Characterizing the sponge grounds of Grays Canyon, Washington, USA

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Abstract

Deep-sea sponge grounds are relatively understudied ecosystems that may provide key habitats for a large number of fish and invertebrates including commercial species. Glass sponge grounds have been discovered from the tropics to polar regions but there are only a few places with high densities of dictyonine sponges. Dictyonine glass sponges have a fused skeleton, which stays intact when they die and in some areas the accumulation of successive generations of sponges leads to the formation of reefs. In 2010 and 2016, we surveyed an area near Grays Canyon in Washington, USA, where dense aggregations of glass sponges and potential sponge reefs were discovered in 2007. Our primary aims were to make a preliminary assessment of whether the glass sponges form reefs at this location, characterize the sponge assemblage present at this site and examine associations between the sponges and commercially important species. Multibeam mapping and sub-bottom profiling indicate that the glass sponges at this site do not form reefs and are mostly attached to hard substrates. Analysis of photographs collected by an autonomous underwater vehicle and samples collected by a remotely operated vehicle guided by telepresence revealed the presence of two abundant dictyonine sponge species at this site, *Heterochone calyx* and *Aphrocallistes vastus* (mean densities = 1.43 ± 0.057 per 10 m^2, max = 24 per 10 m^2). We also observed a large number of non-reef-building glass sponges and various demosponges including a potentially new species in the genus *Acarnus*. A diverse fish assemblage was recorded at this site including eight species of rockfish. Rockfish abundance was positively related to sponge abundance. Spot prawns (*Pandalus platyceros)* were also abundant and were strongly associated with sponges. Despite not finding sponge reefs, this is an ecologically significant area. Further research is necessary to determine the environmental factors that give rise to the abundance of large dictyonine sponges at this location and also to determine if other similar sponge grounds exist along the west coast of the United States.

1. Introduction

Sponges are abundant benthic filter-feeding invertebrates that play important functional roles in marine ecosystems globally. They occur from the intertidal zone to abyssal depths and are involved in processes such as nutrient cycling, spatial competition, bioerosion, habitat provision, predation and mineralization (Bell, 2008). Under certain geographical and environmental conditions, they can form dense aggregations that may provide key habitats for large numbers of associated fauna. There are many types of sponge grounds characterized by differences in species composition, organizational characteristics and the environmental conditions where they occur (see Maldonado et al., 2016 for a recent review).

In deep-sea environments, some of the best-known sponge grounds occur in the North Atlantic where dense aggregations of astrophorid sponges dominated by species in the genus *Geodia* have been found from the Barents Sea to Labrador and Newfoundland (Klitgaard and Tendal, 2004; Knudby et al., 2013; Murillo et al., 2012). These deep-sea sponge grounds contribute a large proportion of benthic biomass (over 90% in some areas excluding fishes) and act as biodiversity hotspots (Murillo et al., 2012). Beazley et al. (2015) found that densities of more than 15 sponges per m^2 resulted in a significant increase in the number of associated fauna. Deep-sea sponge assemblages have also been discovered at temperate and tropical latitudes, including dense aggregations of *Asconema setubalense* on Mediterranean seamounts and *Sericolophus hawaiicus* sponge grounds at depths of 350-450 m off Kona, Hawaii (Maldonado et al., 2016; Parrish et al., 2015).

Some of the most unusual sponge aggregations are glass sponge reefs formed by sponges in the order Sceptrulophora (class Hexactinellida). The first glass sponge reefs were discovered off the west coast of Canada in the 1980s (Conway et al., 1991). These Canadian reefs have been mapped with a combination of submersible and remotely operated vehicle (ROV) dives, sidescan sonar and sub-bottom profiling and cover an area of approximately 700 km^2 (Conway et al., 2001). They have been described as 'living fossils' similar to sponge reefs that were common during the Mesozoic (Conway et al., 2001). The three main reef-building or dictyonine species are *Heterochone calyx, Aphrocallistes vastus* and *Farrea occa* (Krautter et al., 2001). These sponges have spicules that are fused into a rigid 3D silica framework, which means that the skeletons of dead sponges remain intact and provide a substrate for the attachment of the next generation, leading to reef growth. Reefs typically start as small individual mounds that coalesce and grow into larger structures (Krautter et al., 2001). They can form bioherms (fossilized mounds of dead sponge skeletons encased in a matrix of clay that support living sponges) up to 19 m tall with steep flanks. In other areas they form sponge biostromes (lower profile biogenic constructions) 2-10 m thick over a number of kilometers (Krautter et al., 2001). Canadian sponge reefs have a distinctive acoustic signature due to their high clay content which make them less reflective than the gravelly glacial sediments beneath the reefs (Conway et al., 2001). Cores of sponge reefs show that reef sediments are soft near the surface becoming firm below about 1 m but remain unconsolidated to the base of the reefs (Krautter et al., 2001). Since the discovery of the glass sponge reefs off Canada in the 1980s, more sponge reefs have been discovered in the Strait of Georgia, further north in Portland Canal on the border between Alaska and British Columbia and in Lynn Canal in Alaska (Conway et al., 2005a; Stone et al., 2013).

In 2007, aggregations of reef-building glass sponges were discovered west of Grays Harbor off the coast of Washington State by a team led by Paul Johnson at the University of Washington (Dybas, 2008). Since their discovery, many have wondered whether these aggregations form glass sponge reefs similar to those found in British Columbia (BC) and Alaska (Dybas, 2008). If they do form bioherms these would be the southernmost reefs of this kind. Alternatively, they may be more similar to hexactinellid "sponge gardens" found in BC where dense populations of glass sponges occur attached to hard substrates (Marliave et al., 2009). Another distinctive characteristic of the Grays Canyon sponge aggregation is that it is located close to methane seeps raising the possibility that methanotrophic bacteria might be an important food source (Salmi et al., 2011). Despite its unusual features, the ecology of this sponge aggregation is relatively unknown. Sources of information on glass sponge distributions in this region include early collections of the steamer *Albatross* (Schulze, 1899), species lists compiled in the 1930s and 2000s (Laubenfels, 1932; Lee et al., 2007) and the West Coast Groundfish Bottom Trawl Survey (Clarke et al., 2015), however, detailed information on hexactinellid distributions and ecology remains scarce. The main aims of the present study are to: i) make a preliminary assessment of whether the glass sponges at this site form reefs, ii) characterize the sponge assemblages at Grays Canyon in terms of species composition, distribution and abundance, and iii) evaluate their potential importance as fish and spot-prawn habitats.

