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Formation, Persistence, and Recovery of Glass Sponge Reefs: A Case Study

Jeffrey B. Marliave, Laura A. Borden, Jessica A. Schultz, Donna M. Gibbs and Glen J. Dennison

Abstract

Glass sponge reefs (bioherms) are known to occur on glacial deposits but have not previously been observed to develop on fjord bedrock ridges. It is assumed that sexual reproduction dominates reef recruitment and that sedimentation can cover intact sponge skeletons. Over a decade of scuba diving research at a small fjordic bioherm, including installation of bar-coded marker stakes, transplants of loose fragments and survey transects of substrate depth with an avalanche probe have led to new insights into the dynamics of bioherm formation and persistence. We present evidence for recovery of sponge growth from scree slopes of collapsed fragments and logged the temporal changes associated with sponge fragmentation and recovery. Bar-coded stakes were installed in 2014 to enable verification of location and sponge identity through time. Photo documentation of growth, collapse, and regrowth is presented. Research on a sponge garden on glacial sediments reveals that earliest sedimentation may center around prostrate boot sponges and bristly tunicates among the cloud and vase sponges. Although hexactinellid boot sponges do not contribute to the geologic base of bioherms, they may take part as a successional community in the substrate conditioning that could result in the genesis of a glass sponge reef or bioherm.

Keywords: bioherm, cloud sponge, reattachment, regeneration, tissue recovery, asexual reproduction, geologic reef substrate, transplants, ecological succession, temperature cycles

1. Introduction

Glass sponge reefs (bioherms) existed across present-day Europe during the Jurassic 201–145 million years ago [1], but today, only coastal British Columbia and its northern coastal boundary with Alaska have such reefs. The same glass sponges grow on rocks as sponge gardens over a broader geographic range [2]. The differences in growth and longevity of such sponges in the two types of habitat settings merit consideration. Specifically, the long-term persistence of bioherms may relate to the geomorphological base of such reefs and the growth dynamics that relate to that substrate, in contrast to the sponge garden rock substrate. The geological stabilization of glass sponge skeletons by clay sedimentation creates a nonliving

base that provides stability to the living reef, stabilizes dead sponge skeletons, and enables living sponges to attach to this substrate.

Bioherms are considered “bedrock averse” in terms of underlying geologic substrate [3]; glacial sediments are the normal underlying substrate for bioherm formation. Depth data for the shallowest extent of an inshore bioherm are interpreted as indicating a bedrock substrate for at least a peripheral part of the reef we have studied. Observations at a sponge garden suggest a possible successional community including sediment-accumulating species that could develop the substrate of sedimented dictyonine sponge fragments that constitutes the geomorphologic base of a bioherm.

The present study spanned climate events that may relate to trends in sponge mortality. The El Niño of 2015/2016 started in November of 2014 and lasted until May of 2016 with anomalies as high as 2.6 (<http://tinyurl.com/NOAAONI>). Two modest La Niña climate events occurred from August to December 2016 (maximum anomaly of -0.7) and from October 2017 to March 2018 (maximum anomaly of -1.0).

The literature indicates that dead sponge skeletons on a bioherm become embedded intact by sediment and that new sponge growth is based on planktonic settlement of sexually produced sponge propagules that settle on dead sponge skeletons [1, 4]. Not all growth is based on newly settled sponges, since recovery of damaged sponge tissue also occurs [5]. As well, fallen fragments of cloud sponge (*Aphrocallistes vastus*) have capacity to reattach and resume growth [6]. The consequences of collapse and potential for recovery, reattachment, and continued growth have not been compared for glass sponge gardens versus glass sponge reefs. This book chapter presents a theory of scree slope drift formation at sponge reefs as a means of relatively rapid growth for bioherms and further posits that such recovery does not ordinarily occur at sponge gardens.

2. Methods

Over 100 scuba dives were conducted from 2007 to 2018 at the inshore Defence Island bioherm (**Figure 1**) in Howe Sound, British Columbia ($49^{\circ}34.66$ N, $123^{\circ}16.41$ W). Difficulty in relating video frames to individually identifiable sponges led to installation of 12 bar-coded locator stakes [5] in 2014 that also had a mark to indicate the depth of the reef substrate at the time of installation. Growth and death of sponges near these marker stakes were monitored with video recordings. All photographs and videos used for analysis in this chapter include one of these locator stakes or some other landmarks such as a temperature logger, a sonde oceanographic buoy, or a pair of pipes called the “pipe vee” which had been installed in 2009 for camera positioning.

Divers with the Underwater Council of British Columbia inserted temperature loggers in the seabed of various sponge reefs in Howe Sound from 2014 through 2018, including the present site. Loggers were replaced at intervals so that most sites had nearly continuous records. The observations spanned El Niño (2015/2016) and La Niña (2016/2017, 2017/2018) climate events. Beginning in May 2014, Thermochron[®] iButton temperature loggers (version DS1921Z-F5; accuracy = $\pm 1.0^{\circ}\text{C}$) were deployed at six sponge reefs in Howe Sound, data from four of which are presented here. Loggers were placed in among the sponges using PVC pipe holders and left there for up to 1 year, logging at intervals of either 2, 3, or 4 hours. Loggers were collected and data downloaded as often as possible, though weather and boating restricted the collection of some loggers such that gaps in data occurred. Two of the six reefs had significant gaps in data so are not presented here.

