly thin, and canal spaces are very wide compared to those in demosponges. Although the first pores the water encounters in the glass sponge (the ostia) are only 4-8 microns in diameter, the large incurrent canals can be nearly 500 microns in diameter. Canals then diminish in diameter until they reach the flagellated chambers – the pumps. The glass sponge chambers are larger than in the demosponges studied so far (Reiswig, 1975) (approximately 3x the number of pump units/chamber), but there far fewer chambers ($1/6^{th}$) in the equivalent volume of sponge tissue ($1,880/mm^3$ vs $12,000/mm^3$ in demosponges) (Leys et al., 2011). Because there is more resistance to flow through small diameter passages than there is through larger diameter passages, the wide canals of glass sponges provide less resistance than is expected in demosponges. It requires energy to overcome the resistance, and therefore glass sponges seem constructed to reduce resistance and reduce the cost or energy required to filter.

3.4.2. How much water is processed by reef sponges?

A Cloud Sponge (*Aphrocallistes vastus*) with a large osculum processes water at 1-8cm/s (180-1400 L/hr) (Yahel et al., 2007). In still water (in tanks and *in situ* at slack currents) *Aphrocallistes* with a 4 cm diameter osculum can pump at 1-4 cm/s (similar rates were found for pumping of *Sericolophus hawaiicus* at 1.6-3.5 cm/s; Pile and Young, 2006). Note that where the diameter of the osculum was not measured in situ, it is not possible to give volumetric filtration rates. The higher velocities (4-8 cm/s) recorded by acoustic Doppler velocimeters over tide cycles *in situ* must be achieved either by the pumps being triggered to work faster or harder during high ambient velocities, or by passive flow. Passive flow is determined by the ability of the ambient current to draw water through the sponge by viscous entrainment or sucking of the water out of the osculum (chimney/vent). Faster moving water over the top of the sponge opening bends the plume of water moving out of the sponge and generates a low pressure region, drawing water up through the sponge to replace it.

Experiments *in situ* and in tanks have shown that at maximum ambient flow (which occurs during maximum flood tides at the Fraser Ridge Sponge Reef), the velocity out of the sponge is increased by 3-8 times its velocity at slack tide (Figure 6; Leys et al., 2011). In this way at high ambient current velocities, glass sponges are able to process more water and filter more bacteria, presumably without expending additional energy by pumping. Only concurrent oxygen recording would allow us to determine whether the sponge increases its pumping rate and consumes more oxygen or whether increased flow out of the sponge osculum comes with no increase in energy expended.