2. Methods

2.1 Site description

The study site was located offshore of Grays Harbor, a large coastal plain estuary that consists of multiple channels surrounded by mud and sand flats. Surveys were focused on the continental shelf near Grays Canyon where the glass sponge aggregations were first observed in 2007, at a depth of around 150 m (fig. 1). The continental shelf where the sponge aggregation is located is an accretionary wedge formed on the North American

Plate from sediments scraped off the subducting Juan de Fuca Plate and sediments in this area range in age from the Miocene to Pliocene (Ritger et al., 1987). A major source of modern sediments is the Columbia River plume (Twichell et al., 2010). Methane seep sites have been described along the Oregon and Washington continental margins including an actively venting methane seep at 150 m depth near Grays Canyon (Collier and Lilley, 2005; Salmi et al., 2011).

The oceanographic currents in this region are driven by strong alongshore winds. The California Current System flows southward from the shelf break to approximately 1000 km from the coast, while the California Undercurrent flows northward over the continental slope at a depth of 100-400 m (Hickey and Banas, 2003). Seasonal coastal upwelling in spring and summer brings colder, saltier, nutrient-rich (nitrates and phosphates) waters to the continental shelf and to the ocean surface. Water column properties measured in 2007 revealed elevated methane concentrations in this area (Salmi et al., 2011).

2.2 Geophysical survey and ROV sample collections

In 2016, multibeam surveys and high-resolution seismic sub-bottom profiling of the study area were carried out by the Exploration Vessel (E/V) *Nautilus* using the hull-mounted Kongsberg EM-302 multibeam and Knudsen 3260 Chirp sonars. In addition, the E/V *Nautilus* collected substrate and sponge samples via its *Hercules* remotely operated vehicle (ROV). Sample collection was directed using the live video telepresence feed. Samples of all the most common sponges were collected and sent to the Royal British Columbia Museum in Canada for identification.

2.3 Benthic surveys

Surveys were carried out from 20-23 September 2010 from Oregon State University's research vessel (R/V) *Pacific Storm*. Images of the study area were collected at five sites over three days using a SeaBed-type bottom-tracking Autonomous Underwater Vehicle

(AUV) that was deployed from the *Pacific Storm* (fig. 1). Five dives were carried out at depths of approximately 140 to 170 m (fig. 1). The second dive was unsuccessful so this dive was excluded from the analysis.

The AUV was equipped with several sensors that either aided in vehicle navigation and subsurface communication or collected environmental data. Navigation is an inertial system integrating a suite of sensors that precisely and accurately measure depth, altitude and relative speed and direction over the sea floor. Altitude and relative speed are measured by a 1200 kHz Navigator Doppler Velocity Log (Teledyne RD Instruments); heading, pitch and roll are measured by an OCTANS fiber optic gyrocompass and motion sensor (iXblue); and depth is determined by a Series 8000 Digiquartz® depth sensor (Paroscientific, Inc.). Range and bearing of the AUV relative to the support vessel were provided by a TrackLink 1510 medium accuracy ultrashort baseline acoustic tracking system (LinkQuest, Inc.). Once the AUV was at its target altitude above the sea floor, the live USBL data stream was used to position the vehicle as close as possible to the intended dive start point. Subsurface communication and telemetry data were provided by the WHOI 256008 acoustic micromodem and surface communication by a FreeWave FGR-115 RCRF radio modem. All topside navigational data streams including vessel GPS and heading were integrated in real time and logged using custom software written for Matlab (Simulink, Inc.). Salinity, temperature and pressure were collected using a model 49 FastCat CTD (Seabird Electronics, Inc.) mounted on the AUV.

To image the seafloor, the AUV was equipped with two 5 megapixel Prosilica GigE digital cameras (12 bit dynamic range) and a xenon strobe synced with the cameras. Each camera captured approximately the same field of view, but one of the cameras was angled straight down and the other pointed forward at an angle of 30°. Two downward parallel lasers (10 cm apart) were used to estimate the size of organisms in photographs. The AUV was programmed to take photographs once every 4.5-5 seconds from a consistent altitude of 3 m above the seafloor. Several pre-programmed survey patterns were used depending on the area to be explored. Images were downloaded after each dive and color corrected prior to analysis.

2.4 Image analysis

Images from the downward camera were used for organism counts, whereas images from the angled camera were used to confirm identifications. In total, 9722 images were collected with the downward camera. At the image rate used on the dives, some photographs overlapped so these were excluded from the analysis resulting in a dataset of 3185 non-overlapping images from the downward camera. All fishes were identified to the lowest possible taxonomic level and counted. The only invertebrates counted were sponges, spot-prawns and corals. All sponges were assigned an ID code, which were considered operational taxonomic units (OTUs) for this study (see supplementary material, S1). The habitat in each image was also classified using a two-code system by type of substratum as described in Greene et al. (1999). The observer selected the two most important substrate types in terms of surface area for each image (substrate categories: rock ridge, boulder, cobble, pebble, gravel, flat rock, sand, mud). The two codes were then aggregated into two broad habitat categories: soft (which included mud and sand) and mixed (which included various proportions of mud, gravel, pebble, cobble, boulder and rock). To determine if fish were associated with sponges at a fine scale (< 1 m), we also recorded where each fish was found as i) touching, ii) near (less than one fish length away) or iii) away (over one fish length away) from a sponge.

2.5 Statistical analysis

Analyses were performed in R version 3.3.2 (R Core Team 2016). Multivariate analyses were based on resemblance matrices calculated using Bray-Curtis similarity coefficients. Non-metric multidimensional scaling (MDS) was used to visualize differences in sponge assemblage composition on mixed and soft substrates (a dummy variable was used as a large number of samples had low counts and a Wisconsin double standardization was applied so that the similarities did not just reflect differences in the most abundant OTUs). A one-factor permutational multivariate analysis of variance (PERMANOVA) was used to test for differences in sponge assemblage composition between substrates

(Anderson, 2001). A similarity percentage (SIMPER) analysis was used to identify the species that contributed most to differences between sponge assemblages. Generalized linear models (GLM) were used to test for significant differences in sponge abundance on soft and mixed substrates and to examine the relationships between fish and sponge abundance. Gaussian, Poisson and negative binomial distributions were trialed and the results are presented for the distribution that resulted in the lowest Akaike's Information Criterion (AIC). Image area was included as an offset term in the models to account for slight differences in the area of each photograph. Odds ratios were also used to determine if fish and spot prawns were associated with sponges. The odds of observing a target taxon in the same image as a sponge were compared to the odds of observing it in images that did not contain sponges (see Stone, 2014 for a more complete description of the method).

