

The dorid nudibranchs *Peltodoris lentiginosa* and *Archidoris odhneri* as predators of glass sponges

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Abstract. The dorid nudibranchs *Peltodoris lentiginosa* and *Archidoris odhneri* were found on glass sponges (Porifera, Hexactinellida) during remotely operated vehicle surveys of three reefs in the Strait of Georgia, British Columbia, Canada. Eight nudibranchs were sampled from 2009 to 2011. Identification of sponge spicules found in their gut and fecal contents confirmed the nudibranchs to be predators of the reef-forming hexactinellids *Aphrocallistes vastus* and *Heterochone calyx*, as well as of the demosponge *Desmacella austini*, which encrusts skeletons of the glass sponges. Four of five nudibranchs dissected for gut content analysis had stomachs containing sponge spicules. Counts from high-definition video footage taken during systematic surveys done in 2009 showed that nudibranchs were found in only two of the three glass sponge reefs. These data provide the first quantitative evidence of a molluscan predator on glass sponges found outside of Antarctica, and establish the first trophic link between glass sponges and their associated community of animals in a sponge reef ecosystem on the western Canadian continental shelf.

Additional key words: hexactinellid, Porifera, *Aphrocallistes*, *Heterochone*, *Desmacella*

Glass sponges (Porifera, Hexactinellida) have important ecological roles in creating benthic habitats (Dayton et al. 1974; McClintock et al. 2005; Chu & Leys 2010). They are usually found in deeper waters (>200 m) and are heavily silicified, with 80–95% of their body volume composed of inorganic spicules (Barthel 1995; Whitney et al. 2005; Chu et al. 2011). Because of the high content of siliceous skeleton and low amounts of living tissue found in glass sponges, they are of relatively low mass-specific nutritional value, and thus few animals are expected to feed on them (Barthel 1995). In the Strait of Georgia (SOG), Canada, populations of the hexactinellids *Aphrocallistes vastus* SCHULZE 1887 and *Heterochone calyx* SCHULZE 1886 form giant reefs covering kilometers of the seafloor (Conway et al. 2007; Chu & Leys 2010), with the demosponge *Desmacella austini* LEHNERT 2005 existing as an epizoid sponge on the skeletons of *H. calyx* (Lehnert et al. 2005). The first of these glass sponge reefs were discovered in 1988 in Hecate Strait (Conway et al. 1991), and 12 additional reefs were discovered in the SOG from

2001 to 2007 (Conway et al. 2004, 2007). To date, such reefs are only found on the western Canadian continental shelf.

Although a diverse assemblage of megafauna is found within a glass sponge reef, the basic predator–prey interactions within the reef community have not yet been addressed. Within the reef community, only crustaceans and fish are normally seen in contact with the live glass sponges (Chu & Leys 2010). Conspicuous soft-bodied inhabitants, such as sea stars and anemones, are usually found on the skeletons of dead sponges and on small patches of bare substrate rather than on the live sponges (Chu & Leys 2010). However, during detailed surveys of three glass sponge reefs (Fig. 1a) in the SOG with the remotely operated vehicle (ROV) remote operated platform for ocean sciences (ROPOS), we discovered the dorid nudibranchs *Peltodoris lentiginosa* MILLEN 1982 (Fig. 1b) and *Archidoris odhneri* MACFARLAND 1966 (Fig. 1c) on the two reef-forming glass sponges *A. vastus* and *H. calyx* at two of the reefs. Since many nudibranchs feed on demosponges, we hypothesized that the nudibranchs were predators of the reef-forming glass sponges. We sampled individuals of *P. lentiginosa* and *A. odhneri* and examined the spicule fragments in their fecal

