Dynamic change, recruitment and resilience in reef-forming glass sponges

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Glass sponge reefs on the continental shelf of western Canada and south-east Alaska are considered stable deep-sea habitats that do not change significantly over time. Research cruises using a remotely operated vehicle equipped with accurate GPS positioning have allowed us to observe the same sponges at two reefs in the Strait of Georgia, British Columbia to document recruitment, growth and response to damage over time. Spermatocysts and putative embryos found in winter suggest annual, asynchronous reproduction. Juvenile sponges (2–10 cm in osculum diameter) in densities up to 1 m^{-2} were more concentrated near live sponges and sponge skeletons than away (Spearman rank correlations, P < 0.0001 for live cover and for skeletons), suggesting that recruitment occurs in particular regions using sponge skeletons as substrate. Most sponges showed no change in shape or size over 2–3 years, but some had died while others showed growth of 1–9 cm $year^{-1}$. Deposition rates of reef-cementing sediments were 97 mm $year^{-1}$ at Galiano Reef and 137 mm $year^{-1}$ at Fraser Reef, but sediments eroded so that there was no net gain or loss over time. Sponges recovered within 1 year from small-scale damage that mimicked bites by fish or nudibranchs; however sponges did not recover from crushing of a large area (1.5 × 2 m^2) even 3 years later. These observations and experiments show that while recruitment and growth of sponge reefs is more dynamic than previously thought, the reefs are not resilient in the face of larger-scale disturbances such as might be inflicted by trawling.

INTRODUCTION

Glass sponges (Class Hexactinellida) are conspicuous members of the deep-sea fauna and are thought to be adapted to the long-term constancy of deep water. Glass sponges are estimated to live up to 400 years (Leys & Lauzon, 1998; Fallon *et al.*, 2010), yet yearly monitoring has also revealed rapid responses to changing conditions and seasonal or annual spurts of growth in both shallow and deep-water populations (Leys & Lauzon, 1998; Kahn *et al.*, 2012; Dayton *et al.*, 2013; Fillinger *et al.*, 2013).

Glass sponges are typical members of deep-sea fauna, but on the Pacific coast of North America they are highly abundant in fjord habitats and also form reefs covering hundreds of kilometres of seafloor on the continental shelf. Glass sponge reefs are thought to have formed between 6000 and 9000 years ago after glaciers retreated from the continental shelf of western Canada and south-east Alaska (Conway *et al.*, 1991). Since their first discovery during seafloor mapping of the shelf waters in the late 1980s, it is known that four large reefs exist in Hecate Strait and Queen Charlotte Sound, British Columbia and over 12 more are known in southern waters of the Strait of Georgia.

Whereas in northern reefs three glass sponge species make up the reef structure – *Aphrocallistes vastus*, *Heterochone calyx* and *Farrea occa* – in the Strait of Georgia *F. occa* is absent. These three species differ from most glass sponges in having secondary silica deposition that fuses their spicules into a three-dimensional scaffold. When the sponge dies the scaffold resists decay and is eventually buried by sediment. Before burial however, larvae settle and grow up to form the next generation (Krautter *et al.*, 2006). In the Strait of Georgia *A. vastus* and *H. calyx* settle and grow upon previous generations forming mounds up to 21 m high cemented together by sediment (Conway *et al.*, 2005).

Glass sponge reefs and sponge gardens serve important ecosystem functions: they are important nursery habitats for commercially important species (Cook, 2005; Marliave *et al.*, 2009; Chu & Leys, 2010; Miller *et al.*, 2012), they contribute to local silica cycling (Chu *et al.*, 2011), and they are major grazers of plankton in deep water (Kahn *et al.*, 2015). Glass sponges throughout the north-east Pacific are easily damaged by trawl and other fishing activity (Freese *et al.*, 1999; Heifetz *et al.*, 2009). In western Canadian waters glass sponges have been recorded as bycatch with between 0.086 kg^{-1} and 6.041 kg min^{-1} catch per unit effort in trawls through reefs (Jamieson & Chew, 2002); there are also many anecdotal records of damage to sponges by recreational prawn fisheries. What is not known is how resilient glass sponges are to damage, nor generally how dynamic growth and regeneration of individuals and populations are.

We used a remotely operated vehicle (ROV) with highly accurate GPS navigation underwater to monitor change over time at two sponge reefs in the Strait of Georgia. Our aim was to observe and document reproduction and recruitment events, measure normal growth rates, and to determine whether dense glass sponge communities are resilient to disturbance.