3. Results

3.1 Geophysical survey

Multibeam bathymetric data show the presence of mounds in the study area that are similar to the shape of bioherms observed off British Columbia (fig. 4 A). However, sub-bottom profiler data show the complex seafloor morphology of the Grays Canyon sponge site to be controlled by fractured outcrops of folded Pliocene-Quaternary strata that form the limbs of breached and truncated folds (McNeill et al., 1997). Hummocky seafloor ridges/mounds visible in the sub-bottom profiler records at the Grays Canyon site (fig. 4 B), lack the distinctive acoustic signature of the sponge bioherms off British Columbia, where an amorphous acoustically-transparent central mass is encapsulated by strong bounding reflections (Conway et al., 1991; Conway et al., 2005b). The substrate below these ridges/mounds is often poorly resolved in the sub-bottom profiles, but where visible on several lines, they appear to occur where folded strata are truncated at the seafloor. Video footage captured by the *Hercules* ROV revealed sponges growing along several of these low-relief seafloor ridges, which appeared to consist of loose or poorly consolidated material (see fig. 5 c). Using the ROV, attempts were made to take push-core samples of the ledges where the sponges were growing to determine if they were made up of the skeletons of dead glass sponges. However, the ledges were too solid to sample in this way, which indicates that they are unlikely to be sponge bioherms.

3.2 Sponge densities and community composition

Six sponge OTUs were identified from the photographs (see supplementary material S1). These included two dictyonine reef-building glass sponges, *Aphrocallistes vastus* (OTU 1) and *Heterochone calyx* (OTU 2). We also recorded abundant lyssacine glass sponge species (OTU 3) which are non-reef-building glass sponges that do not have a fused skeleton. Analysis of the samples collected in 2016 confirmed that one of the species in OTU 3 was *Rhabdocalyptus dawsoni* also known as the common 'boot sponge'. However, there are a number of species not easily distinguished from *R. dawsoni* in photographs (Leys et al., 2004; Stone et al., 2011), therefore this was considered a species complex. The demosponge *Poecillastra tenuilaminaris* (OTU 4) was common at the Grays Canyon site. OTU 5 could not be identified from the photographs but examination of the samples collected in 2016 revealed that it was a demosponge in the genus *Acarnus* and may be a new species. OTU 6 was a common unidentified encrusting sponge (see supplementary material for images). Finally, there were a large number of unidentified sponges that were mostly small encrusting patches and small tube-shaped sponges (possibly juveniles). These were included in our total sponge count but excluded from the multivariate community analysis.

The sponges that occurred in the highest densities at our study site (excluding the large numbers of small unidentified sponges) were the lyssacine sponges followed by the dictyonine sponge *Heterochone calyx* and the demosponge *Poecillastra tenuilaminaris* (see fig. 2). The maximum density of sponges per 10 m^2 was 133 with a mean of 9.71 ± 0.25 SE per 10 m^2 (see table 1). The mean density of reef-building sponges was 1.43 ± 0.057 SE per 10 m^2 with 1898 observed in total. Sponge assemblage composition was significantly different between mixed and soft bottom substrates (PERMANOVA, pseudo $F = 38.07$, $p < 0.001$). These differences are visible on the nMDS ordination (fig. 3). The results of the SIMPER analysis showed that the species that contributed most to these differences were the lyssacine sponges, *H. calyx* and *P. tenuilaminaris* (table 2). The other sponge groups contributed less than 25 % of the dissimilarity between sponge assemblages on mixed and soft bottom substrates. Sponge abundance was significantly higher on mixed substrates than soft substrates (GLM, $z = -65.12$, $p < 0.001$). Mean sponge abundance on mixed substrates was 19.6 ± 0.48 SE per 10 m^2 compared with 4.04 ± 0.19 SE per 10 m^2 on soft bottom substrates. High sponge densities were observed on rock, boulders, and along low relief sediment covered ridges (see fig. 5).

3.3 Fish and non-sponge invertebrate densities and assemblage composition

In total, 4996 fish were identified belonging to 22 different groups (table 3). Mean fish density was 1.98 ± 0.091 SE per 10 m^2. The most abundant group were rockfish with a mean density of 1.63 ± 0.09 SE per 10 m^2 and a maximum of 35 individuals observed in a single image. The rockfish assemblage (genus *Sebastes*) was dominated by *S. helvomaculatus* (rosethorn rockfish), *S. elongatus* (greenstriped rockfish) and a large number of rockfish species that could not easily be distinguished from each other in the photographs (*S. zacentrus*, *S. wilsoni*, *S. proriger, S. diploproa, S. alutus*) and juveniles. The second most abundant group of fish was flatfishes (mean density = 0.18 ± 0.012 SE per 10 m^2) which included *Lyopsetta exilis* (slender sole), *Glyptocephalus zachirus* (rex sole) and *Microstomus pacificus* (dover sole). We also observed *Ophiodon elongatus* (lingcod), *Raja rhina* (longnose skate), *Hydrolagus collieri* (spotted ratfish), *Eptatretus stoutii* (Pacific hagfish) and unidentified Cottidae (sculpins), Agonidae (poachers) and Zoarcidae (eelpouts). The non-sponge invertebrates enumerated were corals and spot prawns (*Pandalus platyceros*). The corals included unidentified sea whips (order Alcyonacea) and two types of hard corals, unidentified small branching corals and cup corals (order Scleractinia). Corals were much less abundant than sponges at this site with a mean density of 0.19 ± 0.018 SE per 10 m^2 (n=264). Spot-prawn density was 0.14 ± 0.014 SE per 10 m^2 with a maximum of six observed in a single image.

3.4 Fish and spot-prawn associations with sponges

In each case, the best fitting GLM models (lowest AIC) of species counts were based on negative binomial distributions (table 4). This was because most of our images had low counts but some had high abundances. This is not uncommon for biological count data as species often have patchy distributions and are well described by the negative binomial distribution which allows for the variance of the data to be greater than the mean (Bliss and Fisher, 1953). Total fish abundance was higher in areas with greater sponge abundance (GLM, % variation explained = 19%). Rockfish abundance (GLM, % variation explained = 25%) was more strongly associated sponge abundance than total fish abundance was related to sponge abundance. The abundance of fish other than rockfish was lower in areas with greater sponge abundance, however, this relationship was not strong (GLM, % variation explained = 2%). Spot-prawn abundance was higher in areas with greater sponge abundance.

Of the groups that we examined, spot prawns were the most strongly associated with sponges (odds ratio = 15.14), and sponges were present in 94% of the images with spot prawns (see table 5). Rockfish were also associated with sponges (odds ratio = 5.75), and sponges were observed in 82% of photographs that contained rockfish. Flatfish (odds ratio = 0.69) and “other fish” (odds ratio = 0.98) showed lower frequencies of sponge association. However, sponges were present in 69% and 41% of images with “other fish” and flatfish respectively. Only 1% of flatfish were observed touching or within one fish length of a sponge compared with 16% of “other fish” and 39% of rockfish.

4. Discussion

The primary aims of this research were to investigate whether sponges form reefs at Grays Canyon, characterize the sponge assemblages at this location and begin to determine their role as habitat for commercial species.