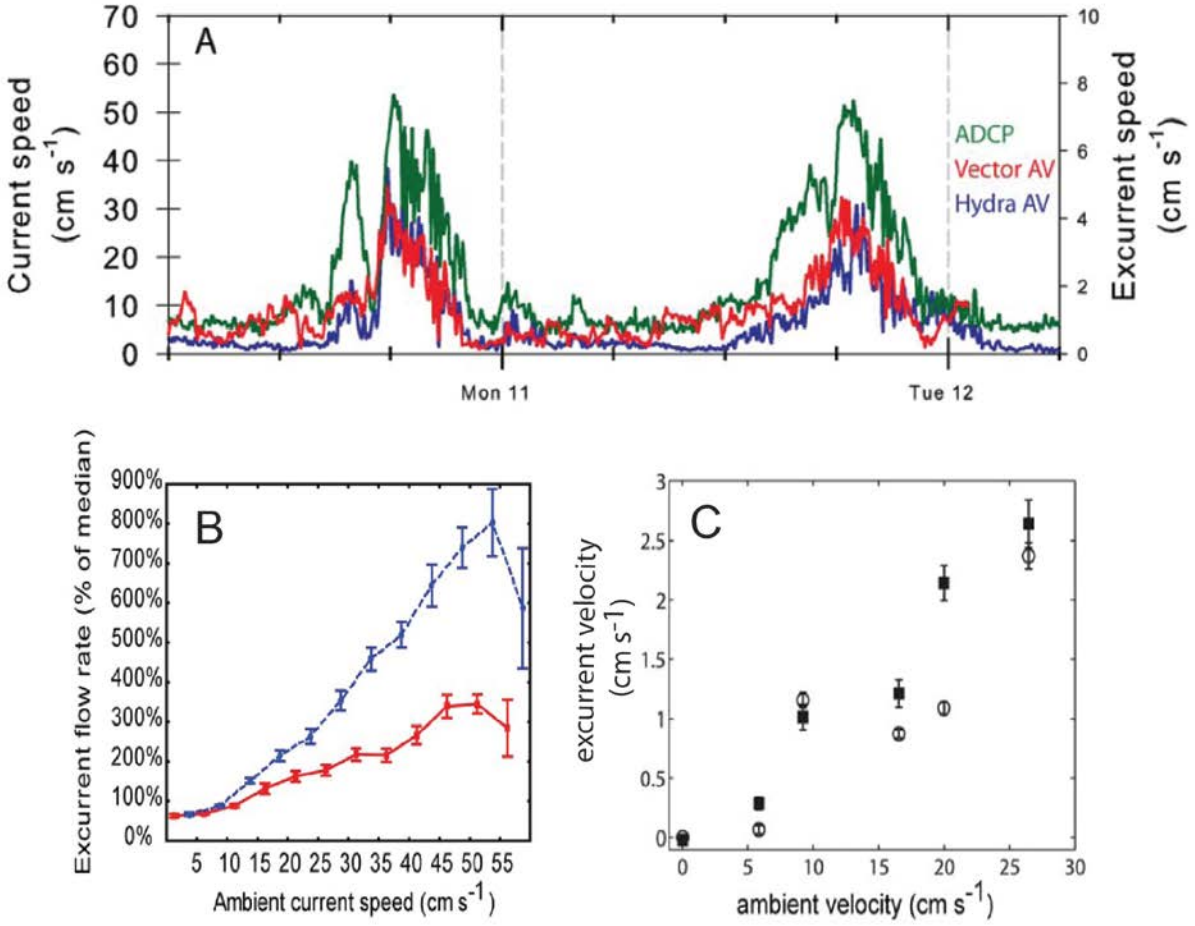

Figure 6. Correlation of sponge excurrent flow velocities with ambient flow (from Leys et al. 2011). A, Increased excurrent flow from the sponge [recorded by the Vector (red) and Hydra (blue) acoustic Doppler velocimeters] was synchronized with increases in ambient flow over the sponge reef [recorded by an Accoustic Doppler Current Profiler (ADCP, green)]. B, Both the Vector and Hydra recordings were highly correlated with the ambient current speed. C, In a flow flume the excurrent velocity from the reef sponge Aphrocallistes vastus increased with higher ambient velocities.

Estimates of filtration capacity were made for a 2 km long stretch of a single sponge reef in the Strait of Georgia (Galiano Ridge reef). This reef has 17 oscula per m^2, with an average oscula area of 25 cm^2. At an excurrent velocity of 1 cm/s, the whole reef pumps 83,000 liters of water each second. Other reefs in the Strait of Georgia are less dense, but the oscula of sponges are larger, and therefore the volume processed is roughly equivalent if excurrent velocities are estimated to be 1 cm/s. The 13 reefs in the SOG together have some 100 million oscula and process 6 billion liters of water per hour, or about 1.7 million liters per second, which is 17 percent of the volume of the Fraser freshet at maximum flow (10 million liters per second or 10,000 m^3/s) (Kahn et al., 2013).

3.4.3. Energetics of filtration

It is calculated that during the brief period of maximum ambient flow (approximately only 20% of the time in NE Pacific coastal waters with a strong diurnal tidal exchange), the sponge is able to process 66% (two thirds) of the water it filters daily (Leys et al., 2011). Taking into account the

normal cost of pumping over that period of time, this suggests that 50-60% of the food captured by the sponge is done at reduced or no energetic expense.

3.4.4. Feeding and cost of filtration - Summary

Glass sponges are tube, vase and plate-shaped, and in deeper water many morphologies occur on stalks raising the body up into the water column; each of these shapes allows higher velocity water over the sponge surface (osculum) presumably generating passive flow through the collar filter (Vogel, 1974). In British Columbia fjords and shelf regions, glass sponges are most common at points of rock wall, and on raised topography on the seafloor. These areas have accelerated water, and enhance the flow over the sponge at flood and ebb tides. The glass sponge filter appears to take advantage of induced current so as to reduce the cost of pumping. This morphology and physiology is expected to be an adaptation to food-poor habitats. The corollary is that if pumping becomes costly, or if passive flow is reduced, for example due to increased resistance through the sponge body due to clogging, the sponge would not meet its energetic requirements.

