Long-term effects of bottom trawling on large sponges in the Gulf of Alaska

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ABSTRACT

Manipulative studies that characterize short-term effects of bottom trawls on seafloor habitats are numerous, but studies that examine long-term effects are rare. The long-term (13 years) effects of a single bottom trawl on large (>20 cm) erect sponges were investigated by revisiting the site of prior experimental trawling studies. In prior studies, large sponges were assessed immediately after trawling and 1 yr post-trawling. Thirteen years post-trawling, the average density of large sponges was 31.7% lower (range 1.5%-53.0%) and the incidence of sponge damage (torn, necrotic, missing tissue, prone) was 58.8% higher within strip transects in trawled versus untrawled reference areas. For all sponge species combined, the mean density of large sponges was 3.19 individuals 100 m^{-2} in trawled areas and 4.67 individuals 100 m^{-2} in reference areas. The most abundant sponge species in both trawled and reference areas was *Rhabdocalyptus dawsoni*. Mean density of this species differed greatly between trawled (1.57 individuals 100 m^{-2}) and reference areas (2.91 individuals 100 m^{-2}). Thirteen years after trawling, the mean percentage of damaged sponges on strip transects was 15.3% in trawled areas and 6.3%

in reference areas. The rate of damage in trawled areas was less than that observed both immediately after trawling and 1 year later. The persistence of damage (lower sponge densities and higher rates of injury in trawled areas) and the potential resultant changes to benthic communities where deepwater habitat-forming biota, such as large erect sponges, are present provide rationale for cautious management of the long term effects of bottom trawling.

Keywords

Trawling, Sponge, *Rhabdocalyptus dawsoni*, *Mycale loveni*, Benthic Habitat, Fishing

1. Introduction

Over 200 sponge species from the Classes Calcarea, Hexactinellida and Demospongiae are known to occur in Alaskan waters (Stone et al. 2011, Lenhert and Stone 2013, Reiswig and Stone 2013). These sponges are broadly distributed on the Continental shelf and slope throughout the Gulf of Alaska, Bering Sea, and along the Aleutian Islands (Malecha et al. 2005) from intertidal depths to at least 2800 m (Stone et al. 2011). Reef-like bioherms, composed mostly of hexactinellids, have been described in the Gulf of Alaska (Conway et al. 1991, 2001, 2005, Krautter et al. 2001, Stone et al. 2013) and demosponge-dominated “gardens” occur along the Aleutian Islands (Stone et al. 2011). Large (>20 cm) erect sponges also occur in lower densities, patchily distributed on hard bottom substrates in the Gulf of Alaska and along the Aleutian Islands (Stone et al. 2011). These sponges usually occur amongst a mix of benthic invertebrates and have varying morphologies including vase-like, tubular, barrel-shaped, and plate-like. Despite slow growth rates, some species attain sizes exceeding 1 meter and may be as old as 220 yrs (Dayton 1979, Ayling 1983, Hoppe 1988, Marliave 1992, Leys and Lauzon 1998). Individually and collectively sponges form high-relief complex habitat that is thought to foster increased biological diversity (Klitgaard 1995, Buhl-Mortensen et al 2010, Hogg et al. 2010, Beazley et al. 2013) and productivity by providing cover and food aggregations for juvenile and adult fish, especially rockfish (e.g., Auster et al. 2003, Freese & Wing 2003, Stone et al. 2005, Marliave et al. 2009, Miller et al. 2012).

Deepwater habitat-forming biota, such as sponges, is sensitive to anthropogenic disturbance (ICES 2009). Interactions between bottom trawls and seafloor habitat has been extensively documented (for reviews see Watling & Norse 1998, Auster & Langton 1999, Collie et al. 2000, National Research Council 2002, Kaiser et al. 2006, Clark et al. 2016). The relative effect of bottom trawls on benthic habitat depends on many factors including gear configuration, the geological characteristics of the seafloor, depth, and sensitivity of the habitat-forming species present (Collie et al. 2000, Kaiser et al. 2006). In general, deepwater (>100 m) habitats experience relatively low levels of natural disturbance, are more susceptible to trawl effects and recover more slowly than shallow water habitats (Kaiser et al. 2002). The response of sessile benthic epifauna to trawl disturbance varies among taxa. In the short-term, deepwater sponges are particularly sensitive to trawl disturbances (Sainsbury et al. 1997, Freese et al. 1999, Freese 2001, Wassenburg et al. 2002). Less is known about the long-term effects of trawl-induced damage on deepwater sponges and their abilities to recover. In the Barents Sea, sponge biomass is lower in trawled areas (Jørgensen et al. 2016) and sponge density has been negatively correlated with fishing intensity (Buhl-Mortensen et al. 2016). Using a logistic model, Rooper et al. (2011) predicted that it would take 20 years for an Aleutian sponge population to return to 80% of its original biomass following a single trawl pass and that intrinsic growth rates of sponges were slow ($r=0.107\ yr^{-1}$).