4.1 Comparison of the Grays Canyon sponge ground to known glass sponge reefs

The multibeam-derived bathymetry of the Grays Canyon site shows mounds and hummocky features that look similar to the sponge reefs in areas further north, however, the high-resolution seismic profiling suggests that these are unlikely to be bioherms and may be the result of different processes. Canadian sponge reef growth is due to a combination of processes including the trapping of suspended sediments by sponges and the attachment of juveniles to the skeletons of dead sponges resulting in the formation of mounds (Krautter et al., 2006). The reefs also typically occur along glacial troughs that cross the continental shelf providing the substrate for the initial attachment of reef forming sponges (Krautter et al., 2006). As a result, the acoustic signature of the glass sponge reefs in Canada is quite distinctive (Conway et al., 2001) with a well-defined top and bottom with acoustically transparent material in between. In contrast, the seismic profiles from the Grays Canyon site indicate that the mounds are outcrops or boulders, which is consistent with the habitat features we observed in the ROV video.

In terms of species composition, the Grays Canyon sponge assemblage shared similarities with known sponge reefs but sponge densities were lower. We recorded two of the three known species of reef-building sponges (*Heterochone calyx* and *Aphrocallistes vastus)* at Grays Canyon. We did not observe the third reef building species, *Farrea occa,* a species that is present on Canadian reefs in the Hecate Strait (Conway et al., 2001) but has not been recorded on the sponge reefs in the Strait of Georgia (Leys et al., 2004). We observed abundant lyssacine sponges at the Grays Canyon site, which are also commonly present on Canadian reefs. Conway et al. (2005b) recorded *Rhabdocalyptus dawsoni*, *Staurocalyptus dowlingi*, *Acanthascus platei, A. cactus* and the demosponge *Poecillastra tenuilaminaris* during their surveys of sponge reefs in the Queen Charlotte Basin. Hexactinellid densities at the Grays Canyon site appear lower than those on the Canadian sponge reefs. At sponge reefs in the Strait of Georgia, *A. vastus* and *H. calyx* can grow in very dense patches within a reef where it is difficult to distinguish individual sponges so the density of live oscula has been used as indicator of sponge density (Chu and Leys, 2010; Chu et al., 2011). The densities of live oscula on these reefs ranges from 17.4 per m^2 at Galiano reef to 5.5 per m^2 at Howe reef (Chu and Leys, 2010). The maximum density of reef-building sponges that we observed at the Grays Canyon site was 24.75

individuals per 10 m^2 with a mean of 1.43 ± 0.057 SE per 10 m^2. When compared with sponge gardens in British Columbian fjords the densities at Grays Canyon are lower than at Jervis Inlet and Howe Sound where densities reach up to 250 per 10 m^2 and 60 per 10 m^2 respectively but higher than at Saanich Inlet where the density is less than 8 per 10 m^2.

The reasons why glass sponges do not seem to form reefs at Grays Canyon are currently unclear but may be related to differences in environmental factors. The local sedimentation regime appears to play a key role in sponge reef formation. Sediment is required to cement reef structures but high sedimentation rates can have a number of detrimental effects on sponges including reducing their pumping rates, lowering their reproductive output and reducing the success of young recruits (Gerodette and Flechsig, 1979; Roberts et al., 2006; Maldonado et al., 2008). Sedimentation rates on sponge reefs in the Queen Charlotte basin are low and most of the sediments in the reef framework are trapped by the reef sponges (Conway et al., 2005b). We expect sedimentation rates for Grays Canyon to be higher because of the influence of the Columbia River plume, an important sediment source at this location (Hickey and Banas, 2003; Nittrouer, 1978) which could explain the lack of bioherms. However, reefs do occur on Fraser Ridge and in Howe Sound where the Fraser River delivers large amounts of sediment into the water column so the extent to which sedimentation controls sponge reef distributions is not fully understood.

4.2 Characterizing the Grays Canyon sponge ground

Sponges were the dominant sessile invertebrates at Grays Canyon with large individuals concentrated along ledges, ridges, boulders and exposed bedrock. The sponge grounds at this location appear similar to hexactinellid “sponge gardens” in British Columbia where numerous sponges also occur on exposed bedrock, gravel substrate, cliffs and ledges (Marliave et al., 2009). The most abundant group that we identified were the non-reef-forming lyssacine sponges. Since lyssacine species are difficult to distinguish in photographs, we did not estimate density for individual species. However, samples taken in 2016 confirmed the presence of the *Rhabdocalyptus dawsoni,* a common species that occurs from Alaska to southern California. The reef-building glass sponge species, *Heterochone calyx* and *Aphrocallistes vastus,* were among the most common and largest species that were observed. One of the most common demosponges that we recorded was *Poecillastra tenuilaminaris,* a relatively common species in the Bering Sea and eastern Gulf of Alaska and thought to have a circumboreal distribution (Stone et al., 2011). Preliminary examination of the unidentified species of *Acarnus* indicates that it differs from the known 26 species of the genus. It also represents a new depth extension for the genus, which is usually considered a shallow water genus, from 91 m to 152 m (Bruce Ott, personal communication, July 27 2017).

There are a number of environmental factors that could contribute to the abundance of large hexactinellid sponges at Grays Canyon. The distribution of hexactinellids is influenced by the amount of dissolved silica in seawater. High abundances of glass sponges are found in regions with high dissolved silica, including the Antarctic and northeast Pacific. Leys et al. (2004) suggest that silica concentrations below 30 to 40 μM could limit glass sponge distributions. Silica concentrations measured near the seabed at the Grays Canyon were well above this threshold (55-60 μM, Salmi et al., 2011), and could contribute to the large numbers of glass sponges observed. Increased nutrient availability in the proximity of Grays Canyon could also contribute to high glass-sponge abundance. Deeper water sources are drawn upwards when a canyon is present than in areas with a uniform slope (Connolly and Hickey, 2014). Upwelling of nutrient rich water is enhanced in areas where the continental shelf is intersected by canyons. Finally, the presence of methane seeps also raises the possibility that sponges derive some of their nutrition from methane-oxidizing bacteria at this site. Bacterial associates are generally less common in glass sponges than demosponges (Leys et al., 2008) and communities associated with methane seeps are typically dominated by bivalves in the families Mytilidae and Vesicomyidae (Sibuet and Olu, 1998) and not by sponges. However, large numbers of sponges in the genus *Cladorhiza* that contain methanotrophic bacteria have been recorded at cold seeps on mud volcanoes in the Barbados Trench (Olu et al., 1997; Vacelet et al., 1996). Of the species recorded at Grays Canyon, previous work on the ultrastructure and feeding of *Rhabdocalyptus dawsoni* have not found evidence of bacterial symbionts (Mackie & Singla, 1983, Yahel et al., 2007). Feeding experiments on *Aphrocallistes vastus* from British Columbian fjords also found no evidence of symbiotic bacteria, however, bacteria have been observed along the inner surface of the collar microvilli of this species (Leys et al., 2008). Further research is necessary to determine whether methanotrophic symbionts are present in the tissues or spicule coats of the sponges in the Grays Canyon area and if this contributes to the large size and abundance of glass sponges at this location.