4. SEDIMENT AND GLASS SPONGES

4.1. SEDIMENT AT GLASS SPONGE HABITATS

Glass sponge habitats range from clear to turbid (turbidity is a measure of suspended solids in the water). Antarctic water and deep sea habitats are nutrient poor and 'clear' but experience periodic fallout from phytoplankton blooms. Disturbance by fish or currents, or by slumps (e.g. Porcupine Sea Bight – *Pheronema*) can resuspend sediment and generate temporarily turbid water (Lampitt, 1985).

In comparison, continental shelf and fjord habitats in British Columbia are clear in winter months and turbid during summer months due to fall out from the highly productive surface waters. Two peak periods of plankton/sediment fallout occur, one in mid-summer (July-August) and the other in mid-fall (Sept-October) (Sancetta and Calvert, 1988; Sancetta, 1989b; Sancetta, 1989a). Material falling to the lower depths includes marine snow (largely organic matter consisting of fecal pellets of zooplankton which have some organic nutrients, broken pieces of silica from crushed diatoms, and bacteria) as well as clays and silts of terrestrial origin (runoff from rivers and activities on land).

4.1.1. Sediment at Northern Sponge reef habitats

Along Moreseby Trough (Hecate Strait) transmissivity (the ability of light to penetrate water) in summer months was 38-55% at 5-10m above the bottom (Whitney et al., 2005). Directly above the sponge reefs transmissivity was at the higher end of that range (50-53%), and south (downstream) of the reefs it was 55%; the higher transmissivity – associated with fewer particles in the water – was credited to filtration of particles by the sponges (Figure 7). Sedimentation rates, calculated from the cores at the Queen Charlotte Sound reefs, were 0.3 mm- 0.9 mm/yr. Sediment traps at the reefs captured a quarter to a third of the sediment (by dry weight) compared to a site 3km away, which agrees with the transmissivity data. At the northern sponge reefs, sediment grain size analyzed from cores consisted of 44-58% clays (<63 microns) and 20% sand (Whitney et al., 2005).

4.1.2. Sediment in BC fjord and Strait of Georgia reef habitats

In the fjord sponge habitat (Barkley Sound, B.C.) transmissivity in summer months was even lower than in Hecate Strait, at <35%, with high suspended solids 7.11 mg/L ± 0.94 mg/L (Yahel

et al 2007). Transmissivity measured in the Strait of Georgia above the Fraser Ridge sponge reef was also low (often below 30%) but despite the location of the reef close to the Fraser River freshet, the concentrations of total suspended solids was a maximum of 8.25 mg/L.