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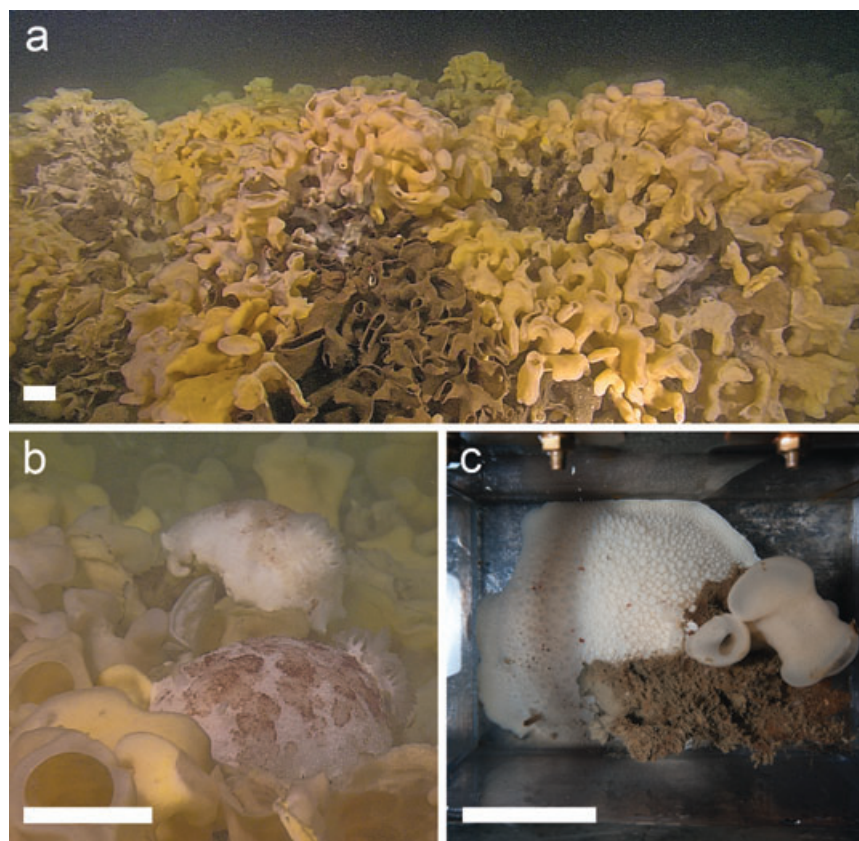


Fig. 1. Glass sponge reefs and dorid nudibranchs in the Strait of Georgia. **a.** The glass sponges *Aphrocallistes vastus* and *Heterochone calyx* build large reefs in the Strait of Georgia. Scalebar=10 cm. The dorid nudibranchs **(b)** *Peltodoris lentiginosa* and **(c)** *Archidoris odhneri* are predators on both glass sponge species. Scalebars in b and c=5 cm.

and gut contents. Our analyses confirmed that both nudibranchs feed on both reef-forming hexactinellids, *A. vastus* and *H. calyx*, and also on the demosponge *D. austini*. Our discovery is an important first step in understanding the food web of the unique glass sponge reef ecosystem.

Methods

In situ observations and sampling were carried out in the SOG with ROPOS onboard the Canadian Coast Guard Ship (CCGS) John P. Tully from 30 September to 3 October 2009 and the CCGS Vector from 29 October to 6 November 2011. Three of the larger glass sponge reef systems in the SOG, Howe Reef (49°20'0"N, 123°17'40"W, mean depth 80 m), Fraser Reef (49°9'16"N, 123°23'4"W, mean depth 164 m), and Galiano Reef (48°54'40"N, 123°19'40"W, mean depth 90 m) were surveyed in 2009 (Fig. 2). The distribution and abundance of the glass sponge populations were described in a separate study (Chu & Leys 2010).

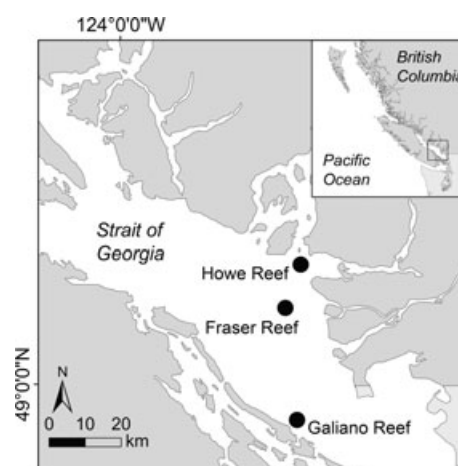


Fig. 2. Map of the three studied glass sponge reefs in the Strait of Georgia.