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MATERIALS AND METHODS

Fraser and Galiano sponge reefs were visited in 2005, 2007, 2009, 2011, 2013 and 2014 during cruises on the 'CCGS Vector' and 'CCGS Tully' (Fraser Reef: $49°9'15.7''$N $123°23'3.7''$W; Galiano Reef: $48°54'51.5''$N $123°19'27.7''$W). Work was carried out using the ROV ROPOS (http://ropos.com) which uses an ultra-short baseline navigation (USBL) Global Acoustic Positioning System (GAPS) with a LOKI Kalman filter that allows positioning within 1 m.

Recruitment and growth

Both Fraser and Galiano sponge reefs were mapped extensively using grids of non-overlapping photos taken 1 m above the sea-floor in 2005 and 2007 (Galiano Reef: 214 photos covering 594 m²; Fraser Reef: 109 photos covering 69 m²) (Chu & Leys, 2010). From the same set of ROV photos juvenile sponges – those with maximum osculum width of <10 cm and minimal branching – were counted and osculum diameters measured using ImageJ software. No attempt was made to differentiate between the two species because *Heterochone calyx* and *Aphrocallistes vastus* cannot be distinguished from photos alone. The density of juvenile sponges was calculated from the total photo area for each survey grid point, plotted on maps of the reefs using ArcGIS (ArcInfo version 10.2, ESRI), and compared to the distribution of adult sponges documented by Chu & Leys (2010) using Spearman rank correlation (SYSTAT 12).

To look for evidence of reproduction (whether as spermatocysts, eggs or embryos in tissue), pieces of *Aphrocallistes vastus* collected by scuba in Saanich Inlet, BC and by ROV at the two reefs were preserved in a cocktail fixative of 1% OsO_4, 2% glutaraldehyde and 0.45 M sodium acetate buffer with 10% sucrose (Harris & Shaw, 1984). The fixative was replaced after 30 min and specimens were left at $4°C$ overnight. Specimens were dehydrated through a graded ethanol series to 70% ethanol, and then desilicified in 4% HF in 70% ethanol. Following desilicification, samples were rinsed twice in 70% ethanol, dehydrated to 100% ethanol and fractured in liquid nitrogen. Fractured pieces were critical point dried (Bal-Tec CPD 030), mounted on aluminium stubs, sputter-coated with gold (Xenosput XE200), and viewed in either a Hitachi S-3500N at the University of Victoria, or a JEOL 6301F at the University of Alberta.

To monitor growth (changes in size of branches) or death (loss of live tissue) over time, the ROV was positioned at the exact same heading and same GPS position to match the camera's view to photos from previous years. Lasers 10 cm apart fixed to the camera provided a scale.

Sediment accumulation

To determine how much sediment accumulates at the reefs, sediment traps and erosion markers were placed at Fraser and Galiano Reefs between 2007 and 2009. Sediment traps were PVC tubes 0.5 m long with 45-cm² opening attached to stakes that were pushed into the sediment until the bottom of the tube was at the sediment surface. Each tube trap was pre-filled with hypersaline water and capped with a lacrosse ball that was removed by an elastic cord after the trap was positioned. Traps and markers were placed adjacent to and about 2–3 m away from clumps of sponges in 2007. In 2009 sediment traps were re-sealed with lacrosse balls to prevent loss of contents, recovered using the ROV, and frozen at $-20°C$ for transport to the University of Alberta. The sediment was pushed out of the traps while still frozen and the total height of accumulated sediment measured. Sediments were dried in an oven at $60°C$ until less than 3% change in mass was achieved for 2 days in a row.

Erosion markers were PVC poles with 2.5-cm wide black and white markings. Not all 14 erosion poles were found each cruise but for those revisited the number of markings above- and below-ground were counted for each pole.

Recovery after disturbance

Disturbance experiments were carried out in 2011, 2013 and 2014. First a clump of sponges was selected for large-scale disturbance at Galiano Reef using an asymmetrical BACI design, with one treatment patch and two control patches to minimize damage to the reef (Underwood, 1994). Two PVC markers, described above, were placed on either side of the clump. Overlapping still images of the entire clump including the marker poles were taken 1 m above the seafloor as the ROV moved around and across the clump. Then the ROV was lowered onto the sponges to crush an approximately 1.5 × 2 m large area. A second image series was captured after damaging the sponges. Two control sites were surveyed using the same methods. All three sites were revisited in 2013 and 2014 and an identical image survey carried out. Seventy photos were selected from each survey based on clarity, image quality and coverage of the site and adjusted for optimal contrast using Photoshop. Three-dimensional structure-from-motion reconstructions of each BACI site were created using 123d Catch (Autodesk, http://www.123dapp.com/catch) to visualize changes to the sites from all angles.