In the Gulf of Alaska, near Salisbury Sound, the immediate effects of trawling on large erect sponges were described by Freese et al. (1999). A follow-up study at the same site documented the status of the sponges roughly one year later (Freese 2001). In the present study, we revisited those trawled areas 13 years later. Our objective was to characterize the long-term effects of trawling by assessing the density and condition of large erect sponges. So that our results could be directly compared with the previous studies, we utilized identical methods to observe sponge density in trawled and untrawled reference areas. We also observed sponges for evidence of disturbance (necrosis, tissue damage, and changes in physical orientation) and compared incidence of injuries between the trawled and reference areas.

2. Methods

2.1. *Study Area*

The study area (Fig. 1) is located on a moderate slope (approximately 22 km southwest of Salisbury Sound in the eastern Gulf of Alaska near the continental shelf break between 200-212 m depth. The site was originally selected after consulting commercial fishing records that identified an area where zero or minimal trawling had occurred since the 1970s (Freese et al. 1999). In 1998, the entire eastern Gulf of Alaska, including the study area, was officially closed to trawling. The seafloor in the study area consists mainly of sand, pebbles, and cobble with a few scattered boulders and the site supports an array of large erect sponge species. Generally, the geological characteristics of the study area are representative of the habitat preferred by numerous rockfish species including Pacific ocean perch *S. alutus*, northern rockfish *S. polyspinis*, and redstripe rockfish *S. proriger* (Love et al. 2002). Rougheye *S. aleutianus*, blackspotted *S. melanostictus* and shortraker rockfish *S. borealis* occupy similar habitats but usually at deeper depths and on steeper slopes (Krieger & Ito 1992).

2.2. Previous Studies (1996 and 1997)

In 1996, distinct locations in the study area were trawled with single passes of a 4-seam, high-opening polyethylene Nor-eastern bottom trawl equipped with tire gear similar to that used in the commercial rockfish *Sebastes* spp. fishery (Freese et al. 1999). Efforts were made to trawl along isobaths over uniform bottom. Data from 8 strip transects within trawl paths (Table 1) were compared with 8 paired strip transects in adjacent reference areas (16 total transects) to determine the immediate effects of trawling on sponge density and incidence of injury (Freese et al. 1999). Numbered flags were placed on the seafloor at the beginnings and ends of each trawl path and differential global positioning system (DGPS) coordinates of the flag locations and compass bearings between flags were noted to facilitate relocation of trawl paths and allow subsequent observations. In 1997 (roughly 1 yr after trawling took place), the study area was revisited and 3 of the original trawl paths were observed; sponge density and the incidence of injury within trawl paths was once again compared to adjacent reference areas (Freese 2001).

2.3. Current Study (2009)

Observational methods identical to those employed by Freese et al. (1999) and Freese (2001) were used in 2009 to enable direct comparison of our results with the earlier studies. Likewise, we used the submersible *Delta* to complete video transects along the seafloor (Figure 1). The 2-person *Delta* traveled at an average speed of 2.01 kmh^{-1}, maintained constant contact with the seafloor, and was equipped with an oblique-facing camera and halogen lighting. Parallel lasers 20 cm apart provided a scaling measure on the recorded video for determining sponge sizes in the laboratory. An observer inside the submersible narrated the videotape in real-time by verbally describing biota and geological features passing through the camera's field of view. Observations in paired trawl and reference areas were obtained on 5 strip transects (Table 1) as well as on 5 close-up observations (Table 2). The suite of strip transects observed differed slightly from the suite of close-up observations due to technical issues with the submersible that interrupted video recording during two dives. Therefore, Transect A was observed during strip transect observations but not during close-up observations and Transect G was observed during close-up observations but not during strip transects.