Counts of nudibranchs were made from 27 h of high-definition digital video (Ikegami HDL 40 with a Fujinon HA10×5.2BERD-S48 lens, Insite Pacific Inc., Solana Beach, CA, USA) and still images (DSC,

Sony Cyber-Shot DSC F707, Sony Electronics Inc., Oradell, NJ, USA) taken during the systematic surveys performed in 2009 (see Chu & Leys 2010). Because *Peltodoris lentiginosa* and *Archidoris odhneri* both appear as large, white nudibranchs, we were unable to reliably differentiate them in the video. Data on the area covered in the survey and the location and depths at which nudibranchs were seen were extracted from the ROV navigation files corresponding to the time stamp on the video and images. Both video and still images had 10-cm laser dot scales that were used to measure nudibranch sizes using Adobe Photoshop CS3 (Adobe Systems Inc., San Jose, CA, USA). Spatial distributions of the nudibranchs were mapped and analyzed using ArcGIS v10.0 (ESRI, Redlands, CA, USA).

Nudibranchs were sampled at Galiano Reef. Four individuals of *P. lentiginosa* were collected in 2009, and two individuals of *A. odhneri* and an additional two *P. lentiginosa* were collected in 2011. Of the individuals of *P. lentiginosa* collected in 2009, one collected with a manipulator arm was crushed, and therefore, we immediately fixed it in 4% formaldehyde; all other nudibranchs were collected without damage using a low force suction sampler and placed in a collection box with a sealing lid.

In 2009, the three live specimens of *P. lentiginosa* were kept in flowing seawater on board the ship before being transported in sealed buckets with seawater to the Bamfield Marine Sciences Centre in Bamfield, BC. These three individuals were placed in separate aquaria with flow-through seawater pumped from a depth of 25 m from Bamfield Inlet. After observations, the nudibranchs were returned to the SOG. Fecal matter was collected daily from each nudibranch and studied with a compound microscope for the presence of sponge spicules. Fecal samples containing spicules were cleaned with nitric acid at 95°C for 5 min, diluted with distilled water, and filtered through 0.22-µm Millipore membrane filter papers. Spicules were then lightly rinsed in Petri dishes with distilled water, mounted wet on glass

slides, and imaged using QCapture Pro with an Olympus CX41 microscope (Olympus America Inc., Center Valley, PA, USA) and an Infinity 1 camera (Lumenera Corporation, Ottawa, ON, Canada). The nudibranch fixed in formaldehyde from 2009 and the four individuals collected in 2011 were dissected and their gut contents studied by microscopy.

Members of *Aphrocallistes vastus* and *Heterochone calyx* have similar suites of spicules, but the two species can be distinguished by the distinct morphologies of specific spicules: only *A. vastus* has oxyhex-aster microscleres (Reiswig 2002), and while both *A. vastus* and *H. calyx* have pinnular hexactin microscleres, the ornamental ray of the pinnular hexactins of *A. vastus* has distinctly spinier projections as opposed to the rounded scales on those of *H. calyx* (H.M. Reiswig, pers. comm.; see fig. 1–5 in Chu 2010). Both *A. vastus* and *H. calyx* can fuse certain spicules with secondary silica deposition, creating a “dictyonine” skeleton (Leys et al. 2007). *Desmacella austini* can be identified by its tylostyle megascleres, as well as the presence of a range of sigma microsclere sizes. Thus far, it is the only demosponge species known to encrust members of reef populations of *H. calyx* (Lehnert et al. 2005).

Results

Analysis of the high-definition video showed that nudibranchs were present at Howe Reef and Galiano Reef, but not at Fraser Reef (Table 1). Despite the large areas covered by our systematic surveys, and the large and therefore conspicuous nature of these nudibranchs, only 26 individuals were observed (Table 1). The small sizes of the observed populations prevented a meaningful statistical analysis of their distributions; however, 19 of the 26 nudibranchs seen were found on top of live glass sponges, while one was seen on muddy substrate, and four pairs were copulating (one pair at Howe, three pairs at Galiano; Fig. 3). The three live specimens of *P. lentiginosa* collected in 2009 had wet weights and body

Table 1. Video observations of abundance and density of *Peltodoris lentiginosa* and *Archidoris odhneri* at each glass sponge reef. Individuals were not distinguished to species from the video. Area represents the area covered by the systematic reef surveys and is described in Chu & Leys (2010). No nudibranchs were observed in the survey video from Fraser Reef. Units are in meters.