Second, in 2013 four sponges adjacent to PVC erosion markers were selected for small-scale damage experiments at Galiano Reef. Images were captured of 'mitten'-like extensions and then the ROV manipulator arm was used to remove 3–10 cm portions from the tips of the sponges and images captured again. The same sponges were revisited in 2014 using heading and GPS coordinates to match the view from images from 2013. Images were captured of the same view.

RESULTS

Recruitment of new sponges

The smallest sponges visible on the reef using high-definition (HD) video from the ROV were less than 5 cm in overall height and width with oscula as small as 2 cm in diameter. All juvenile sponges observed were attached to dead skeleton, had centrally placed oscula, and had broad ridges indicating the first growth of mitten-like projections.

The density of juvenile sponges (0.4 ± 0.9 juveniles m^{-2}; mean $\pm$ standard deviation, SD) was greater in areas where adult sponge density was highest (Figure 1A; Spearman rank correlation, $\rho = 0.299$, $P < 0.0001$) and where dead sponge cover (skeletons) was highest (Spearman rank correlation, $\rho = 0.272$, $P < 0.0001$). Live and dead sponge cover were strongly correlated (Spearman rank correlation, $\rho = 0.666$, $P < 0.00001$). While density did not differ between reefs (Mann–Whitney U-test, $U = 10,905$, df $= 1$, $P = 0.218$), juveniles found at Fraser Reef were significantly smaller

(1.6 ± 0.8 cm maximum osculum width, mean ± SD) than juveniles at Galiano (2.6 ± 1.7 cm; Mann–Whitney U-test, U = 1376.5, df = 1, P = 0.004) and had a narrower size distribution (Figure 1B–D).

Adult tissues from one ROV collection in November 2011 had spermatocysts by December of the same year, and tissue collected by scuba in a nearby fjord (Saanich Inlet) in December 2012 and February 2013 also contained spermatocysts (Figure 1E). Developing embryos were found in a single specimen of *Aphrocallistes vastus* collected by scuba by one of us (Leys) in November 1995 (Supplemental Figure S1).

Growth

Because *Aphrocallistes vastus* and *Heterochone calyx* grow in three dimensions and extend mitten-like projections to increase surface area, it is difficult to find an accurate growth parameter to measure. We compared images captured at the same angle (ROV heading) each year to measure changes in shape and change in either height of an osculum or length of a projection. Changes included one sponge found growing around a pole in 2013 that had been absent in 2011, and was dying in 2014 (Figure 2A). Individual oscula grew in diameter in a multicoloured clump of sponges in 2011, 2013 and 2014 but a portion of that clump died back between 2013 and 2014 (Figure 2B). A juvenile grew an estimated 3 cm year^{-1} (Figure 2C). Three large sponges grew between 1 and 3 cm year^{-1} taller while projections from oscula grew more, between 7 and 9 cm year^{-1} (Figure 2D).

Sediment accumulation

Sediment traps showed sedimentation accumulation of 97 mm year^{-1} at Galiano Reef and 137 mm year^{-1} at Fraser Reef over 2 years (2007–2009); however, the PVC poles showed both accumulation and erosion with no net overall change over the 2 years (Supplemental Figure S2). On some poles at Galiano Reef the markings at sediment level were erased by scouring caused by high currents.

Recovery after disturbance

LARGE-SCALE DAMAGE
The site crushed by the ROV showed no recovery after 3 years (Figure 3, Supplemental Material 3). Large clumps of sponges immediately adjacent to the damaged site survived through 2014 but did not spread into the space vacated by the dead sponges, nor were new juvenile sponges seen anywhere on the damaged skeletons (Figure 4). The two undisturbed control sites showed both new growth and patches of sponges that had died. New growth occurred as overgrowth of skeletons by both glass sponges and by the demosponge *Desmacella austini*.