4.3 Associations with fish and invertebrates

Sponges can provide habitats, protection from predation, feeding opportunities and nursery grounds to sponge associates (Bell, 2008). The internal canals of sponges are used by some invertebrates as microhabitats (e.g. polychaetes and ophiuroids) while others (e.g. bryozoans and ascidians) use sponges as settlement substrates. Numerous marine phyla have been found associated with sponge grounds (Klitgaard and Tendal, 2004; Marliave et al., 2009; Freese and Wing, 2003; Beazley et al., 2013). We recorded a positive relationship between rockfish and sponge abundance at Grays Canyon. Chu and Leys (2010) studied the fauna associated with three sponge reefs in the Strait of Georgia and recorded abundant rockfish on the sponge reefs. Glass sponges are also known to provide important habitats for juvenile rockfishes. Freese and Wing (2003) found that *Aphrocallistes vastus* sponges were an important habitat for juvenile rockfishes (*Sebastes* sp.) in the Gulf of Alaska and suggested that juveniles associated with sponges benefited from increased predator avoidance. Rockfishes appear to be facultative rather than obligate sponge associates as they also occur in areas without sponges, similar to many species that are associated with deep-sea sponge grounds (Beazley et al., 2013; Klitgaard and Tendal, 2004). The increased numbers of rockfish observed in the presence of sponges could be due to large sponges providing physical structure at this site (Buhl-Mortensen et al., 2010; Du Preez and Tunnicliffe, 2011). The availability of hard substrates tends to decrease with depth so increasing habitat complexity is likely to be an important functional role of glass sponges in deep-sea environments.

Our finding that spot prawns (*Pandalus platyceros*) were positively associated with glass sponges has also been observed in other areas. In the Strait of Georgia, Chu and Leys (2010) found that total crustacean abundance was significantly higher in areas where glass sponges were present and that spot prawns were one of the most abundant crustaceans on glass-sponge reefs. Spot prawns are known to be relatively abundant around Grays Canyon, which is one of the primary commercial spot-prawn fishing grounds in the coastal fishery (Wargo et al., 2013). The positive association between spot prawns and glass sponges could be due to the provision of habitat, which increases spot-prawn survival by providing foraging opportunities and shelter from predators. Fishing activity could potentially affect the sponge ground as glass sponges are vulnerable to physical damage (Conway et al., 2001), although not all fishing methods are equally deleterious. The spot-prawn fishery currently operates using pots, which cause less damage to sessile benthic invertebrates than bottom trawling methods (Heifetz et al., 2009). In addition to the spot-prawn fishery, a limited entry groundfish fishery has operated and continues to operates in this region. There are no permanent protections in place that prohibit the use of bottom tending fishing gears but trawl effort at the study site is currently lower than nearby areas.

5. Conclusions

Dense aggregations of large dictyonine sponges thrive on the continental shelf adjacent to Grays Canyon. They do not appear to form glass-sponge reefs at this location but are associated with large numbers of rockfish and spot prawns. Environmental conditions that are likely to favor the development of large glass sponges at this site include, high levels of dissolved silica, the availability of hard substrates for attachment, strong upwelling currents that are enhanced by the presence of Grays Canyon, and possibly methane venting. Key areas for future research include mapping the extent of the sponge grounds, further characterization of the community associated with sponges, collecting additional samples to identify unknown sponges, improved characterization of local environmental conditions including sedimentation rates and investigation of the influence of high methane levels on glass sponges.

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We thank Jeremy Taylor, Chris Murphy, Russell Haner and the crew onboard Oregon State University's Vessel, R/V *Pacific Storm* for their assistance at sea during the 2010 cruise. Thanks also to the scientists and crew of the E/V *Nautilus* and the operators of the ROV *Hercules* for the sub-bottom profiling and sample collections carried out in 2016. Thank you to Melanie Johnson for contributing to the image analysis and to Meredith Everett and Eric LaHood for their assistance shipping the sponge samples. This work was supported by Ocean Exploration Trust Inc.; NOAA Ocean Exploration and Research Program; and NOAA NMFS Deep Sea Coral Research and Technology Program. Any use of trade, product, or firm names is for descriptive purposes only and does not imply endorsement by the U.S. Government.

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Tables

Table 1 Total number of each sponge group observed in the 13687 m^2 survey area and the maximum and mean densities of sponges (# per 10 m^2).

	All sponges	**Dictyonine sponges (*A. vastus* + *H. calyx*)**	***Aphrocallistes vastus***	***Heterochone calyx***	***Lyssacine sponges***	***Poecillastra tenuilaminaris***	***Acarnus sp.***	***OTU 6 (white encrusting sponge)***	***Unidentified sponges***
Total number observed	13283	1898	*599*	*1360*	*1430*	*1090*	*197*	280	8327
Max per 10 m	132.61	24.75	18.86	20.25	32.1	22.8	8.93	18.7	78.26
Mean (± SE) per 10 m2	9.71 ± 0.25	1.43 ± 0.057	0.39 ± 0.024	0.99 ± 0.043	1.046 ± 0.052	0.8 ± 0.042	0.14 ± 0.012	0.204 ± 0.02	6.09 ± 0.17

Table 2 Results from SIMPER analysis comparing sponge assemblages on mixed and soft substrates. Densities of each sponge group on soft and mixed substrates are also reported.

Taxonomic group	**Average dissimilarity**	**%Contribution to dissimilarity**	**Cumulative contribution %**	**Mean (± SE) per 10 m^2 on soft substrates**	**Mean (± SE) per 10 m^2 on mixed substrates**
Lyssacine sponges	0.21	28	28	0.44 ± 0.04	2.11 ± 0.12
Heterochone calyx	0.2	26	54	0.22 ± 0.022	2.35 ± 0.099
Poecillastra tenuilaminaris	0.16	22	76	0.19 ± 0.021	1.85 ± 0.1
Aphrocallistes vastus	0.1	12	88	0.12 ± 0.015	1 ± 0.062
Acarnus sp.	0.05	6	94	0.098 ± 0.013	0.22 ± 0.025
OTU 6 (white encrusting sponge)	0.04	6	100	0.0057 ± 0.003	0.55 ± 0.053

Table 3 Total numbers of fishes observed at the Grays Canyon site and mean densities (# per 10 m^2).