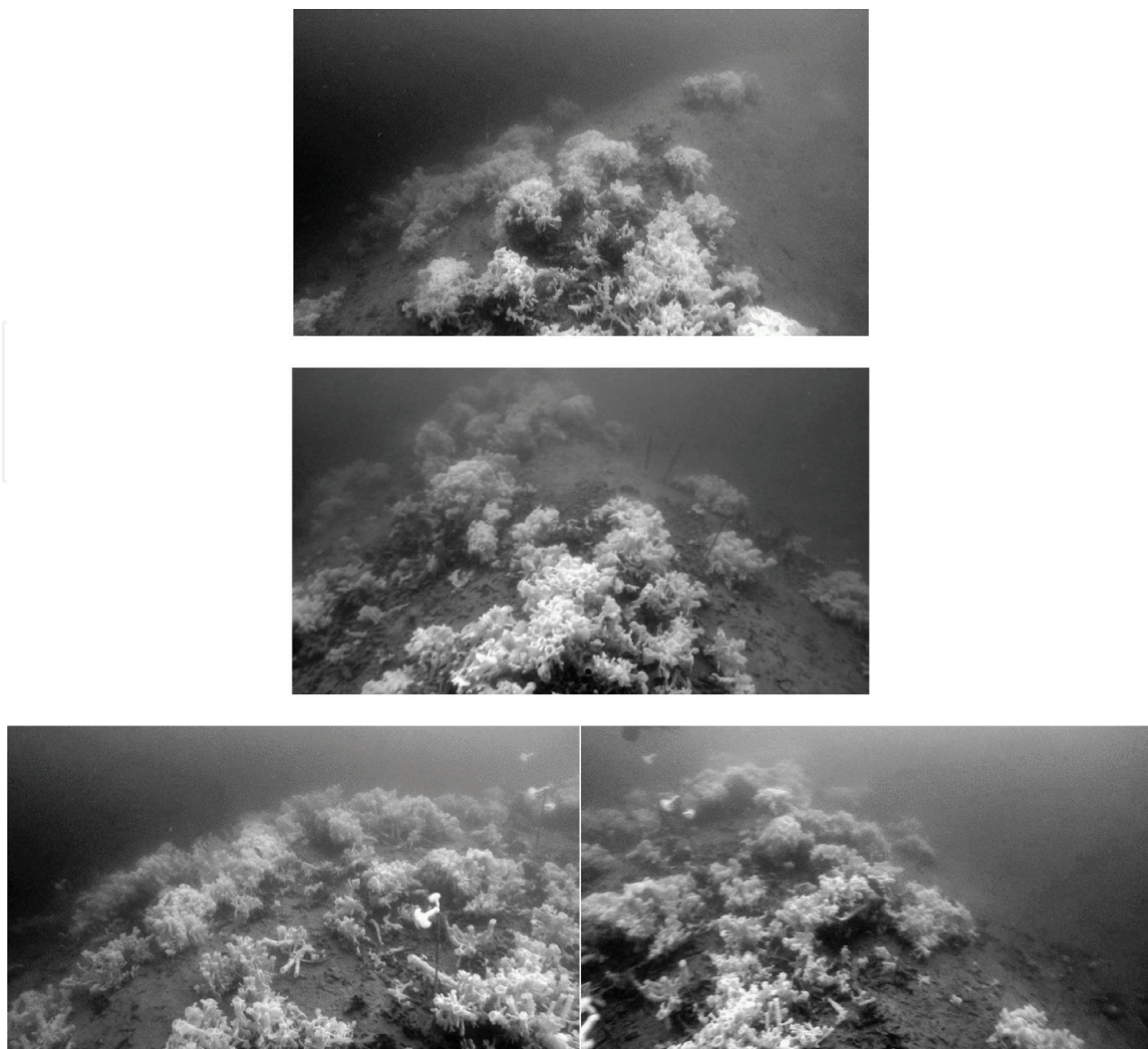


Figure 1.
Defence Island bioherm, GoPro Black (enhanced), April 27, 2018, full sun with ≤ 30 m visibility at all depths. The lower two video frames show the southwestern side of reef, shot from the southwest (N slope left, S slope right). Middle frame is of mid-reef, shot from southwest on the mid-line ridge of the reef. Top photo is of the northeast end of the ridge.

Data collected from 2014 to 2018 were summarized as an average temperature per date and presented graphically.

Unplanned events led to research opportunities. The pipe vee had been installed in July 2009, prior to the 2009/2010 El Niño which coincided with collapse of many sponges through 2010–2012, including formation of a drift of sponge debris that came to rest just below that pipe vee. Recovery and regrowth of that pipe vee sponge drift has since then been monitored with video recordings. Specific video frames are presented to demonstrate shape and relative size at a given date.

In October of 2016, various sponges were found cut off and lying loose after apparent contact with a sport downrigger fishing line that hit the reef. Four complete sponge bushes were fixed to the reef with PVC pipes (uppermost in **Figure 1**), and a sliced section of a sponge head was placed precisely against its intact host sponge, and the healing and reattachment were monitored with video. The transplanted sponges now provide new fixed location identifiers.

Surrounding the transplanted sponges at the shallowest ridge at the east side of the reef (**Figure 1**; top), a grid of half-meter spaced measures with an avalanche probe was conducted to measure depth of bioherm over solid rock. Previous transect measures with that probe had established that the shallowest ridge top where the transplants were installed had the least depth of reef substrate, suitable

for measure with the probe. We used a 3-m avalanche probe to determine the depth of bioherm sediment accumulation on top of the rocky reef. We measured sediment depth within a 300 × 300 cm grid centered on the ridge of transplanted sponges. To ensure the measurements were 50 cm away from one another, we used a 50 × 50 cm quadrat to mark each position before inserting the probe. At each position, we inserted the probe until it hit hard substrate, recorded the bioherm depth to the nearest 5 cm, and recorded the water depth to the nearest 0.1 m. Measurements were taken on August 24, 2018, and September 14, 2018. To correct for variation in tidal height between the 2 days, we measured the water depth at one of the sampling positions twice (i.e., on both days). Because the water was 2.2 m higher on September 14, we subtracted 2.2 m from all water depth measurements taken that day. We then further corrected all measurements to zero tide by subtracting 1.1 m, which was the height of the nearest slack tide on August 24. At 5 of 42 measuring positions within our grid, we could not measure sediment or water depth without risking damage to the sponges. In those instances, we interpolated the measurements by taking the average of the nearest two measurements on either side. Data were plotted using surface plots in Microsoft Excel. The bioherm thickness and the depth of the hard substrate were plotted separately.

A sponge garden on glacial till at west Bowen Island (49°23.26 N, 123°24.76 W) was videotaped in July 2013 and August 2018, capturing images of sedimentation around glass sponges and their dead fragments, along with other marine organisms that accumulated sediment. These videos were reviewed, and all identifiable animal species in the vicinity of glass sponges were recorded. A cluster of cloud sponges (called Baker's Dozen) at this site was videotaped in 2012 and 2015 to document relative growth of various sponge bushes.

3. Results

Temperature logger data for the present study site (inshore Defence Island) and three other sites are detailed in **Figure 2**. All four sites had temperature spikes in late summer of 2015 exceeding 10.0°C, but only the inshore Defence Island site exceeded 9.0°C through spring and summer of 2015 as well, before the intensification of the 2015/2016 El Niño. Note that Passage Island is the only other bioherm site as shallow as the present study site; the location of the Passage site (49°20.27 N, 123°18.89 W) is at the south entry to Howe Sound, whereas the present Defence site is at the inner sill to the north.

At the Defence bioherm, the pipe vee scree drift formed in 2010–2012 and its subsequent recovery, growth, and loss of successive bushes was documented through 2018 (**Figure 3**). The first frame in **Figure 3** (viewed from east end) shows primarily dead sponge tissue in the center of the drift, with small tubes and mittens emerging from the dead tissue. The second frame in **Figure 3** shows the pipe vee and the drift from the east; the third is an overhead shot that includes two transplanted tubes of sponge at the downhill east and west sides (both transplants perished within 2 years). The last frame shows the central portion of the drift continuing to grow, whereas the western cluster of sponge in the foreground had fallen over in the downhill direction. That fallen cluster had grown as vertical tubes without any sideways mittens contacting the surrounding substrate. The eastern head of sponge had been hit by fishing gear in fall of 2016 and had subsequently collapsed and perished.

At the distant Passage Island bioherm site, possible debris drift formation is evident on the east slope of the reef (**Figure 4**). The lower edges of those apparent drifts in **Figure 4** have well-developed sponges, but above the middle drift in the