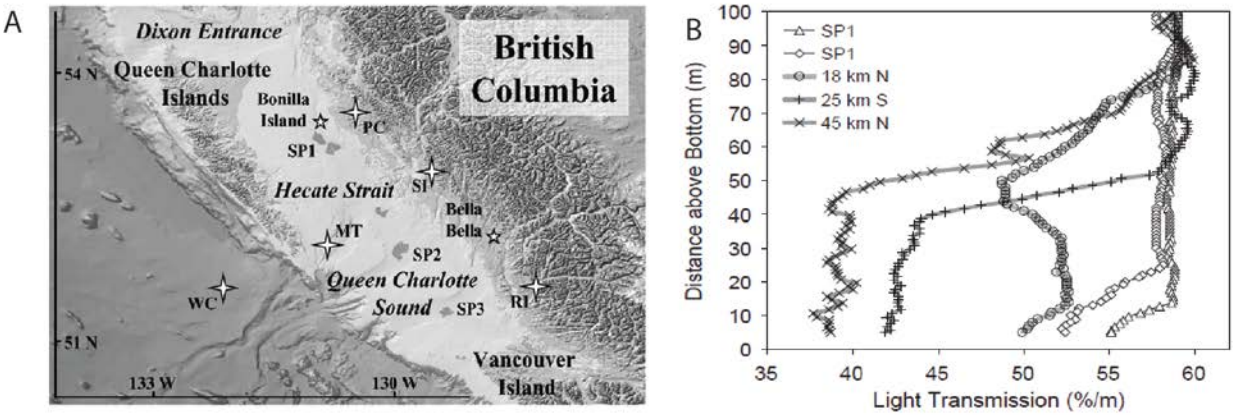

Figure 7. A, Location of glass sponge reefs (SP1, SP2, SP3) in Hecate Strait and Queen Charlotte Sound. B, Transmissivity of the water above the reefs (two right traces) and at three locations to the north and south of the reefs (from Whitney et al., 2005). Light transmission is higher directly above the reefs, possibly due to filtration of particulates by the sponges.

The Fraser River freshet (which has a maximum spring flow of 10,000 m^3s^{-1}) has load of 17.3 million tonnes per year, 35% of which is sand, and 65% clay and silt (Thomson, 1981; Whitney et al., 2005). Sediment traps placed at Galiano and Fraser Ridge Sponge reefs collected 50g and100g (respectively) of sediment per year over 2 years (Leys and colleagues unpublished data). Total accumulation is difficult to assess because of erosion. Tall poles marked with increments placed near the traps showed accumulation of a few centimeters in some places and erosion of up to 10 cm in other locations (Leys et al., unpublished data).

Organic carbon in sediment at the Northern reefs was 3%, which makes the sediment anoxic (Whitney, et al., 2005). Sediment cores from the Fraser Ridge are anoxic after the first 5 mm (Juniper, unpublished data).

4.2. THE EFFECT OF SEDIMENT ON REEF SPONGE PUMPING

Because of the expense and difficulty of accessing glass sponges in their deep habitat, *in situ* experiments on the direct effects of sediment on glass sponge pumping rates and condition are not possible to carry out. Experiments of the effects of sediment have been done on animals kept in tanks at the Bamfield Marine Sciences Centre where unfiltered water is brought directly from 30m depths. The BMSC seawater system is the only place in the world where glass sponges can be kept in healthy condition and experiments on their physiology since 1982 have shown they survive well if kept in a large exchange of seawater, in the dark, and at temperatures below 12ºC (Mackie, 1979; Lawn et al., 1981; Leys et al., 1999; Leys et al., 2007).

4.2.1. Sediment resuspension on reef sponges

The following summary comes from work carried out by G. Tompkins-MacDonald at the Bamfield Marine Sciences Centre in 2004 (Tompkins-MacDonald and Leys, 2008). Sediment used in treatments was collected either from around the glass sponges in fjords, or was obtained from a core of the northern sponge reefs via K. Conway (PGS, Sidney, B.C.).

A single dose of 1 mL of sediment (10 g/L) applied directly onto a sponge in a 2.5 L aquarium caused immediate arrests of the feeding current (Figure 8). Though the final concentration in the aquarium was low (0.4 mg/L) the amount experienced by the surface of the sponge was estimated to reflect an amount of a disturbance caused by resuspension of bottom sediments by fish or other animals. The sponges seemed to be less likely to respond to several small resuspension events but after repeated applications of 5-500 mL of 10 g/L over 60 minutes (such that the concentration in the aquarium had reached over 100mg/L), the sponges arrested repeatedly – stopping and starting pumping, with 3-4 minute arrests and similarly long bouts of pumping. Sponges did not recover normal pumping patterns for 4-5 hours.