SMALL-SCALE DAMAGE
All four sponge projections that were damaged had repaired completely within 1 year. In each instance, the sponge had regenerated a soft growing edge to close the damaged area. On one sponge, the damaged projection had grown into
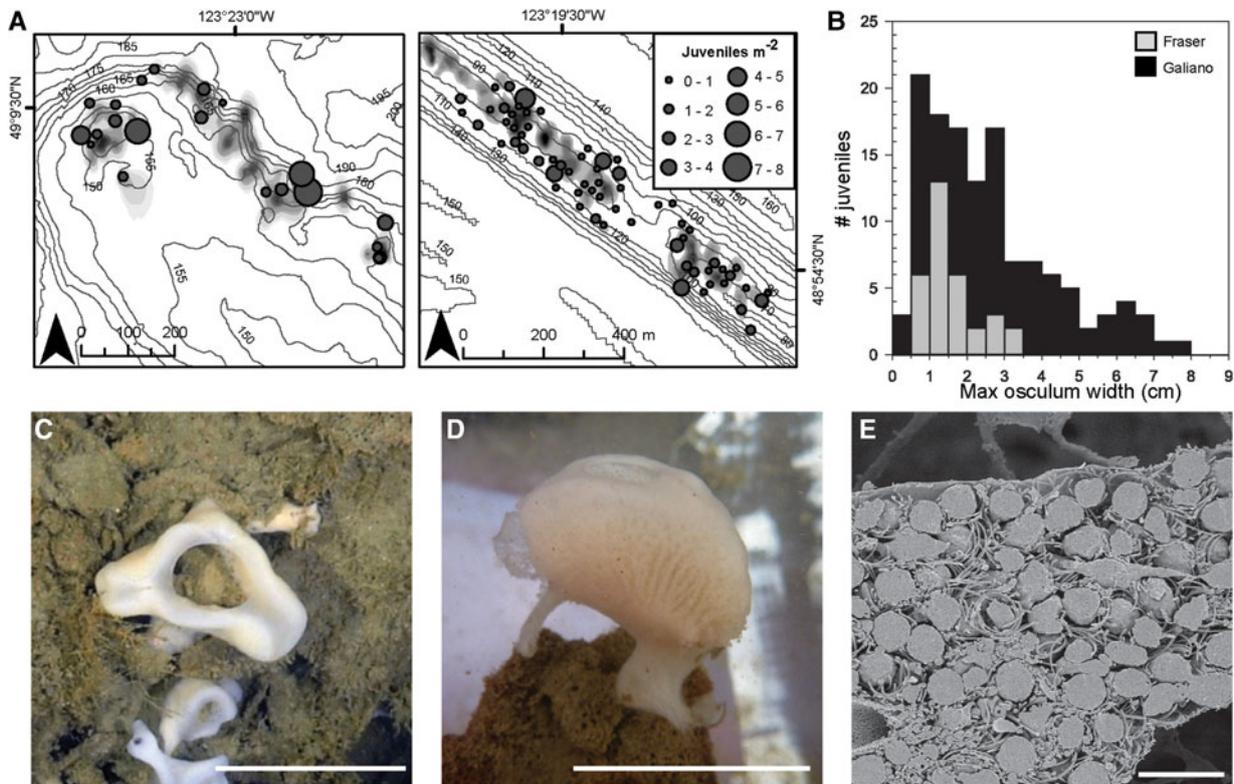