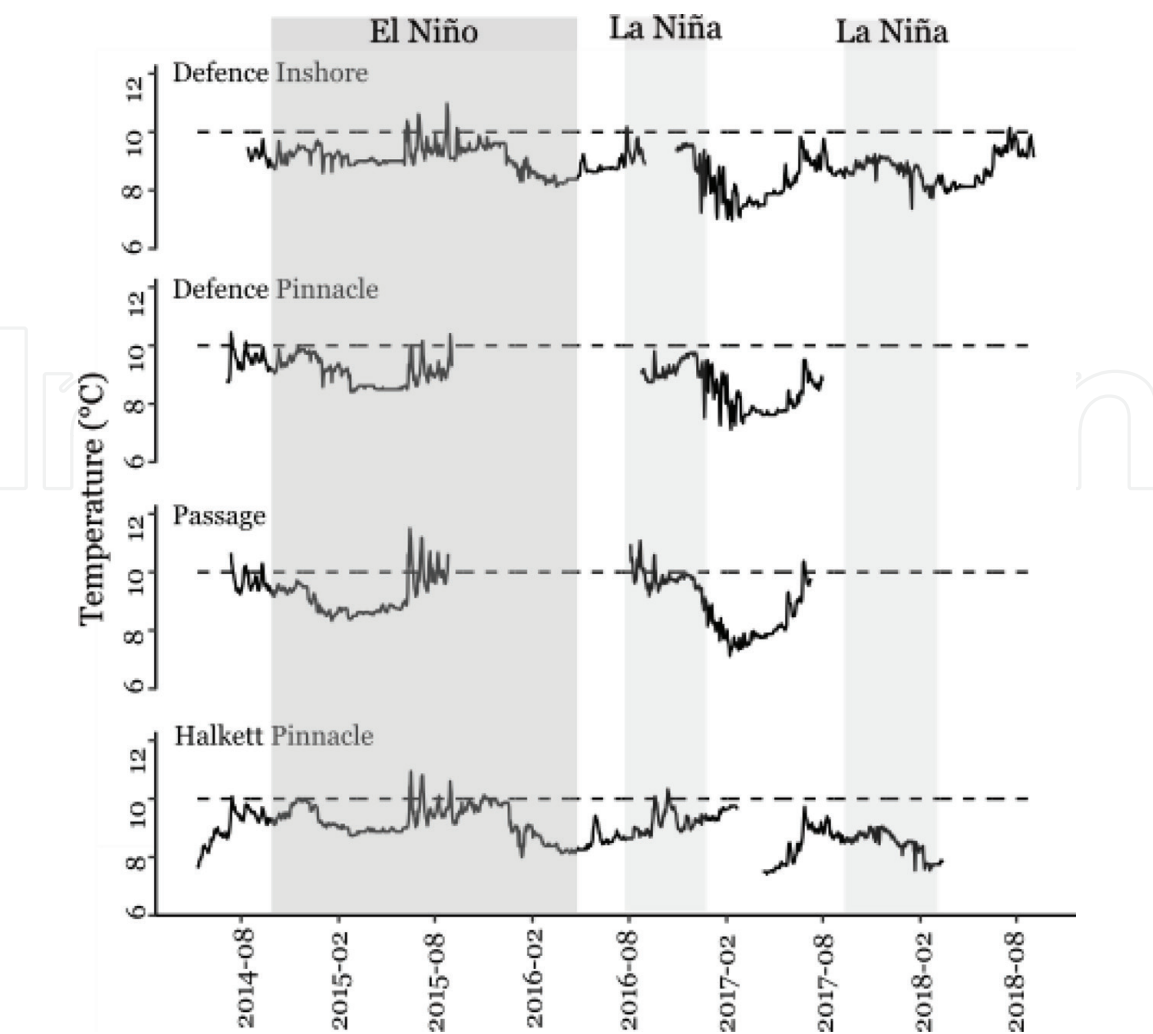


Figure 2.
Temperature at the inshore Defence Island bioherm and three similarly shallow bioherms in Howe Sound, British Columbia, May 2014–September 2018.

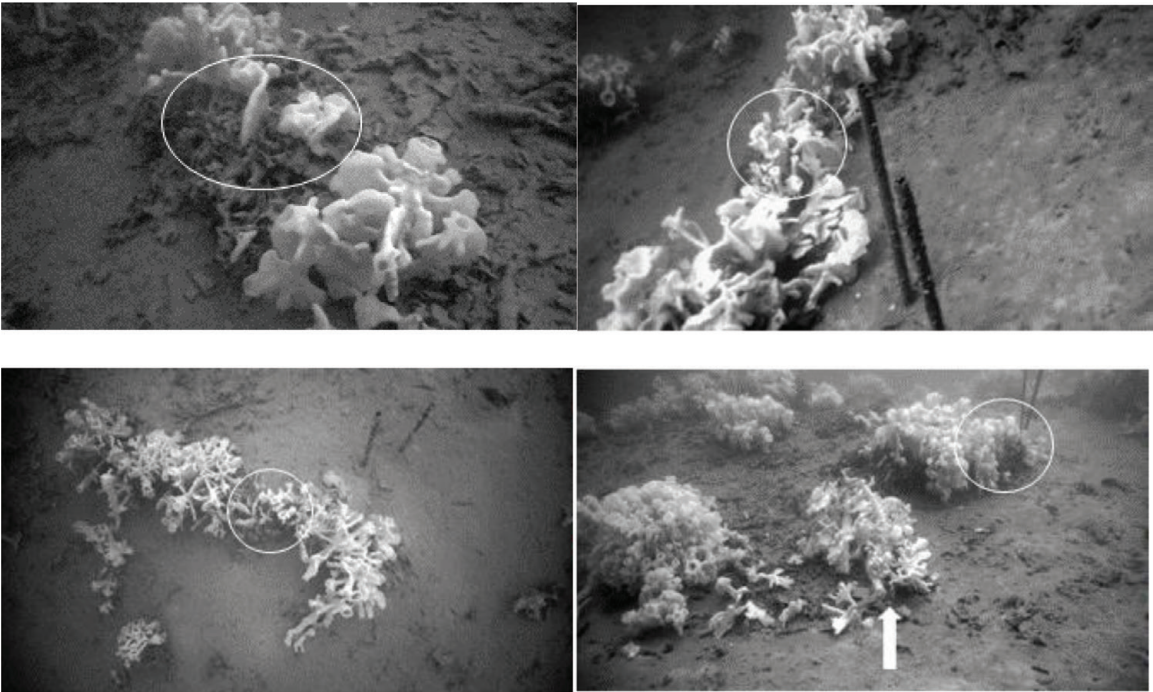


Figure 3.
Pipe vee sponge debris scree drift. Growth and subsequent tissue loss: top left—July 10, 2013; top right—May 1, 2014; bottom left—October 26, 2015; and bottom right—April 27, 2018. Circles identify same sponge. Note foreground center of lowest photo (arrow) shows fallen sponge from debris drift (W end).



Figure 4.
Passage Island bioherm with possible debris drifts at lower elevations on the east slope. Note debris fragments with recent growth (circled) above central sponge row at lower center.

center of the frame, there are disorganized, collapsed sponge fragments and small outgrowths of sponge that may represent tissue recovery rather than rapid growth of newly settled sponges.

The fishing gear damage to the Defence bioherm in fall of 2016 led to opportunistic transplanting of four sponge bushes at the shallowest ridge top (**Figure 5**). A loose fragment of sponge sliced from an otherwise intact host sponge bush was replaced against the host tissue and secured with stakes (**Figure 6**). By 2018 the transplants were growing and had attached to the stakes and to the underlying bioherm substrate (**Figure 5**). The staked slice of tissue was completely healed, and no sign of the slice location was evident. In September 2018, the westernmost transplant was about half dead, possibly indicating the onset of a 2018/2019 El Niño that is not confirmed on the Ocean Niño Index at the time of writing (**Figure 7**). Another