Group	Family	Scientific name	Common name	Mean (± SE) per 10 m^2	Total number observed
	Agonidae		Poachers	0.035 ± 0.0056	48
	Chimaeridae	*Hydrolagus colliei*	Spotted ratfish	0.0022 ± 0.0013	3
	Cottidae		Sculpins	0.023 ± 0.004	31
	Hexagrammidae	*Ophiodon elongatus*	Lingcod	0.02 ± 0.0038	27
	Myxinidae	*Eptatretus stoutii*	Pacific hagfish	0.0029 ± 0.0015	4
	Pleuronectidae	*Lyopsetta exilis*	Slender sole	0.091 ± 0.0084	125
	Pleuronectidae	*Microstomus pacificus*	Dover sole	0.031 ± 0.0048	43
	Pleuronectidae	*Eopsetta jordani*	Petrale sole	0.0067 ± 0.0022	9
	Pleuronectidae	*Glyptocephalus zachirus*	Rex sole	0.038 ± 0.0053	52
	Rajidae	*Raja rhina*	Longnose skate	0.0044 ± 0.0018	6
	Sebastidae	*Sebastes aleutianus*	Rougheye rockfish	0.00073 ± 0.00073	1
	Sebastidae	*Sebastes alutus*	Pacific ocean perch	0.0015 ± 0.0011	2
	Sebastidae	*Sebastes babcocki*	Redbanded rockfish	0.00073 ± 0.00073	1
	Sebastidae	*Sebastes diploproa*	Splitnose rockfish	0.012 ± 0.0033	17
	Sebastidae	*Sebastes elongatus*	Greenstriped rockfish	0.19 ± 0.012	255
	Sebastidae	*Sebastes flavidus*	Yellowtail rockfish	0.003 ± 0.0015	4
	Sebastidae	*Sebastes helvomaculatus*	Rosethorn rockfish	0.27 ± 0.015	367
	Sebastidae	*Sebastes proriger*	Redstripe rockfish	0.02 ± 0.0073	26
	Zoarcidae		Eelpouts	0.00075 ± 0.00075	1
Unidentified fishes				0.079 ± 0.0083	109
Unidentified flatfishes				0.013 ± 0.0033	18
Unidentified rockfishes				1.14 ± 0.085	1561
All rockfishes				1.63 ± 0.09	2234
All fishes				1.98 ± 0.091	2710

Table 4 Summary of the GLM results showing the nature of relationship (+/-), amount of variability explained (%) and Akaike's Information Criterion (AIC) (negative binomial with a log link used for all models).

Response variable (# per image)	Predictor variable (# per image)	AIC	Variability explained (%)	Parameter estimates (95% CI in brackets)	Relationship
Fish (all species)	Sponges	7284	19%	Intercept: -5.16 (-5.25, -5.08) Sponges: 0.11 (0.09, 0.12)	positive
Rockfish	Sponges	6025	25%	Intercept: -5.67 (-5.78, -5.57) Sponges: 0.14 (0.13, 0.16)	positive
Other fish	Sponges	2812	2%	Intercept: -6.03 (-6.15, -5.92) Sponges:-0.05 (-0.07, -0.03)	negative
Spot prawns	Sponges	1296	15%	Intercept: -7.96 (-8.24, -7.7) Sponges: 0.13 (0.1, 0.16)	positive

Table 5 Odds ratios for fish and spot prawns, the number of images where each taxon was observed, the percentage of images where sponges were also present and the percentage of individuals observed near or touching sponges. The total number of individuals and densities are also reported.

Taxonomic Group	Odds ratio	Number of images where each taxon was observed	% of images where sponges were also present (# of images shown in brackets)	% of individuals observed touching or near sponges	Total number of individuals observed	Mean per 10m2 (SE)
All rockfishes	5.75	883	82 (n=728)	39	2234	1.63 0.09
All flatfishes	0.69	232	41 (n=96)	1	247	0.18 0.0012
Other fish	0.98	207	69 (n=143)	16	229	0.17 0.0012
Spot prawns	15.14	140	94 (n=131)	NA	193	0.14 0.0014

List of figures

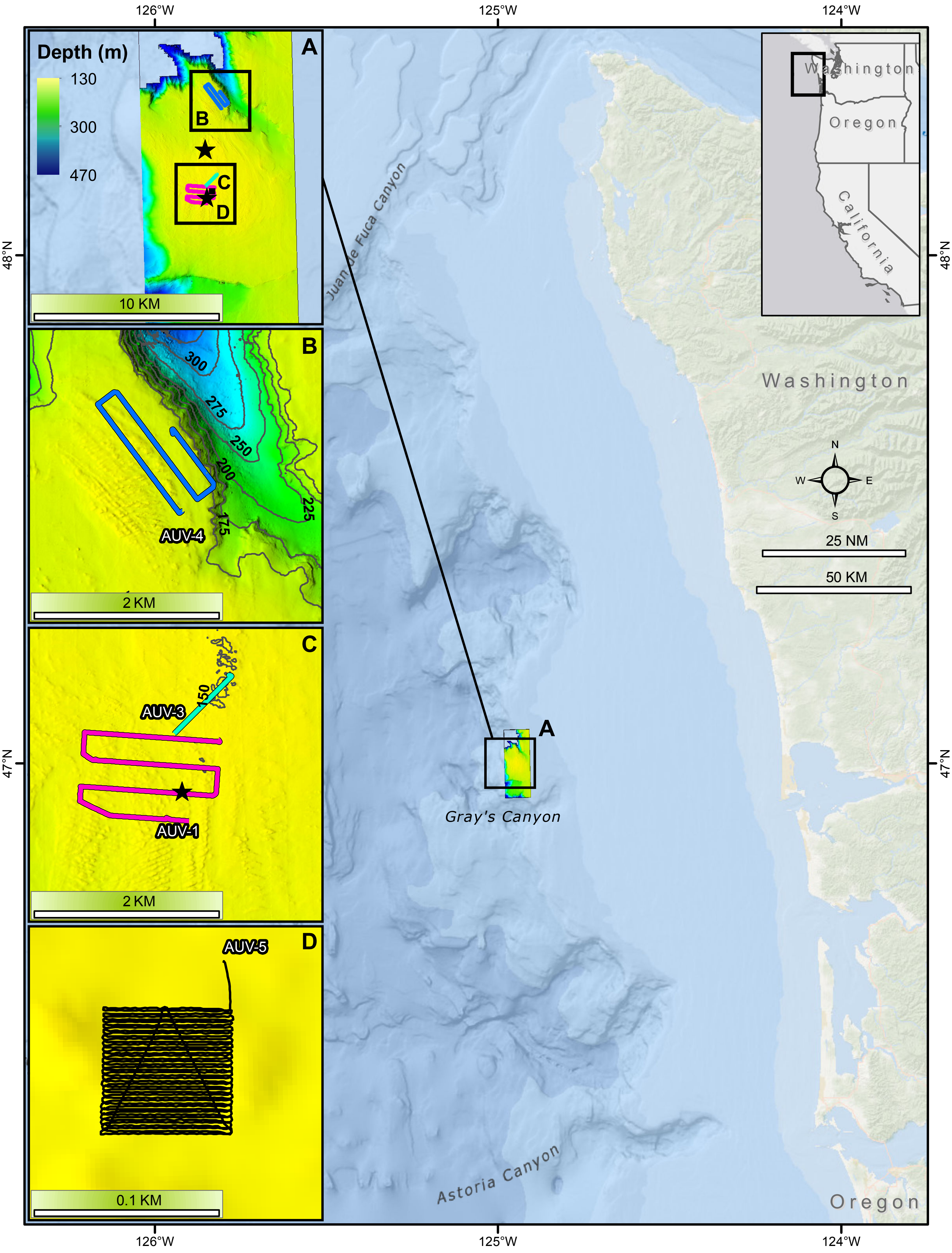
Fig. 1. Location of the study area near Grays Canyon, off the coast of Washington state. Inset A) shows the main areas where the AUV dives were carried out. Insets B), C), and D) show the tracks of the five dives (AUV 1 to AUV 5) over multibeam sonar derived bathymetry of the seafloor (data sources: Oregon State Univ. Active Tectonics and Seafloor Mapping Lab; Environmental Systems Research Institute, Inc.). The track of fifth dive (AUV 5) is unlike the others because it was used to create a photo mosaic, however, for the purposes of this study only non-overlapping images were used. Black stars show sample collection sites.