Fig. 1. Recruitment in glass sponge reefs. (A) Map of the density of juvenile sponges at Fraser Reef and Galiano Reef. Juvenile density is correlated with adult sponge density (shaded grey). (B) Size distributions of juveniles found at Fraser (grey) and Galiano Reefs (black). (C, D) Juvenile sponges have a maximum osculum width less than 10 cm. (E) Spermatocysts from a specimen of *Aphrocallistes vastus* collected in November, kept alive in seawater tables at Bamfield Marine Sciences Centre, and fixed in December. Scale bars: C: 5 cm, D: 2 cm, E: 10 μm.
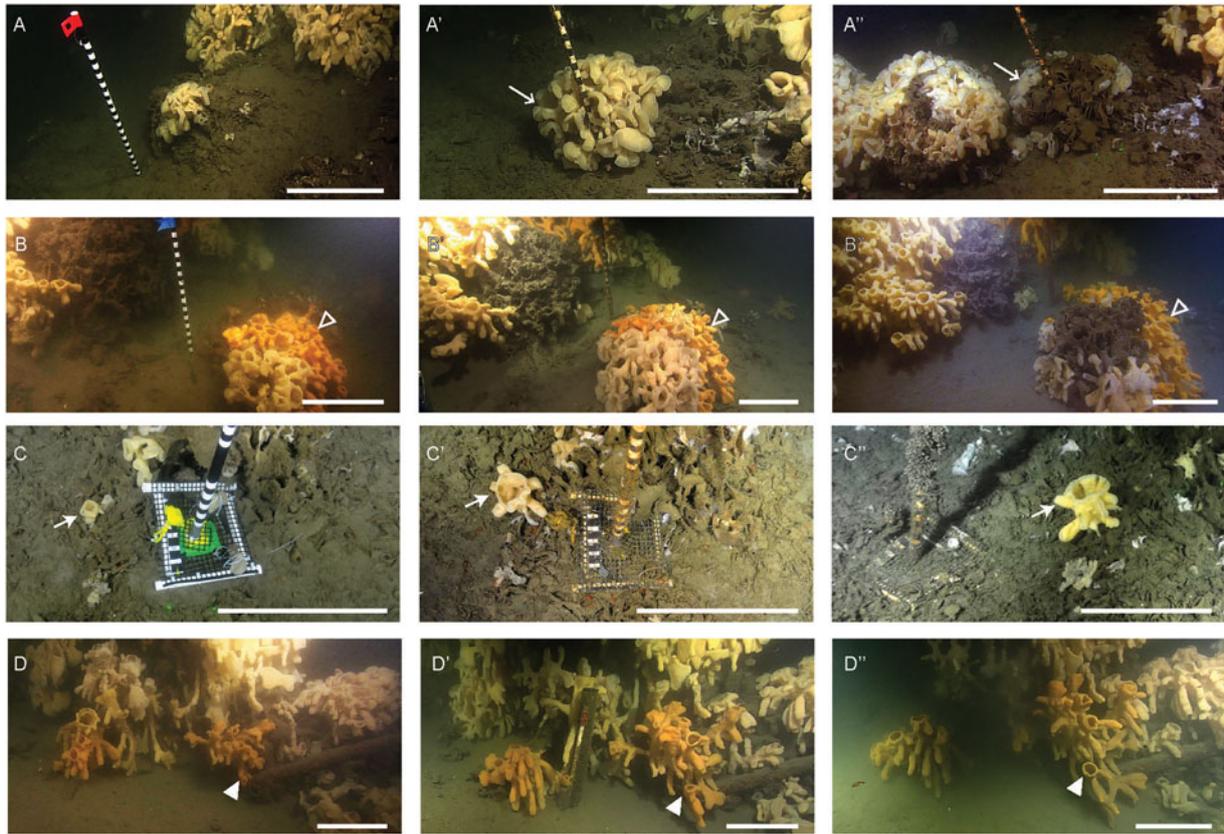
Fig. 2. Growth and change in glass sponge reefs. (A) A marker pole planted in open sediments in 2011 (A) had a 20-cm tall sponge (arrow) surrounding it in 2013 (A′), probably dislodged by the ROV. In 2014 (A″), the sponge had died but other sponges had grown up nearby. The photo from 2011 was rotated to provide the same view as in 2013 and 2014. (B) A clump of sponges (arrowhead) adjacent to a sediment marker persisted from 2011 (B) to 2013 (B′), but was dead in 2014 (B″). (C) Growth of a small sponge (filled arrow) beside a marker. The marker was moved after imaging in 2013, so it now is to the left of the sponge and a juvenile appeared on the settlement plate in 2014 (C: 2011, C′: 2013, C″: 2014). (D) Several sponges (filled arrowheads) overgrew a discarded cable we encountered at Fraser Reef. The projections on these sponges grew 7–9 cm year^{-1} (D: 2011, D′: 2013, D″: 2014). All scale bars: 50 cm.

what appeared to be an osculum while an undamaged projection of the same sponge had grown 9 cm in length (Figure 4).

DISCUSSION

We took advantage of repeat visits to the glass sponge reefs in the Strait of Georgia British Columbia using a ROV to observe recruitment and changes to individual sponges over time. We found that the changes were similar to those that occur to sponges in shallow-water habitats including growth, death and resilience to disturbance.

Recruitment of new sponges

The many juvenile sponges observed on the reefs with one distinct size class of osculum diameter (1–3 cm) are indicative of one or more reproductive events per year. We have looked for signs of reproduction in reef sponge tissues during every visit by scuba or ROV since the late 1990s. Although putative embryos have only been found in one specimen collected in November 1995 and not in tissues collected in July 2005, October 2007, 2009, 2011 or November 2011, 2013, 2014, nevertheless we found spermatocysts in tissue collected in December 2012 and February 2013. From these three observations of spermatocysts and embryos we conclude that gametes

develop asynchronously within a single individual of *Aphrocallistes vastus* and that reproduction is asynchronous among individuals, with spawning of sperm and development of embryos by brooding occurring over winter months.