Reef	Area (m ²)	N	Density (ind. m ⁻²)	Depth distributions		
				Mean±SD	Maximum	Minimum
Howe Reef	166,500	9	0.00005	77.4±11.7	102	66
Fraser Reef	142,775	0	0	—	—	—
Galiano Reef	25,966	17	0.0007	91.1±2.0	94	89

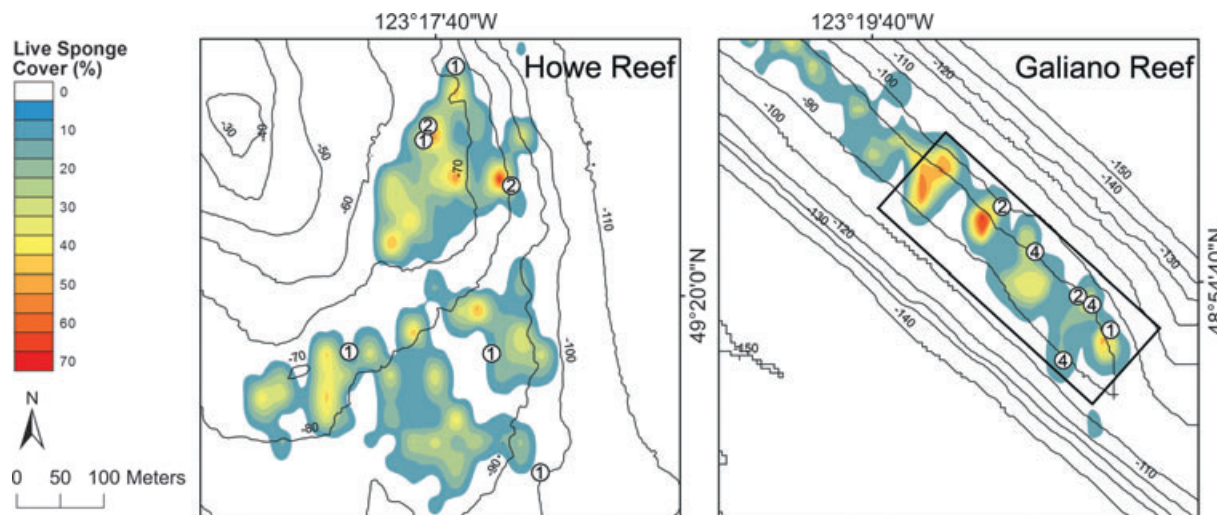


Fig. 3. Spatial distributions of dorid nudibranchs on glass sponge reefs. A total of 26 nudibranchs were observed, with nine seen at Howe Reef and 17 at Galiano Reef. No nudibranchs were observed at Fraser Reef. Numbers indicate spatially overlapping individuals. The box indicates the area covered by the survey video at Galiano Reef. Live sponge coverage is redrawn from Chu & Leys (2010). Contours are in 10-m depth intervals.