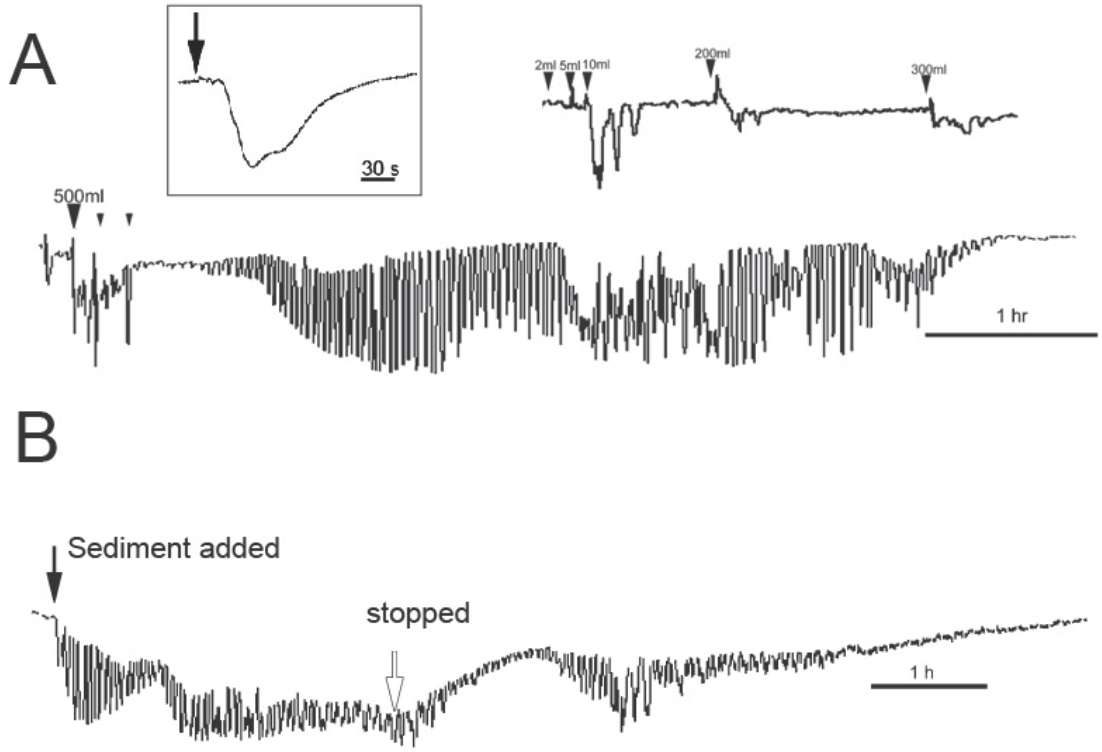

Figure 8. Effect of sediment on the reef sponge Aphrocallistes vastus (from Tompkins-MacDonald and Leys, 2008). A, Sediment applied as though resuspended from the bottom, in a single dose of 100g per liter, caused an immediate arrest of the feeding current followed by a train of arrests lasting several hours. Inset shows a single arrest. B, Sediment applied slowly but continuously for 3 hours caused a reduction in pumping by 50-80%.

4.2.2. Continuous application of sediment to reef sponges

Sediment was added to tanks containing sponges using a continuous supply via a peristaltic pump. The reef sponge *Aphrocallistes vastus* began to arrest pumping when sediment concentrations reached 36 mg/L. Arrests followed the same sequence above (with repeated on/off attempts to pump) but after 17 minutes the pumping rate was nearly zero. If addition of sediment stopped at that time, the sponges recovered full pumping rates quite quickly, but if sediment continued to be added to the water the excurrent velocity from the reef sponges pumped remained less than 50% of normal rates. Excurrent velocities remained low until sediment was no longer added to the water. The 3 reef sponges tested recovered normal pumping rates only 6 hours after sediment was no longer added to water.

4.2.3. Clogging of the sponge filter by sediment

Reef sediment consisted of smaller particles than fjord sediment. More than 75% of the particles in reef sediment were smaller than 3 microns in size; in contrast less than 50% of particles in fjord sediment were smaller than 3 microns. Reef sponge tissues studied by Scanning Electron Microscopy after treatment by sediment showed that whereas sponges treated for less than 40 minutes had very few particles of clay in their chambers and canals, in sponges treated for more than 40 minutes with fjord sediment many chambers were completely filled with clays and silt.

4.3. EFFECT OF SEDIMENT ON PUMPING AND ENERGETICS

4.3.1. Expected residence time of suspended particles near reefs

Residence time refers to the amount of time water spends traversing a region; its relevance here is to the amount of time water carrying suspended sediment loads will be in contact with the sponge reefs. On the Pacific continental shelf of Canada, current velocities near the sponge reefs of approximately 5 cm/s or 4 km/day would generate a residence time of approximately 6 days over the reefs (Whitney et al. 2005). During this period any body of water traversing the shelf, including suspended sediment and low oxygen water, will cover the sponges. Whitney and colleagues (2005) estimated that with any cessation of flow all oxygen would be used up in less than two months. The residence time can be used to estimate the time sponges would be exposed to fine sediments suspended in the water column as in 4.3.2 (c) below.