Finding so many very small sponges gives new insight into reproduction and recruitment at the reefs. Given a growth rate of 1–3 cm year^{-1}, juveniles (2–10 cm) seen on the reefs in November 2013 and 2014 may have settled the previous year. Because larvae recruit to dead sponge skeleton we wondered whether high sedimentation might impede settlement and recruitment. Our two methods of measuring sediment accumulation suggest this is not the case. First, the density of juveniles was independent of sedimentation rates: Fraser Reef had double the sediment fallout of Galiano Reef, but density of juvenile sponges at both reefs did not differ. Second, the erosion markers showed very little accumulation of sediment even over several years, which explains why reef skeletons remain exposed as a good substrate for recruitment.

The fact that juveniles were found near both adult sponges and dead skeleton suggests that either larvae settle close to their site of release as found by Uriz and colleagues for a demosponge (Uriz *et al.*, 1998), or that larvae settle gregariously based on chemical cues from the material growing on dead skeletons (Ettinger-Epstein *et al.*, 2008). A third possibility is that those skeletons and live sponges provide both good substrate and good growing conditions for sponges. These
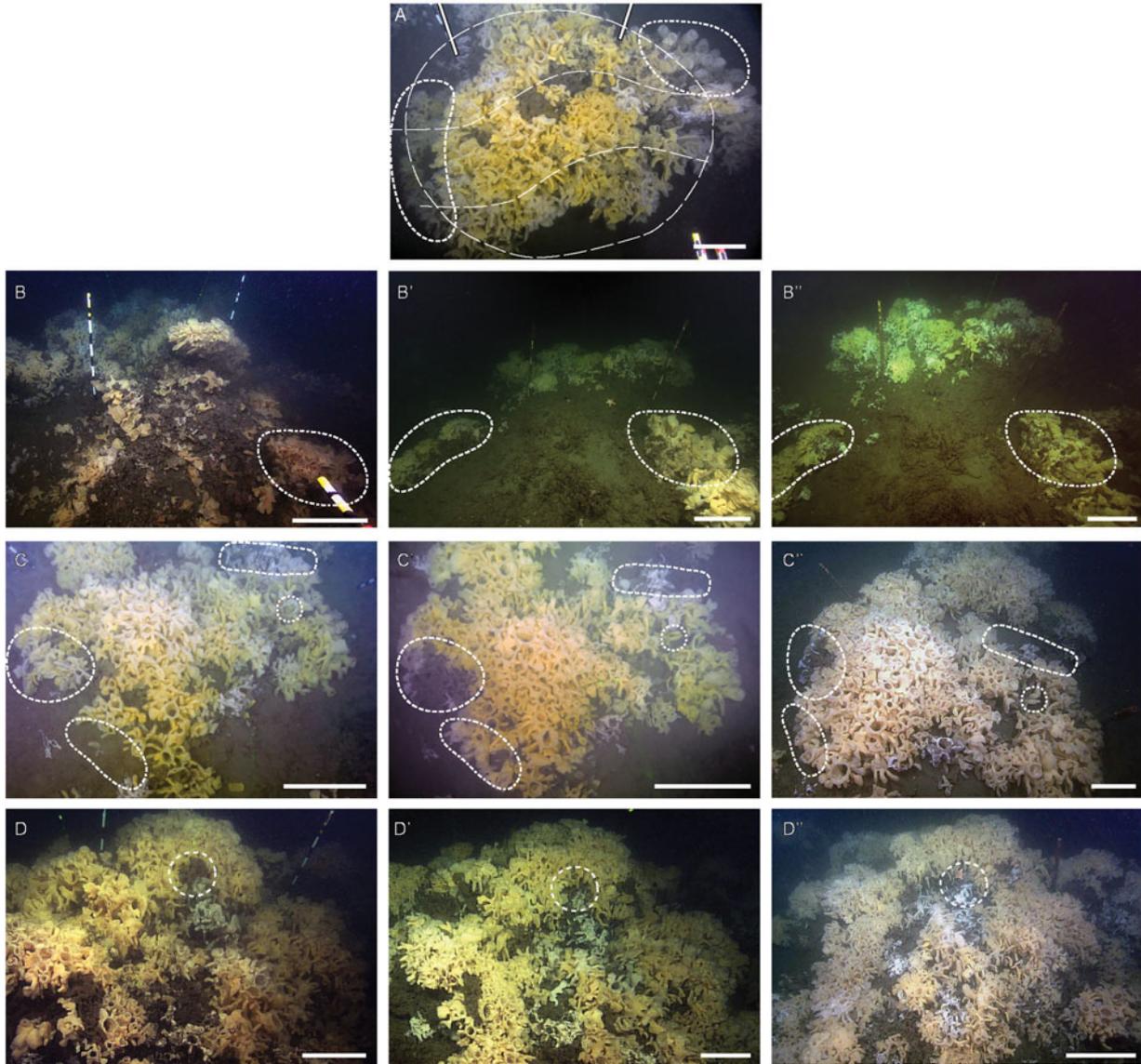
Fig. 3. Disturbances to the sponge reefs using an asymmetrical BACI design. (A) Images of 'impacted' site in 2011 before physical disturbance with paths for ROV surveys shown by dashed lines. (B, B′, B″) Image surveys following disturbance in 2011, 2013 and 2014 show little recovery, though adjacent sponges appeared unaffected. Control sites 1 (C: 2011, C′: 2013, C″: 2014) and 2 (D: 2011, D′: 2013, D″: 2014) showed overgrowth of sponge tissue, death of other tissue, and colonization by *Desmacella*. Dotted circles indicate regions of growth or death between years. All scale bars: 50 cm.