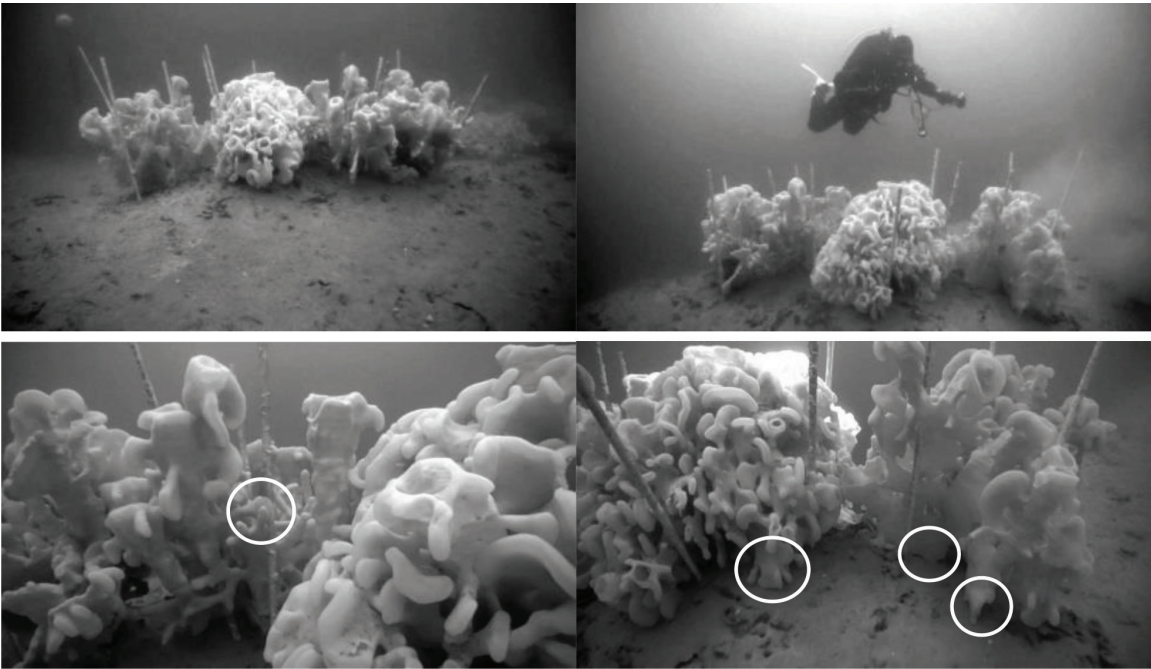


Figure 5.
Ridge top transplants (conducted October 2016), February 13, 2018. Top left photo viewed from north; top right photo viewed from south. Note attachments (circled) of sponge mittens to substrate (bottom right photo) and to stake (bottom left photo).

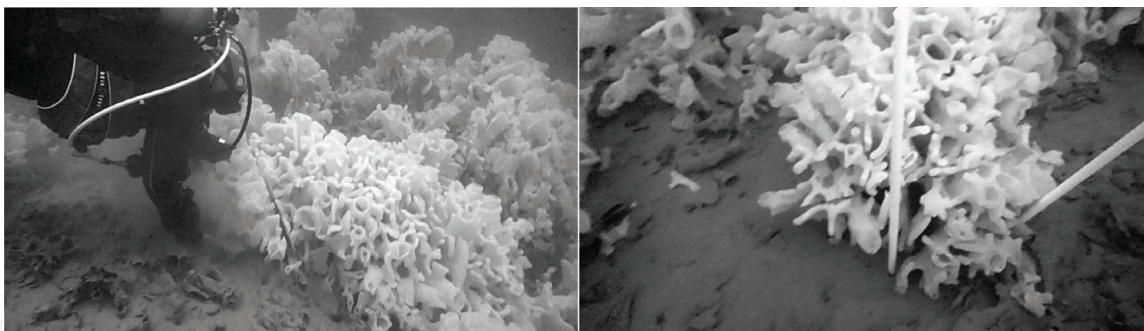


Figure 6.
 Loose slice of sponge replaced against host tissue and secured with pipe stakes in October 2016.

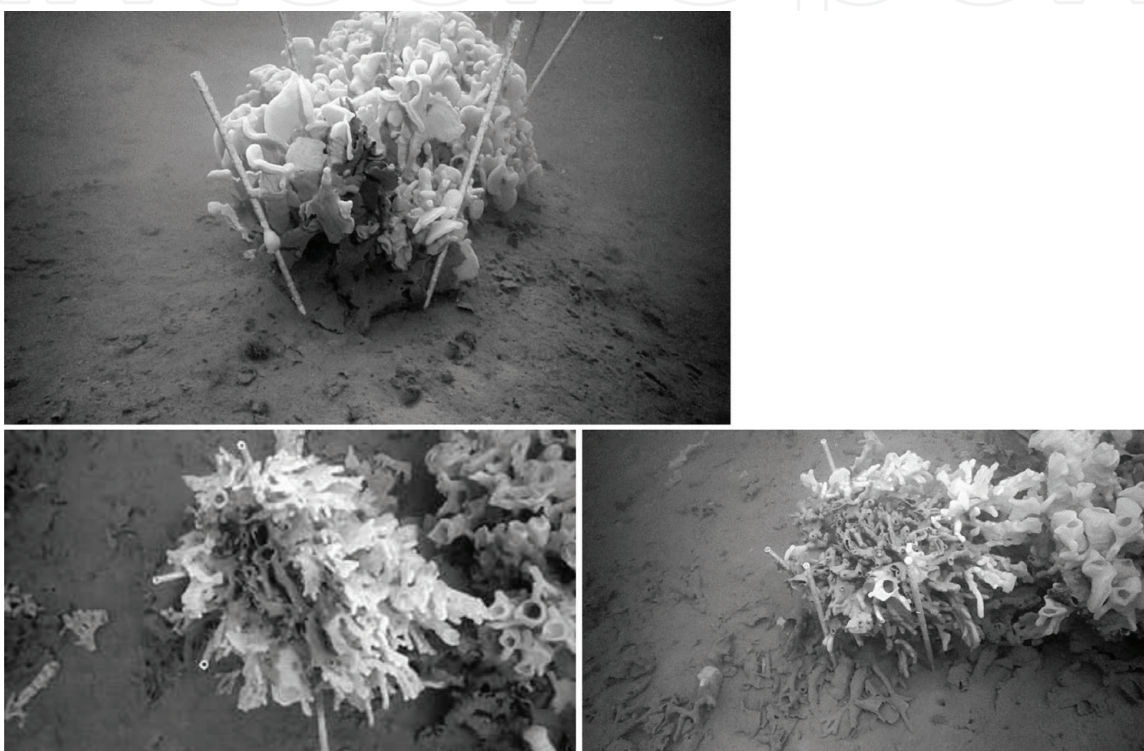


Figure 7.
 Upper photo: west transplant at ridge top dying, October 9, 2018. Lower left photo, transplant by 2-blue with dead core on July 24, 2017. Lower right, October 9, 2018, same transplant largely dead.

loose sponge head that had been staked in place at another part of the reef also died suddenly in the August/September period of 2018.

At the west Bowen Island sponge garden, four sponge heads labeled (A), (B), (C), and (D) in **Figure 8** grew relatively rapidly between September 2012 and May 2015. During fall of 2015, these sponges suffered tissue loss during the record 2015/2016 El Niño. Growth has been negligible in the subsequent 3 years.

Examples of rapid mortality at the inshore Defence bioherm were identified by means of the bar-coded locator stakes (**Figures 9–11**). At the stake with 1-black stripe (at stake top), we saw rapid necrosis of part of a sponge head over a 3-month period during spring 2015, with no subsequent spread of mortality over the next 3 years (**Figure 9**). **Figure 10** shows the sponge tissue marked at the 2-black stake in 2014 that had died adjacent to the stake by May 2015; tissue growth was evident upslope from that dead sponge by 2018. In **Figure 11** the sponge tissue at 1-green had largely died by 2017.