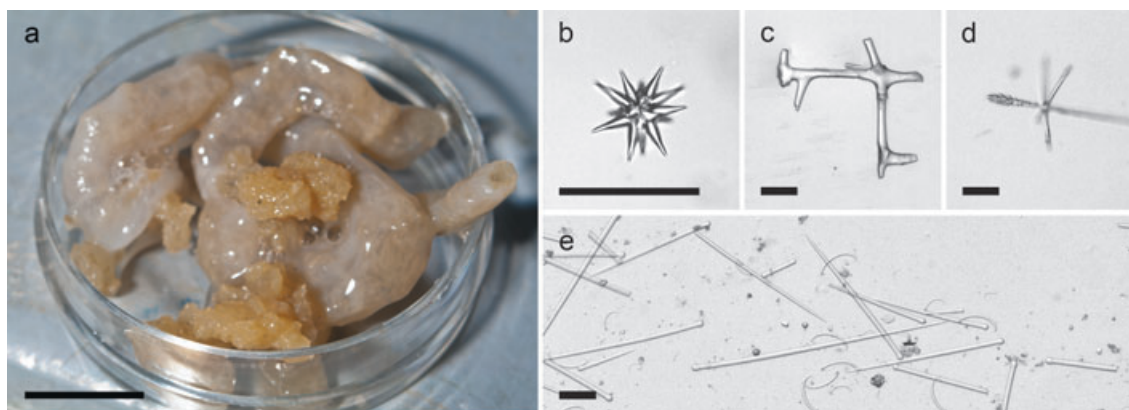


Fig. 4. Sponge spicules found in gut and fecal content analyses of *Peltodoris lentiginosa* and *Archidoris odhneri*. **a.** The stomachs of *P. lentiginosa* were found to be completely engorged with skeletons of the glass sponges *Aphrocallistes vastus* and *Heterochone calyx*. Scalebar=10 cm. Inspection of individual spicules from stomach and fecal contents revealed **(b)** oxyhexaster microscleres of *A. vastus*, **(c)** fused dictyonine skeletons of *A. vastus* and *H. calyx*, **(d)** pinnular hexactin microscleres of *A. vastus* and *H. calyx*, and **(e)** tylostyle megascleres and sigma microscleres of *Desmacella austini*. Scalebars in b–e=50 μ m.

lengths of 142.3 g and 10.5 cm, 286.1 g and 15.4 cm, and 329.4 g and 15.8 cm. From the analysis of the video footage and photos, the accurately measurable nudibranchs from all reefs had average body lengths of 13.9 ± 4.4 cm ($n=17$), with the largest individual, found at Howe Reef at 102-m depth, measuring 24.4 cm.

Fecal samples from all three live nudibranchs contained the same representative set of spicules from *Aphrocallistes vastus*, *Heterochone calyx*, and *Desmacella austini*. Spicules were found in fecal

matter collected each day for ≤ 1 week after sampling. Of the five specimens dissected for gut content analysis, four had spicules in their stomachs. Two of these individuals (both *Peltodoris lentiginosa*) had stomachs that were fully engorged with glass sponge skeletons (Fig. 4a). The bleach-cleaned, engorged stomach contents from these two individuals contained 0.4 g of hexactinellid spicules (dry weight). Gut contents analysis of spicules also confirmed *A. vastus*, *H. calyx*, and *D. austini* to be a part of both nudibranchs' diets (Fig. 4b–e).

Discussion

Glass sponges are primarily known as structuring agents for otherwise flat benthic areas and are not considered important components in the diet of predators because they possess miniscule amounts of organic tissue per body volume (Barthel 1995). Although nudibranchs are known to eat demosponges, the only previous record of a nudibranch predator of glass sponges was that of Dayton et al. (1974), who followed Antarctic populations of glass sponges for several years and found the dorid *Austrodoris mcmurdensis* ODHNER 1934 to be a major predator of the rossellid glass sponges *Scolymastra joubini* TOPSENT 1916 and *Rossella nuda* TOPSENT 1901. Dayton et al. (1974) described the sea star *Acodontaster conspicuus* KOEHLER 1920 as the other major predator of these Antarctic glass sponges. Observations from other studies suggest sea stars may be the more common predators of glass sponges (McClintock 1987; Leys & Lauzon 1998). Also in Antarctica, the sea star *Odontaster validus* KOEHLER 1906 preferentially feeds on *R. nuda* (McClintock 1987). On the Pacific coast of Canada, individuals of the sea star *Pteraster tessellatus* IVES 1888 have been observed sitting on live individuals of *Aphrocallistes vastus* (Chu, unpubl. data), and have been reported to feed on the glass sponge *Rhabdocalyptus dawsoni* LAMBE 1892 (Leys et al. 2007). Individuals of *P. militaris* MÜLLER 1776 have also been observed with their stomachs everted onto members of *A. vastus* (W.C. Austin, pers. comm.).