4.3.2. Estimated effects on sponge reefs exposed to trawl sediments

a) Smothering: Smothering and reduced recruitment. The energetic costs of mucus production by sponges are unknown, yet this is a common physiological response to stress (Weber et al., 2006). Recruitment is reduced when sponges and substrates are covered by sediment. Studies with demosponges show less recruitment on sediment covered panels (see section 2.2.2); no difference would be expected for hexactinellid (glass) sponges.

b) Clogging: Clogging of the sponge filtration apparatus occurs after 40 minutes exposure to sediment and may be caused by sediment concentrations equivalent to those resuspended by trawl activities. Recovery from sediment, should trawling be only a 3 hour activity, would take 6-12 hours. With up to 6 days residence time over reefs, sponges throughout the reefs would experience reduced pumping for up to 6 days after trawl activity.

c) Reduced feeding: Considerable knowledge of volumes of water processed and food extracted by reef-forming glass sponges is now available from in situ studies, and concrete numbers of the reduction of filtration caused by sediment are known from tank-based studies. Together these provide an important basis for estimating the effects of reduced filtration that would be generated by clogging of the filter.

First, the reef sponge *Aphrocallistes vastus* is known to require passive flow to enhance feeding (Leys et al., 2011), and it is also seen that the greater part (up to 2/3) of the daily volume of water processed and therefore of the sponges' food intake occurs during maximum flood tides (when ambient flow is over 15 cm/s). It has also been shown that glass sponges (like other sponges) are sensitive to suspended sediment concentrations of 11 mg/L and greater, and that filtration rates are reduced by a minimum of 50% while those concentrations persist. Therefore if water disturbed by trawls contained suspended sediment concentrations greater than 11 mg/L and remained over the sponges during periods of maximum current flow, it would reduce filtration to 50% of maximum filtration rates (according to Tompkins-MacDonald and Leys,

2006). Using the upper value of 2/3 of feeding occurring during those periods, this would therefore cause the sponges to lose approximately 30% of their daily food.

At the two northern sponge reefs near bottom currents have been measured in Morseby Trough. Currents at 4.6m above the bottom reach 35 cm/s during maximum flood (northward along the canyon), but are more typically 10-25 cm/s (Whitney et al., 2005). Flood currents are stronger than ebb flows, but both are in the range that would enhance sponge feeding (above 15 cm/s). Suspended particulates in the water during the two peak exchanges (flood and ebb) would result in compromised feeding ability of the sponges as indicated above. For sponges that have other sources of energy (for example, algal or bacterial symbionts), this would not necessarily interfere with metabolism. For reef building glass sponges, loss of 30% of the energy supplies during summer periods of peak feeding is expected to be detrimental to their well-being and risk irreversible harm.

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APPENDIX 1 : TERMINOLOGY

Sponge = phylum Porifera ('pore-bearer').

Four classes (types):

Demospongiae (*demosponges*, most sponges, deep and shallow water);

Homoscleromorpha (with/without siliceous spicules – few species, prev. with demosponges);

Calcarea (sponges with a calcium carbonate skeleton – few, mostly shallow water species);

Hexactinellida or '*Glass Sponges*' (sponges with a siliceous skeleton – SiO_2 – that are restricted to deep water world-wide).

Ostia = pores on the surface of the sponge (about 5-20 µm diameter) for inhalant water.

Choanocytes = 'collar' cells with a flagellum which whips back and forth creating suction to draw water into the sponge. (*Choano* = collar and *cyte* = cell)

Osculum = vent (usually one), large (1-50cm in diameter) for exhalent water. (means 'Mouth' L.)

Deep water = usually means greater than 30m; whereas deep sea >500m

Shallow water = can refer to diving depths to continental shelf 0-30m

Syncytium = single giant cell with many nuclei.

Clearance studies = sponges are put in a closed tank with seawater that has particles in it and the number of particles present in the water (i.e. not filtered out by the sponge) are counted at different time points.

Respiration studies = sponges are put in a closed tank and the oxygen levels at the beginning and end of the experiment are compared.