Upright dead sponges were observed to collapse after some period of time. At the 2-yellow stripe stake (**Figure 12**), a group of intact, dead sponges observed

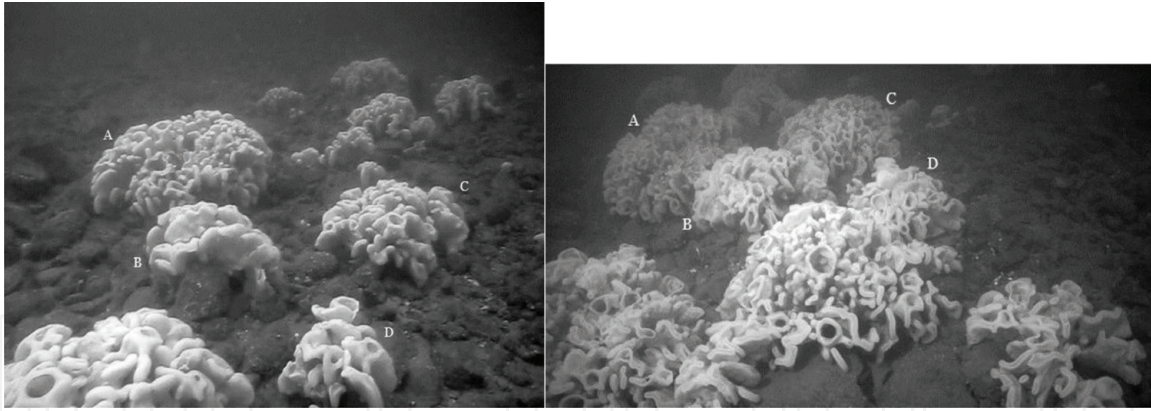


Figure 8. Baker's Dozen center sponges from north, September 26, 2012 (left); and same center sponges from north, May 4, 2015 (right). Letters identify same specific sponges.

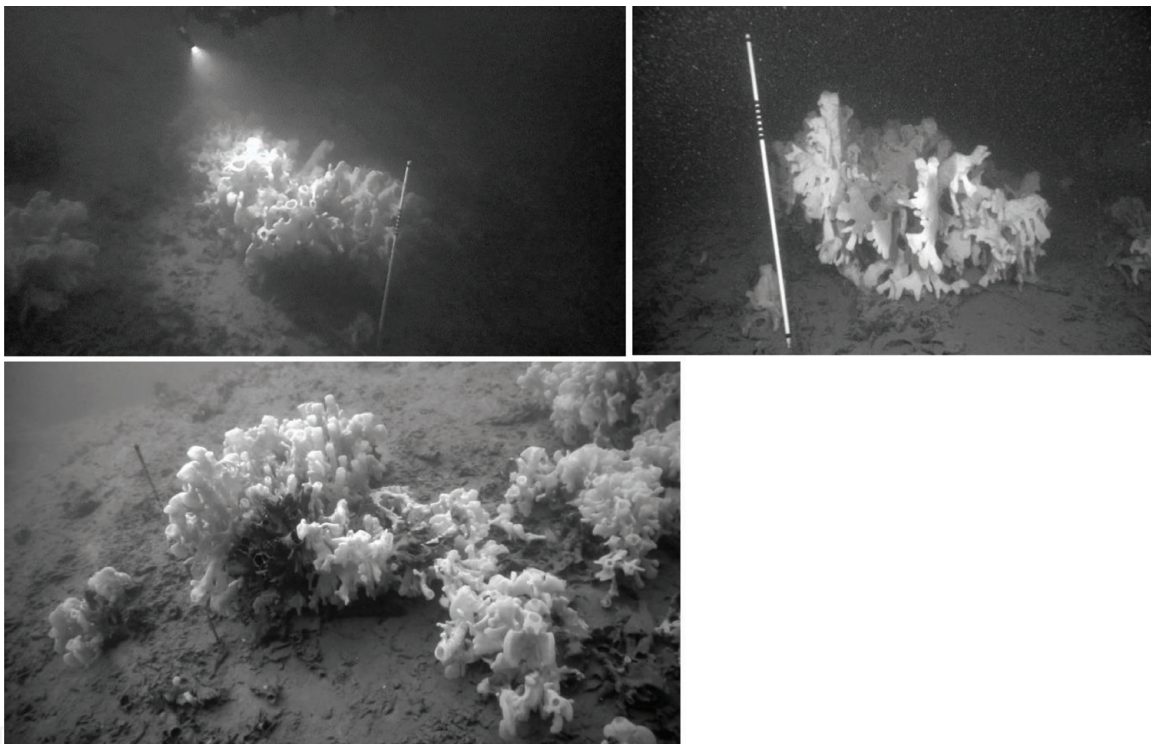


Figure 9. Top left—Defence 1-black: February 20, 2015; top right—May 31, 2015 (Paul Sim photo); and bottom: April 27, 2018.

during 2013 and 2014 had collapsed by 2018. The actual time required for collapse is probably very brief, as upright, dead sponges filmed on the bioherm ridge top on June 17, 2013, had collapsed by July 10, 2013.

Bioherm base layer depth at the upper ridge of the inshore Defence Island sponge reef varied from 0.30 to 1.45 m deep over an area of 3×3 m, with adjacent measures usually varying on the order of 0.1–0.2 m between adjacent probings at distances of 0.5 m (**Table 1**). The plot of hard bottom depth is consistent with bedrock (**Figure 13**) rather than glacial till, in which much more variation in depth would be expected on a recurring basis.

Detailed observations were made at the shallow-sloped west Bowen Island sponge garden with attention to sedimentation around dictyonine hexactinellid sponges on glacial till. Taxonomy of the community occurring at this site in 2013 and 2018 in association with the glass sponges included moderate abundances of rough patch shrimp (*Pandalus stenolepis*), galatheid crab (*Munida quadrispina*),

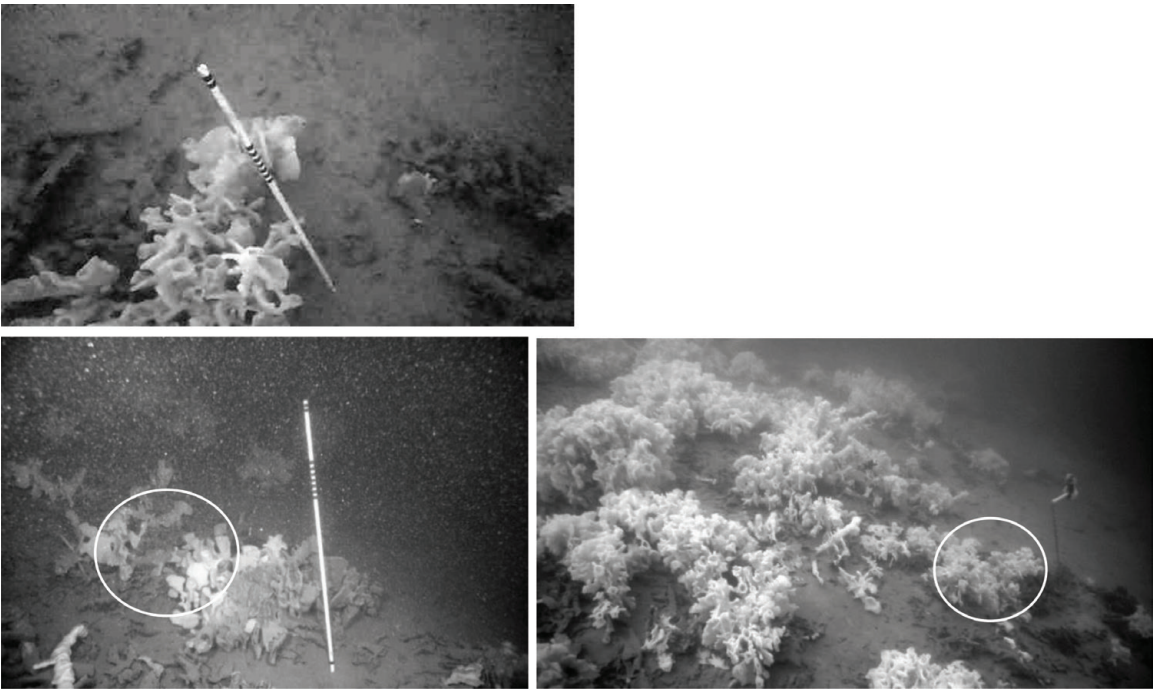


Figure 10.
Rapid necrosis of sponge adjacent to stake with 2-black stripes, intact February 20, 2015 (top), dead May 31, 2015 (middle—Paul Sim photo) and subsequent growth upslope (circled) from dead tissue, April 27, 2018 (note *Metridium anemone* and rockfish at top of stake).