Glass sponge reefs share a similar assemblage of megafauna (e.g., nudibranchs and sea stars) with the well-described Antarctic sponge community, and the interactions of these animals may also be similar in the two systems. In Antarctica, predation is a major cause of mortality of glass sponges, but populations are able to grow to large standing crops because the sea star *O. validus* feeds on newly settled larvae and juveniles of both glass sponge predators, thereby preventing larval recruitment and skewing the predator population to large class sizes (Dayton et al. 1974). It is possible that a similar interaction occurs on NE Pacific sponge reefs. *Aphrocallistes vastus* and *Heterochone calyx* have bodies made of >90% hydrated silicon dioxide, and <10% their biomass is organic (Chu et al. 2011). A full stomach of 0.4 g of dry skeleton would contain <0.04 g of organic material; therefore, adults of *Peltodoris lentiginosa* and *Archidoris odhneri* must consume a substantial amount of glass sponge biomass to sustain their characteristic large sizes. The sea stars *Ceramaster* sp., *Henricia* sp., *Mediaster aequalis* STIMPSON 1857,

and *P. tessellatus* also co-occur with *P. lentiginosa* in the reefs among the large *A. vastus* and *H. calyx* (Chu & Leys 2010), yet their current ecological roles have not been addressed. In shallow water populations of the demosponge *Halichondria panacea* PALLAS 1776, high recruitment of its major predator, the dorid nudibranch *Archidoris montereyensis* COOPER 1862, can lead to the complete elimination of sponge patches by predation (Knowlton & Highsmith 2000). Although these populations of *H. panacea* covered a much smaller benthic area (m² compared with km²), similar top down control on the glass sponge populations could occur within the patches of a glass sponge reef. Our surveys covered a small fraction, <0.5 km², of the 700 km² known to be covered by glass sponge reefs (Conway et al. 1991). An examination of the interactions between the nudibranchs, sea stars, and hexactinellids using manipulative predator removal is needed to determine if the trophic patterns revealed by our study can structure glass sponge reef communities.

Peltodoris lentiginosa and *A. odhneri* are the only conspicuous soft-bodied animals observed to crawl and feed on living individuals *A. vastus*, whose barbed spicules have been suggested to deter contact by most other soft-bodied animals (Austin 2003; Chu & Leys 2010). Many small dendronotid and aeolid nudibranchs are typical members of glass sponge reef communities, but they are usually found on the bedrock and mud substrates on the periphery of the glass sponges (Chu & Leys 2010). The effectiveness of spicules as a predation deterrent in sponges has only been addressed in shallow water demosponges (Jones et al. 2005; Ferguson & Davis 2009). In demosponges, low mass-specific content of living tissue and the presence of secondary metabolites have also been shown to deter predation (Chanas & Pawlik 1995; Uriz et al. 1996). Compared to the abundance of studies that focused on identifying secondary metabolites of shallow water demosponges, few have attempted to identify analogous compounds used for predator defense against in hexactinellids (for a review see Avila et al. 2008). In general, the results of these studies suggest defensive strategies are highly dependent on sponge species, and both spicules and chemical compounds may sometimes function together within a demosponge to deter predation (Burns & Ilan 2003; Hill et al. 2005). However, for *A. vastus* and *H. calyx*, we suggest that physical defences (spicules) are a more likely strategy because they are 80% spicules by dry weight (Whitney et al. 2005; Chu et al. 2011) and live in a low-resource environment (Yahel et al. 2007); thus, organic-based defences (chemicals)

would be a more energetically costly strategy. Furthermore, the morphology of hexactinellid spicules are different than those of demosponges, and certain spicule types, such as the dermal pinnular hexactin spicules of *A. vastus*, easily get impaled in soft tissue that contacts live glass sponges (Austin 2003; Chu, unpubl. data). Despite having a characteristic fleshy foot, members of both *P. lentiginosa* and *A. odhneri* can withstand contact, ingestion, and excretion of these spicules. The live nudibranchs we sampled produced a large amount of mucus during their captivity, which may function as a protective measure against contact with sponge spicules.