hypotheses cannot be tested with our data since the density of live sponges and dead skeletons were strongly correlated. In all visits to the reefs, there was no evidence that reef species reproduce asexually by forming tissue drips as suggested by Austin *et al.* (2007).

Growth

Because we could carry out repeated visits to the same sites on the reefs we could see changes to individual sponges over time. Rates we calculate of 1–3 cm year^{-1} for very young reef sponges are slower than those estimated for overall growth for the hexactinellid *Rhabdocalyptus dawsoni*, which can grow in length by up to 12% per year in small specimens and by 6% per year in larger specimens (Leys & Lauzon, 1998). Projections of reef sponges grew more rapidly, at 7–9 cm year^{-1}, which is in agreement with rates measured by

Austin and colleagues (Austin *et al.*, 2007). Generally it seems then that smaller sponges grow relatively quickly or episodically (Leys & Lauzon, 1998; Dayton *et al.*, 2013; Fillinger *et al.*, 2013). Appearance and growth of new sponges, and death of patches of sponge, indicate that the population is continually renewing and replacing across annual timescales as described for other glass sponge populations (Kahn *et al.*, 2012). In 2013 we re-visited an erosion pole planted in 2011. A large sponge now lay against it (Figure 2A), which suggests that this sponge was dislodged from elsewhere and came to rest against the pole. If the sponge was dislodged in 2011 and was still alive 2 years later then glass sponges can reattach following breakage. There is little chance that this sponge settled and grew from a larva to some 30 cm in diameter in 2 years, although that possibility should not be ruled out. This was a single observation however, and further observations are needed to determine whether this sort of

Fig. 4. Recovery of reef sponges from small-scale damage. All panels show regions with projections of sponges that were damaged in 2013. (A, B) 2013, Still image captured from high-definition (HD) video before damage occurred. A′, B′: 2013, Still image from HD video taken after the projections had been damaged. A″, B″: 2014, Still image from HD video taken 1 year later. All scale bars: 10 cm.

reattachment could happen more often in sponge reefs due to disturbance by sharks or high currents.

Recovery after disturbance

Glass sponges are easily broken with trawls and prawn traps (Freese *et al.*, 1999; Wassenberg *et al.*, 2002; Ardron & Jamieson, 2006; Heifetz *et al.*, 2009), but the ability of reefs to recover from damage is unknown. We therefore took advantage of the ability to make repeat visits to identical sites to determine the ability of reef-forming sponges to regenerate.