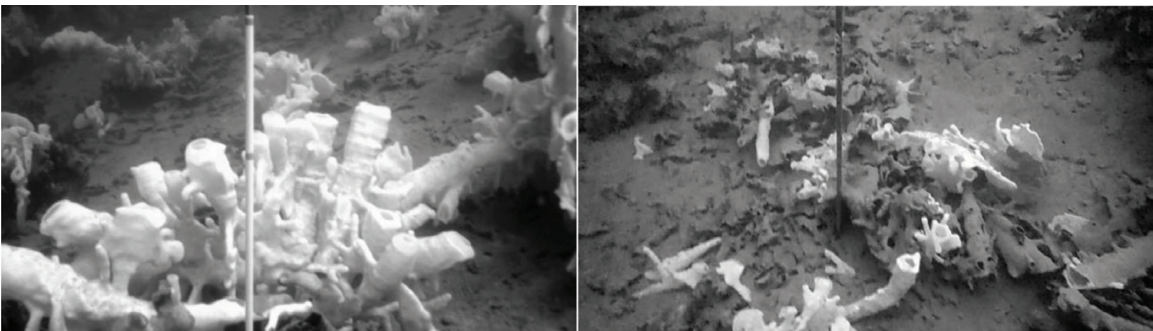


Figure 11.
Marker stake (1-green stripe): May 1, 2014 (left) and July 25, 2017 (right).

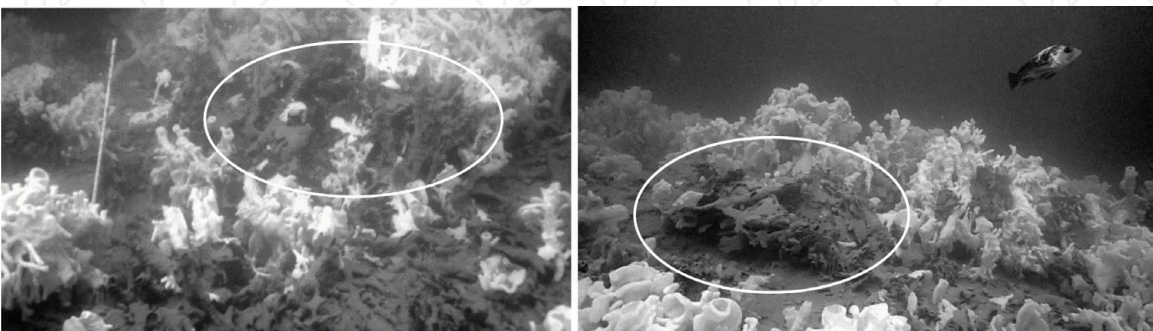


Figure 12.
Dead sponges upright at 2-yellow stake in 2014 (left) and collapsed in 2018 (right).

bristly tunicate (*Halocynthia igaboja*), fan bryozoan (*Dendrobeania murrayana*), vermillion star (*Mediaster aequalis*), white blood star (*Henricia* sp.), giant sea cucumber (*Apostichopus californicus*), and blackeye goby (*Rhinogobius nicholsii*), plus lesser abundances of 40 other animal species, not including sponges. Sponges included over 1000 cloud sponges (*Aphrocallistes vastus*) and over 1000

	A	B	C	D	E	F	G
1	110	145	140	(125)	110	115	120
2	75	70	85	(95)	105	95	95
3	70	70	60	(70)	80	90	70
4	80	70	75	(82.5)	90	70	55
5	55	65	80	(70)	60	45	55
6	80	75	65	60	55	30	40

Row and column labels correspond to the coordinates in **Figure 13**. Numbers in brackets were interpolated based on adjacent values because live sponges growing at these locations prevented the use of the avalanche probe.

Table 1.
Bioherm base thickness (cm) as measured with an avalanche probe.

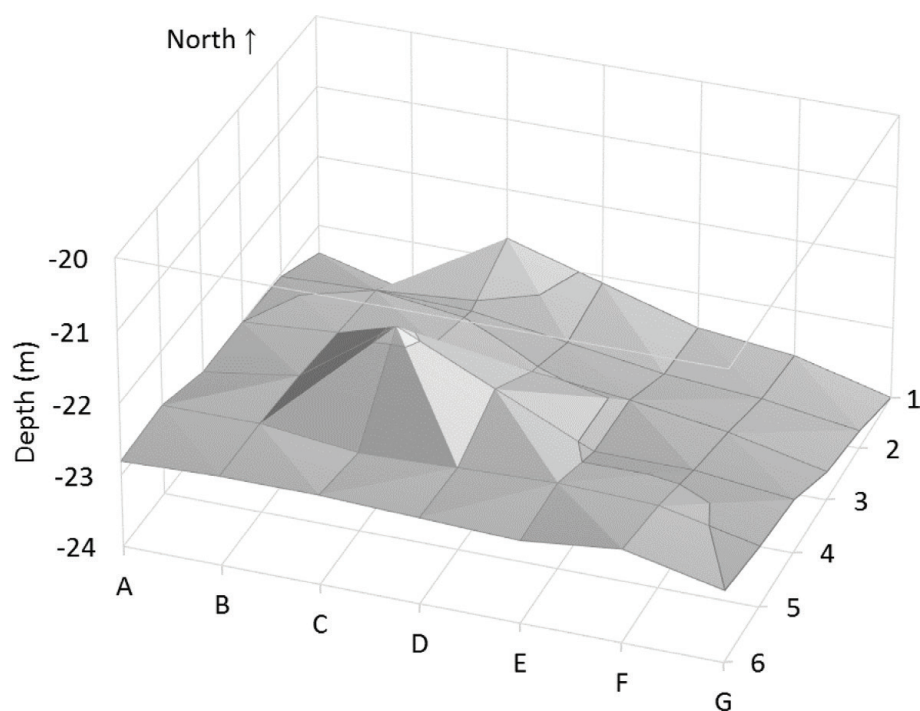


Figure 13.
Depth of the hard substrate beneath the bioherm basal layer at the Defence Island bioherm ridge. Depth was calculated by summing the water depth at zero tide and the bioherm depth, which was determined using an avalanche probe inserted into the sediment at 50 cm increments. North is toward the top and left-most position of the figure.

boot sponges (*Rhabdocalyptus dawsoni*) in each year, plus about 10 vase sponges (*Heterochone calyx*) in 2013 and over 500 in 2018, the increase in apparent numbers owing to the inability to distinguish small cloud and vase sponges in 2013. The yellow boring sponge (*Cliona californiana*) was moderately abundant, and the white meandering sponge (*Haliclona* cf. *mollis*) was at high abundance in both years. Algae included moderate abundance of red rock crust (*Hildenbrandia* spp.) and crustose corallines (*Clathromorphum*, *Lithothamnion*). Video frames in **Figure 14** lead to the hypothesis that the non-reef-forming lyssacine Hexactinellid boot sponge as well as the bristly tunicate may sequester sediment that eventually stabilizes the fallen dictyonine cloud sponge or vase sponge skeletons lying in the same vicinity. Thus, new sponges can settle on sediment-stabilized sponge fragments as well as on rock until eventually all growth might be on a bioherm-type of sedimented base composed of dictyonine sponges and their fragments.