Members of both species of dorids observed on the glass sponge reefs may reach large sizes (e.g., *P. lentiginosa* may reach 45 cm in body length: S.V. Millen, pers. comm.) The individuals documented in our study are certainly some of the largest invertebrate members of the glass sponge reef community. Several other large dorid nudibranchs are common in the waters around the sponge reefs, and these dorids may also be hexactinellid predators whose feeding biology has gone unnoticed due to their characteristic deep-water habitats. Demosponges generally have more organic tissue per body volume than hexactinellids (Barthel 1995), so it is possible that, like other dorids, individuals of *P. lentiginosa* prefer to feed on demosponges such as the desmacellid *D. austini* (Bloom 1976, 1981). Feeding on *A. vastus* and *H. calyx* could be incidental due to the abundance of hexactinellids, or accidental, because *D. austini* grows as a thinly encrusting form on the glass sponges. However, our data suggest the nudibranchs are mostly feeding on the glass sponges because they were primarily observed on live glass sponges (*D. austini* was not observed nearby in the videos), and because microcleres, which are only found in glass sponge tissues, were found in their guts and fecal contents. We were limited by logistical constraints and small sample sizes, but a controlled food preference lab study coupled with caloric measurements of each of the three sponges contributing to the nudibranch diets would aid in determining the specificity of their feeding habits and whether predation could potentially impact the glass sponge populations in a reef.

The absence of *P. lentiginosa* and *A. odhneri* at Fraser Reef illustrates a fundamental difference among the glass sponge reefs in the SOG. There were twice as many animals associated with the glass sponges at Galiano Reef than at either Howe or Fraser Reefs (Chu & Leys 2010). Fraser Reef has an intermediate abundance of sponges (relative to Howe and Galiano Reefs; Chu & Leys 2010), and

D. austini is found at all three reefs (Chu, unpubl. data). Thus, glass sponge density and food availability cannot explain the absence of nudibranchs at that reef. Furthermore, we used identical methods to survey the three reefs within 72 h, and therefore should have detected the nudibranchs if they were present. Although it is possible that we missed seeing a few nudibranchs due to slightly poorer visibility at Fraser Reef during our video surveys, our data illustrate large differences in nudibranch abundance and density among the three reefs. This pattern could arise from differences in recruitment, predation, or other ecological processes. We hypothesize that the different environmental conditions (e.g., sedimentation levels, flow rates, and current patterns) observed among reefs (Chu & Leys 2010) affect the settlement and recruitment of associated animals at each reef.

The direct interactions between molluscan predators and glass sponges revealed in our study are the first observed since the pioneering work of Dayton et al. (1974) in Antarctica. Although the assemblage of animals present is known for glass sponge reef communities (Chu & Leys 2010), other species interactions have yet to be quantified. Because direct and indirect interactions can influence the local species diversity of a system (Paine 1966; Menge 1995), future ecological studies of glass sponge reefs need to address the nature of the species interactions occurring within the community and how they could be structuring the ecosystem.

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References

- Austin WC 2003. Sponge gardens: a hidden treasure in British Columbia. Available at www.mareco.org/khoyatan/spongegardens (accessed 28 November 2011).