Having expected that deep sponge communities change slowly, we were surprised to find that small parts of sponges
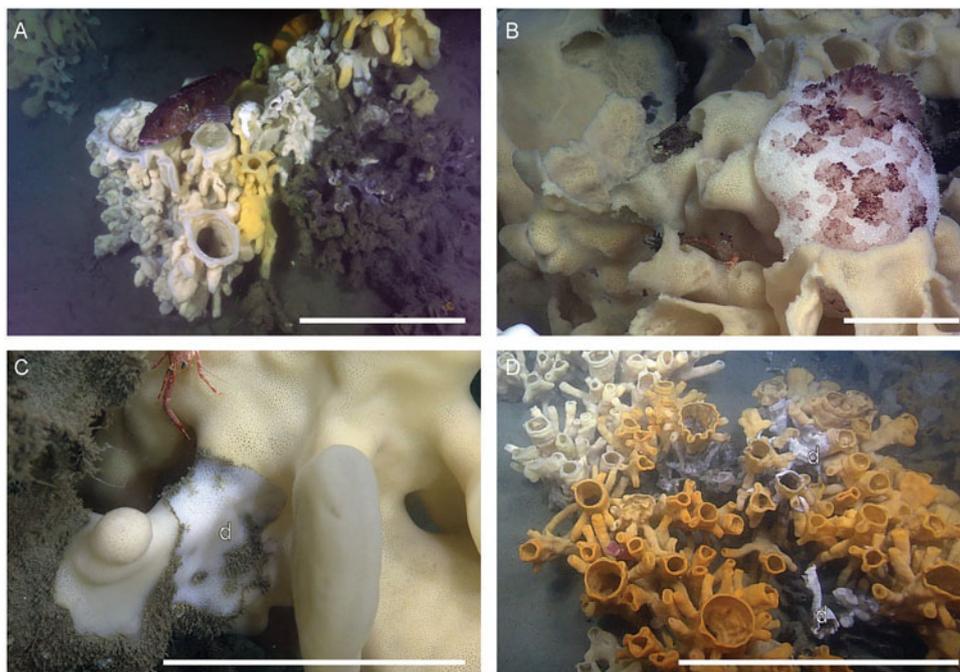

Fig. 5. Other ecological players in sponge reefs. (A) A lingcod (*Ophiodon elongatus*), one of many fish that frequent the reefs and can cause disturbance from bites and knocks, perches on the sponges. (B) The nudibranch *Peltodoris lentiginosa* on a sponge; adjacent oscula showing damage from grazing. (C) *Desmacella austini* (d), a demosponge that occupies the skeleton, here at the base of *Aphrocallistes vastus*. (D) *Desmacella* was commonly seen at the base of glass sponges in the reefs. Scale bars: A & D: 50 cm, B & C: 5 cm. All scale bars are approximations.

intentionally damaged by the ROV could recover completely in 1 year. Similar regeneration rates were found previously in shallower populations of glass sponges wounded experimentally (0.05 cm² day^{-1} or 18 cm² year^{-1}; Leys & Lauzon, 1998). Naturally broken fragments of sponges and damage to oscula and projections were frequently seen on our ROV dives. This damage was thought to be caused by both fish bites and knocks by fish tails (e.g. dogfish, ratfish) because in 2014 we watched as both the Pacific spiny dogfish (*Squalus acanthius*) and the lingcod (*Ophiodon elongatus*) caused this sort of damage when they caught crustacean prey from among the sponges (Figure 5A). Grazing by the nudibranch *Peltodoris lentiginosa* also causes extensive damage to the uppermost projections of sponges (Figure 5B).

We were even more surprised to learn that, in contrast to the quick repair of small parts of the sponges, no new sponges grew into or colonized the 'impacted' BACI site even after 3 years. Because sponges at the edge of the damaged site grew into the area but no new sponges recruited, we suspect that it was the extensive damage to the skeletons, used as substrate by reef sponges, that prevented new recruitment. Trawling has similar effects in removing rugosity and creating flat terrain (Puig *et al.*, 2012), so damage caused by trawling in regions with sponge reefs and gardens is expected to be long lasting.

In addition to anthropogenic disturbance, reef sponges face predation as described above and also by Chu and Leys (2012) as well as competition. The demosponge *Desmacella austini* grows on and takes over the skeletons of reef sponges. Three different colour morphs – possibly different species – of *Desmacella* were seen at both reefs. *Desmacella* was most common on dead glass sponge skeleton (Figure 5A), but careful study of the HD video showed that *Desmacella* occupied the base of many individuals of glass sponges (Figure 5B). Whether *Desmacella* colonizes live glass sponges or takes advantage of areas of skeleton left exposed by regressing tissue as the sponges grow upward is unknown. Its growth on dead skeletons, however, may prevent larvae from settling.

CONCLUSIONS

Three years of observations of deep sponge reefs showed that many aspects of reef ecology – recruitment, growth and resilience to disturbance – were comparable to those of shallower sponges. Recruitment occurs annually with growth rates for the smallest sponges of 1–3 cm year^{-1} and projections of the larger sponges at up to 7 cm year^{-1}. New sponges continually grow and replace sponges that have died. Glass sponge reefs are resilient to minor natural disturbance, but show no signs of recovery from large-scale physical breakage within the timescale of this study.

Supplementary material

To view supplementary material for this article, please visit http://dx.doi.org/10.1017/S0025315415000466.

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