Fig. 2. Mean densities (# per 10 m^2) of observed sponge taxa.

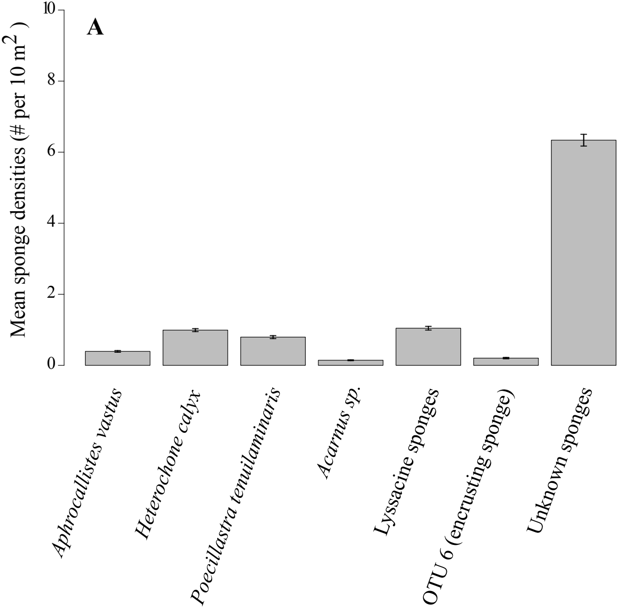
Fig. 3. Non metric MDS ordination (stress = 0.19) of the differences in sponge assemblage composition on hard and soft bottom substrates. The distance between the points on the ordination is related to the similarity in sponge assemblage composition in the samples (points closer together are more similar than those further apart). The position of the names on the ordination represent weighted average scores for each sponge group based on the sample scores from the ordination and species abundances in the original data.

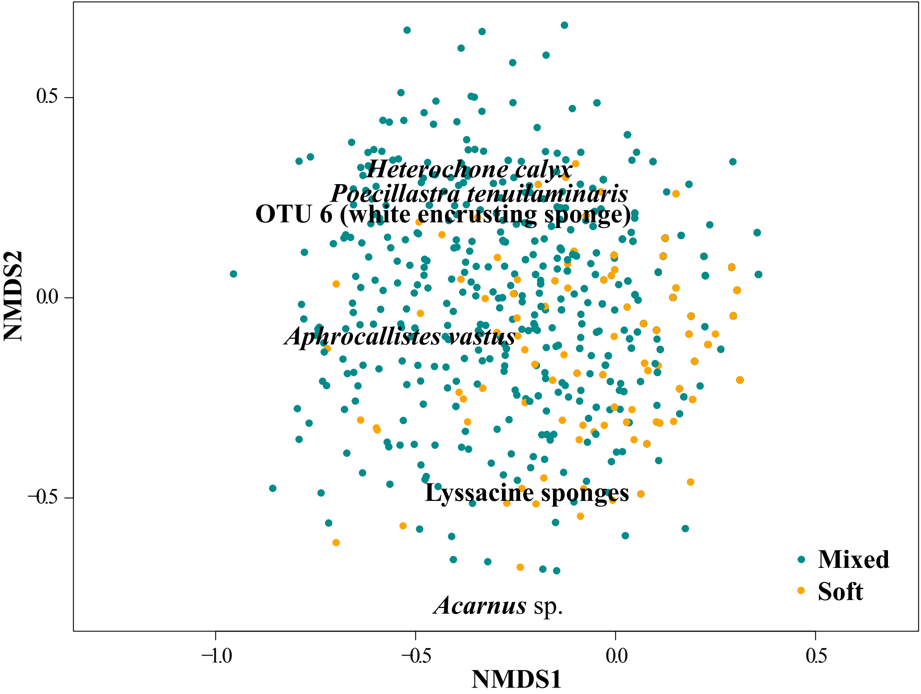
Fig. 4. A) Multibeam-derived bathymetry of part of the study site where rounded elongate features were identified that could correspond to the location of sponge bioherms (circled area). The dotted lines are sub-bottom profile lines collected by the E/V Nautilus and areas in blue correspond to where the features appear on the sub-bottom profile. The red lines are areas we interpret to be exposed sediment layers/fractures. B) Part of sub-bottom profile line 6 showing the elongated, rounded mounds (circled in A) atop acoustically transparent substrate and folded Pliocene-Quaternary sediments to the northeast of the sponge site.