- Avila C, Taboada S & Núñez-Pons L 2008. Antarctic marine chemical ecology: what is next? *Mar. Ecol.* 29: 1–71.
- Barthel D 1995. Tissue composition of sponges from the Weddell Sea Antarctica: not much meat on the bones. *Mar. Ecol. Prog. Ser.* 123: 149–153.
- Bloom SA 1976. Morphological correlations between dorid nudibranch predators and sponge prey. *Veliger* 18: 289–301.
- 1981. Specialization and noncompetitive resource partitioning among sponge-eating dorid nudibranchs. *Oecologia* 49: 305–315.
- Burns E & Ilan M 2003. Comparison of anti-predatory defences of Red Sea and Caribbean sponges. II. Physical defense. *Mar. Ecol. Prog. Ser.* 252: 115–123.
- Chanas B & Pawlik JR 1995. Defenses of Caribbean sponges against predatory reef fish. II. Spicules, tissue toughness, and nutritional quality. *Mar. Ecol. Prog. Ser.* 127: 195–211.
- Chu JWF 2010. Biological patterns and processes of glass sponge reefs. Master thesis, University of Alberta, Edmonton, AB, Canada. 180 pp.
- Chu JWF & Leys SP 2010. High resolution mapping of community structure in three glass sponge reefs (Porifera, Hexactinellida). *Mar. Ecol. Prog. Ser.* 417: 97–113.
- Chu JWF, Maldonado M, Yahel G, & Leys SP 2011. Glass sponge reefs as silicon sinks. *Mar. Ecol. Prog. Ser.* 441: 1–14.
- Conway KW, Barrie JV, Austin WC, & Luterbauer JL 1991. Holocene bioherms on the western Canadian continental shelf. *Cont. Shelf Res.* 11: 771–790.
- Conway KW, Barrie JV, & Krautter M 2004. Modern siliceous sponge reefs in a turbid siliciclastic setting: Fraser River delta, British Columbia, Canada. *Neues Jahrb. Geol. Paläontol. Monatsh.* 6: 335–350.
- Conway KW, Barrie JV, Hill JV, Austin WC, & Picard K 2007. Mapping sensitive benthic habitats in the Strait of Georgia, coastal British Columbia: deep water sponge and coral reefs. *Geol. Surv. Can.* 2007-A2: 1–6.
- Dayton PK, Robilliard GA, Paine RT, & Dayton LB 1974. Biological accommodation in the benthic community at McMurdo Sound, Antarctica. *Ecol. Monogr.* 44: 105–128.
- Ferguson AM & Davis AR 2009. Heart of glass: spicule armament and physical defense in temperate reef sponges. *Mar. Ecol. Prog. Ser.* 372: 77–86.
- Hill MS, Lopez NA, & Young KA 2005. Anti-predator defences in Western North Atlantic sponges with evidence of enhanced defense through interactions between spicules and chemicals. *Mar. Ecol. Prog. Ser.* 291: 93–102.
- Jones AC, Blum JE, & Pawlik JR 2005. Testing for defensive synergy in Caribbean sponges: bad taste or glass spicules? *J. Exp. Mar. Biol. Ecol.* 322: 67–81.
- Knowlton AL & Highsmith RC 2000. Convergence in the time-space continuum: a predator-prey interaction. *Mar. Ecol. Prog. Ser.* 197: 285–291.
- Lehnert H, Conway KW, Barrie JV, & Krautter M 2005. *Desmacella austini* sp. nov. from sponge reefs off the Pacific coast of Canada. *Contrib. Zool.* 74: 265–270.
- Leys SP & Lauzon NRJ 1998. Hexactinellid sponge ecology: growth rates and seasonality in deep water sponges. *J. Exp. Biol. Ecol.* 230: 111–129.
- Leys SP, Mackie GO, & Reiswig HM 2007. The biology of glass sponges. *Adv. Mar. Biol.* 52: 1–145.
- McClintock JB 1987. Investigation of the relationship between invertebrate predation and biochemical composition, energy content, spicule armament and toxicity of benthic sponges at McMurdo Sound, Antarctica. *Mar. Biol.* 94: 479–487.
- McClintock JB, Amsler CD, Baker BJ, & Van Soest RWM 2005. Ecology of Antarctic marine sponges: an overview. *Integr. Comp. Biol.* 45: 359–368.
- Menge BA 1995. Indirect effects in marine rocky intertidal interaction webs: patterns and importance. *Ecol. Monogr.* 65: 21–74.
- Millen SV 1982. A new species of dorid nudibranch (Opisthobranchia: Mollusca) belonging to the genus *Anisodoris*. *Can. J. Zool.* 60: 2694–2705.
- Paine RT 1966. Food web complexity and species diversity. *Am. Nat.* 100: 65–75.
- Reiswig HM 2002. Family Aphrocallistidae Gray, 1867. In: *Systema Porifera: A Guide to the Classification of Sponges*. Hooper JNA & Van Soest RWM, eds., pp. 1282–1286. Plenum, New York.
- Uriz MJ, Turon X, Becerro MA, & Galera J 1996. Feeding deterrence in sponges. The role of toxicity, physical defences, energetic contents, and life-history stage. *J. Exp. Mar. Biol. Ecol.* 205: 187–204.
- Whitney F, Conway KW, Thomson R, Barrie JV, Krautter M, & Mungov G 2005. Oceanographic habitat of sponge reefs on the Western Canadian Continental Shelf. *Cont. Shelf Res.* 25: 211–226.
- Yahel G, Whitney F, Reiswig HM, Eerkes-Medrano DI, & Leys SP 2007. In situ feeding and metabolism of glass sponges (Hexactinellida, Porifera) studied in a deep temperate fjord with a remotely operated submersible. *Limnol. Oceanogr.* 52: 428–440.