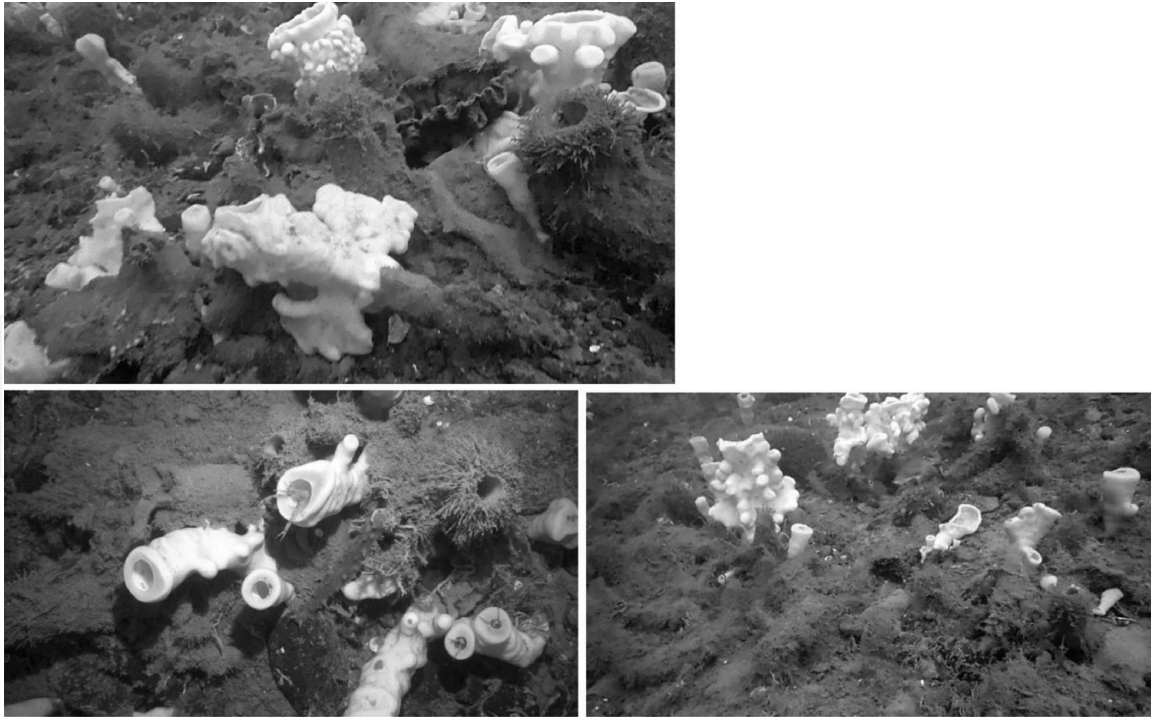


Figure 14.
 Sedimentation around cloud sponges and boot sponges at the west Bowen Island sponge garden. Note sponge side attachment to both rock and dead sponge fragments in the middle photo.

4. Discussion

Glass sponge mortalities occurred at various times throughout the period of dive surveys from 2007 to 2018. Particularly extensive mortalities were associated with the El Niño climate events of 2009/2010 and 2015/2016. Note that the episode of mortality in sponge at the 1-black and 2-black stake sites occurred during the onset of the 2015/2016 El Niño during early spring of 2015 (anomalies of 0.6–1.0). This was during a period when temperatures were higher at this site than at the other three sites (**Figure 2**), whereas other sponge mortalities seemed to coincide with the heightening of that climate event during August/September 2015 (anomalies reaching 1.8 and 2.1). The coincidence of several mortality events during August/September of 2018 may enable a prediction for testing by subsequent Ocean Niño Index records for 2018/2019 if another El Niño occurs. The onset of increased mortalities in August and September of 2018 (**Figure 7**) may relate to temperature spikes associated with the onset of an El Niño climate phase at the shallow bioherms in Howe Sound. It should also be mentioned that the pH of local seawater hit low extreme levels of 7.3 in 2009 and 7.4 in 2015, compared to modal levels of about 7.7 through that period [7]; thus, low pH may interact with elevated temperature in stressing glass sponges. Interaction of climate warming and ocean acidification may soon affect shallow bioherms.

It needs to be emphasized that, without the deployment of markers [5], it would not have been possible to identify specific sponge clusters or the changes that occurred to them over time. Considerable confusion existed in trying to orient to the reef in 2012 after a period of absence during which the damage from the 2009/2010 El Niño reshaped the appearance of the reef; it was in the aftermath of that period that stakes were deployed in winter of 2013/2014. Similarly, the episode of fishing gear damage in fall of 2016 resulted in disorientation on the reef until videos of marker stakes were scrutinized and certain bushes of sponge were identified as loose and others were spotted with cuts through them. The staking of

transplants in 2016 provided additional markers. Unfortunately, all these markers and oceanographic monitoring devices degrade the pristine aspect of the reef, a cost of ongoing study, but this site is remote from the more accessible bioherms used by dive charter boats in southern Howe Sound.

The depth of the present study site is 24 m at the shallowest point. The Passage Island reef is at 24 m, the Defence Island offshore reef at 31 m, and the Halkett Pinnacle reef at 32 m [8]; all other Howe Sound sponge reefs are significantly deeper (38–96 m) [8]. The temperature data (**Figure 2**) indicate that spikes in temperature exceeding 10.5°C occurred at around the heightening of the 2015/2016 El Niño in summer of 2015. By contrast, during the two subsequent La Niña years, the high temperatures were closer to 9.5°C. Cloud sponge mortalities may be associated with high temperature stress. One should note that the bioherms outside Howe Sound are uniformly deeper [1]. Therefore, the present observations represent one of two of the very shallowest known glass sponge reefs in the world, the other being Howe Sound's Passage Island reef. Similarly, the observations of a possible successional community favoring biogenic sedimentation at west Bowen Island are taken from a slightly shallower location of about 22 m depth. The much larger bioherms in northern British Columbia may have different characteristics in growth and recovery of sponge tissues. Whether a bioherm could develop at the 22 m Bowen Island sponge garden would probably depend on the future water conditions at that site. That site should be monitored for sedimentation and sponge attachment characteristics together with close attention to seawater temperature trends.

Temperatures at large sponge reefs on the continental shelf of Hecate Strait were from 5.5 to 7.3°C [9]. Those reefs occur at depths of 140–240 m, much deeper than the Howe Sound reefs at 24–96 m [8]. It is unlikely that the majority of bioherms experience such high summer temperatures as were recorded for the present study site. Therefore, the characteristics of growth and recovery of this shallowest case study site should not be predicted to establish how the deeper bioherms were formed.

If Ocean Niño climate regimes are being affected by global warming, then these two shallowest known glass sponge reefs may be predicted to be at risk of hindered persistence over time (see [10] for review). Continued study will be important to adjudicating the prospects for survival of shallower glass sponge reefs in the future. Beyond direct physiological effects of extreme temperature on glass sponges, another possibility must be considered regarding the food web of sponge reefs. The biodegradation of dying diatoms by bacteria feeds bacteria to glass sponge reefs [4]. Any temperature effect on the dynamics of diatom blooms and their subsequent biodegradation may affect the nutritional status of glass sponges, another possible impact on sponge reef health.