Fig. 5. Images of the different types of substrate where glass sponges were observed and common sponge species A) Exposed rock B) Boulders C) Sediment-covered ledges D) Rockfish inside the osculum of *Aphrocallistes vastus* E) Spot prawn and rockfish associated with *Heterochone calyx.*

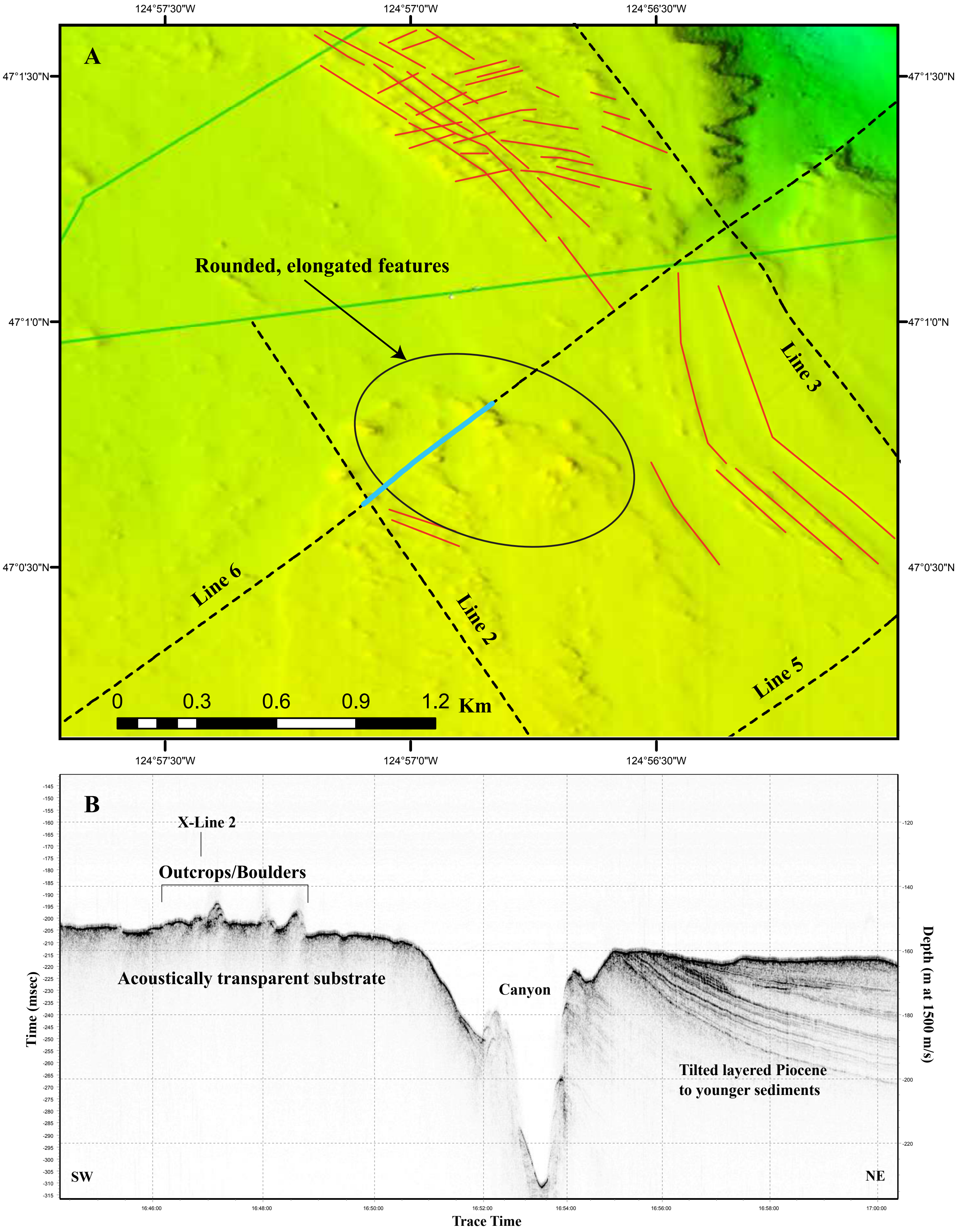


126°W
125°W
124°W
48°N
47°N
Depth (m)
130
300
470
A
B
C
D
10 KM
300
275
250
200
225
175
AUV-4
2 KM
150
AUV-3
AUV-1
2 KM
AUV-5
0.1 KM
Juan de Fuca Canyon
Gray's Canyon
Astoria Canyon
Washington
Oregon
California
Washington
Oregon
N
W
E
S
25 NM
50 KM

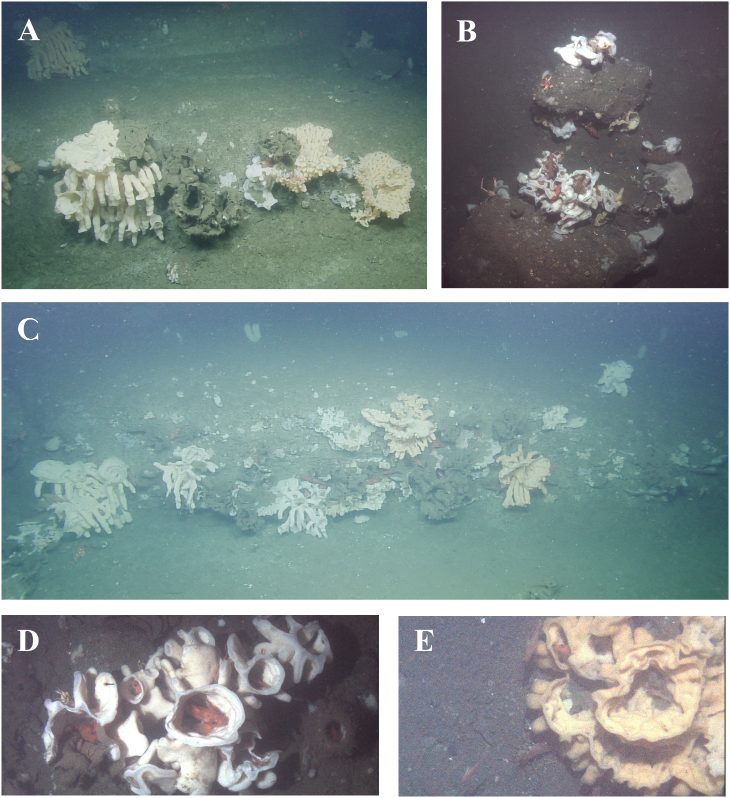

A
Mean sponge densities (# per 10 m^2)
10
8
6
4
2
0
Aphrocallistes vastus
Heterochone calyx
Poecillastra tenuilaminaris
Acarnus sp.
Lyssacine sponges
OTU 6 (encrusting sponge)
Unknown sponges



Heterochone calyx
Poecillastra tenuilaminaris
OTU 6 (white encrusting sponge)
Aphrocallistes vastus
Lyssacine sponges
Acarnus sp.
Mixed
Soft
NMDS2
NMDS1
0.5
0.0
−0.5
−1.0
−0.5
0.0
0.5



A
124°57'30"W
124°57'0"W
124°56'30"W
47°1'30"N
47°1'0"N
47°0'30"N
Rounded, elongated features
Line 3
Line 6
Line 2
Line 5
0
0.3
0.6
0.9
1.2
Km
B
X-Line 2
Outcrops/Boulders
Acoustically transparent substrate
Canyon
Tilted layered Piocene
to younger sediments
Time (msec)
Depth (m at 1500 m/s)
SW
NE
Trace Time


A
B
C
D
E