Sponge reefs consist of dictyonine glass sponges (hexactinellids) growing on a geologically stabilized base of glass sponge skeletal material [1, 3]. Although the lyssacine hexactinellid sponges (boot sponges) do not contribute to the sedimented geologic basal portion of bioherms, they may participate in creation of the original reef base at the level of the glacial till on which the bioherm grows. It may be the relatively flat nature of the glacial till at the west Bowen Island site, together with the turbulent drag of the cobbles and pebbles, which enables the sediment accumulation around the boot sponges and bristly tunicates at that location. Bioherms are characterized by growing on glacial till [3]. It is very likely that the inshore Defence Island bioherm is centered on glacial till because Defence Island is on the Porteau Sill, the inner sill of this fjord, the sill primarily consisting of glacially deposited boulders and cobbles. Therefore, the bedrock underneath the uppermost ridge of this bioherm probably relates to a gradual upward creep of this bioherm onto the bedrock of the island shoreline.

In this case study, glass sponge skeletons were observed to fragment significantly prior to sedimentation of the bioherm base. Thus, the increase in bioherm base depth with generations of sponges at this study site may be a minor fraction of the cumulative average height of the intact, living sponges through time. Previous literature cited here finds that deeper sponge reefs consist of frameworks of intact skeletons, and it is considered that “larger sponge skeletons may persist several hundred years before they become sedimented over” [11]. We have observed sedimentation of sponge fragments in the present study and have never observed a partially buried sponge skeleton. The portions of the sedimented bioherm base that we removed with intact living sponges attached consisted of layers of sponge skeleton lying flat. Intact skeletal specimens of siliceous sponges have been recovered from Jurassic spongiolithic deposits [12], so there undoubtedly are cases where relatively intact sponge skeletons become stabilized with sediments, but stabilization of sponge fragments must also be a component of bioherm geologic growth at the present study site. Fragmentation occurs prior to burial here, partly owing to a typically unstable tubular morphology (**Figure 15**) which may break off due to gravity after continued growth. In addition, we observe many secondary species growing on glass sponge skeletons that degrade skeletons within years (DMG unpublished data), so that collapse into fragments also relates to weakening of skeletons over relatively few years.

The assumption of sexual reproduction and reef growth from settlement of new sponges on skeletal sponge architecture [5, 11] may not be the sole source of new growth. The rapid appearance of relatively large growths out of fallen sponge fragments may have more to do with tissue recovery of stabilized fragments [6]. The experimental crushing of a portion of reef [5] did not show any recovery, but the crushing by an ROV did not leave large intact pieces of sponge as occurs in a debris drift. Many newly settled sponges on the present reef study site simply failed to thrive and disappeared. The few that survived for several years tended to obtain only modest size (<5 cm osculum diameter and height) over a period of several years (DMG, JBM personal observations). The most rapid growth we have seen has been associated with recovery or continued growth of larger sponges, including sponge fragments.

The lack of evidence for a frame-building aspect to this very shallow bioherm may indicate that it is more comparable to a biostrome [1] than to a reef mound

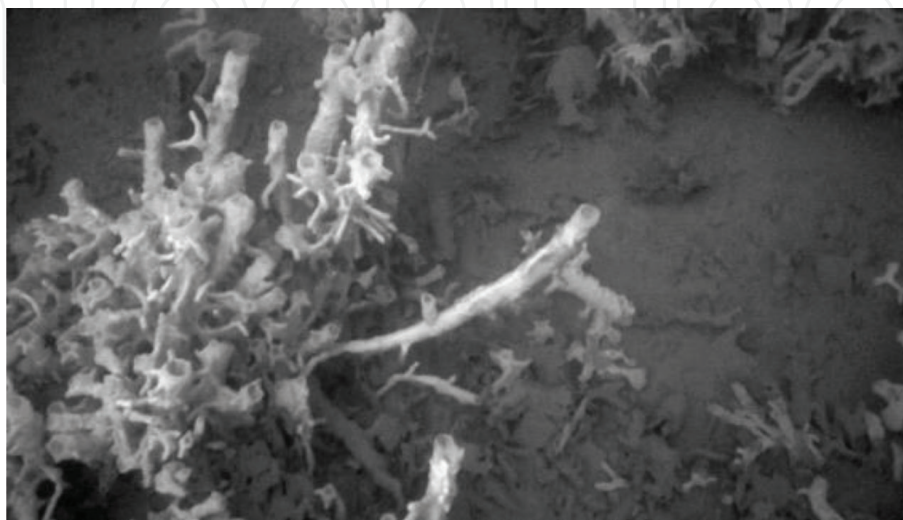


Figure 15.
Unstable tubular morph of cloud sponge (October 2018). This type of angled, elongate tube usually collapses by breaking off, and then dies. Note sedimentation of fallen fragments.

bioherm. It should be noted that the inshore biostromes of Queen Charlotte Sound are relatively flat [1, 13], whereas the shallowest bioherms in the Howe Sound area of the present study have much steeper top slopes than has been documented elsewhere [13]. Early work on glass sponge reefs referred to skeletal fragments in core samples [13], so the question of how intact skeletons are within all bioherms should be held moot. It remains for coring or detailed side-scan work on the shallowest inshore reefs of Howe Sound to be conducted, so whether these bioherms are any deeper in thickness than biostromes remains to be determined. Searching for evidence of frame-building within these shallow Howe Sound bioherms is another topic for future research.

5. Conclusions

A theory of scree slope drift formation at sponge reefs is proposed as a means of relatively rapid growth for bioherms; we further posit that such scree recovery does not ordinarily occur at sponge gardens owing to lack of stabilized position of fragments in garden sites resulting in continued mechanical damage of fragments in gardens. The difference is that currents continually shift and damage sponge fragments on bedrock, whereas the spicules of loose sponges can firmly lock position on a bioherm substrate under favorable circumstances of position.

The present observations indicate that a dead sponge will tend to collapse under its own weight within a few years of the death of living tissue. Similarly, growing, living sponges also have some tendency to become unstable and to collapse in the face of tidal currents, especially tubular morphs with necrosis occurring at the narrow points of attachment to the reef base. Thus, the view that bioherm growth consists of sedimentation of intact, dead skeletons of glass sponges does not fit well with our case study in which episodes occurred of necrosis and collapse of significant portions of the reef. Both the 2009/2010 and 2015/2016 El Niños coincided with certain areas of the reef dying and collapsing. The tissue collapse episode after 2009/2010 led to at least one debris drift forming and subsequently recovering growth (**Figure 3**). This is consistent with results from experimental transplant of fragments [6].

As well, a theory of successional community contribution to bioherm formation is based on observations of an extant ecological community on glacial till where sediment sequestering species of lyssacine sponge and tunicate buildup sediments in which fragments of dead dictyonine glass sponges rest secure from movement by seabed tidal currents. Attachment of live dictyonine sponges to such stabilized dead fragments can occur (**Figure 14**). A major question concerns what variation in rates of sedimentation can occur during formation of sponge reefs. A related question concerns what the dynamic is between ongoing vertical growth, collapse, and regrowth of the living surface of the reef in relation to the vertical growth of the geologically stabilized, sedimented reef base. The present study suggests that the living reef has a more dynamic range of growth, collapse, and regrowth through time than has been presumed.

These very shallow sponge reefs in Howe Sound, the only cases in the world amenable to studies based on scuba diving with compressed air, may afford valuable opportunities for citizen science contributions based on video recordings. It must be cautioned, however, that without landmarking against either geologic features or use of marker stakes, it is nearly impossible to prove identity of a sponge from one point in time to another owing to significant changing of shape and size.

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Conflict of interest

The authors have no conflicts of interest.

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