2.4. Strip Transects

Strip transects were completed within 5 trawl paths and paired reference transects were completed in adjacent areas outside the trawl paths (Table 1). Transects within trawl paths followed a designated bearing from one seafloor marker to another; paired reference transects were completed by maneuvering the submersible perpendicularly at least 100 m away from the trawl transects and observing roughly parallel paths outside the trawled areas.

In the laboratory, video from strip transects was reviewed to determine sponge density and incidence of damage. Like the previous studies, only specimens >20 cm in any dimension and within 5 m of the submersible were enumerated. Area sampled was estimated by multiplying transect distance, as determined from GPS coordinates, by transect width (5 m). Sponges were categorized into 3 groups; 1) undamaged, i.e. erect and intact, 2) erect but with torn, necrotic, or missing tissue, and 3) tipped over with torn or intact tissue. The categories were identical to those used in the previous studies. Tears, necrosis, or missing tissues were only noted if the damage was longer than 10% of the specimen's longest axis. Density and damage data from the 5 paired trawl and reference transects were compared with permutation tests (Noreen 1989, Odiase & Ogbonmwan 2007). The test statistics were the t -statistics generated from one-sided paired t-tests. Permutation tests were used because of the small sample sizes and therefore unknown distributions of the density and damage estimates. Conventional paired t-tests assume that the density estimates are normally distributed.

2.5. Close-up Observations

Unlike the previous studies, a second set of observations were completed in five trawl and reference areas to obtain close-up video of individual sponges (Table 2). These observations were made so that injuries and damage could be characterized in greater detail. On the dives in the trawled areas, the submersible began at one flag and proceeded on a bearing toward the opposite flag. Along the way, large sponges were randomly encountered and the submersible completed full circles around each individual specimen to obtain a 360° view of its full extent. Once the circle was complete, the submersible would continue on its original bearing until it encountered another large sponge. Close-up observations were obtained in a similar manner in paired reference areas by maneuvering the submersible at least 100 m outside of the trawl paths and completing observations on a bearing parallel with the trawl path. Video from the close-up observations was reviewed in the laboratory where damage to each sponge was categorized using the same three criteria used for strip transect analysis. In addition, sponges were evaluated for the percentage (relative to the intact individual) of necrotic and missing tissues and the size (longest axis) of each sponge was visually estimated using the scaling lasers. Incidence of damage and size data from the close-up observations in paired trawl and reference areas were compared with exact permutation tests. Sponge density was not statistically compared among the reference and trawl areas with the close-up observations because the total area sampled was unknown.

2.6. Sponge Identification

Our tentative sponge identifications are somewhat different from those reported in Freese et al. (1999) and Freese (2001). In many cases, current and previous transects occurred along the same stretch of seafloor or were in close proximity and it is likely that many of the same long-lived specimens were observed but identified differently. In the previous studies, sponges were grouped by shape and size in order to facilitate analyses.

Since those studies were completed, the taxonomic literature describing deepsea sponges has expanded. The previous studies identified the demosponges (Class Demospongiae) *Mycale* sp., *Geodia* sp., and *Esperiopsis* sp. They also identified the glass sponges (Class Hexactinellida) *Rhabdocalyptus* sp. and an unidentified “morel” sponge. We agree that the study site contains many *Mycale* sp., presumably *Mycale loveni* (Fig. 3). However, based on spicule examination, we believe that the majority of the specimens previously identified as *Geodia* are likely *Poecillastra tenuilaminaris* (Fig. 2) and those specimens identified as *Esperiopsis* sp. are *Isodictya quatsinoensis* (H. Lehnert, personal communication). The previously unidentified “morel” sponge is likely *Farrea occa* and the sponge previously identified as *Rhabdocalyptus* sp. we identify as *Rhabdocalyptus dawsoni* (Fig. 2). We also observed *Acanthascus koltuni*; a reference specimen was collected and its identity verified under magnification (H. Reiswig, personal communication). This species has only recently been described (Reiswig & Stone 2013). Freese et al. (1999) observed many “finger sponges” that were tentatively identified as *Leuconia* sp. We believe this species to be *Axinella rugosa*, which was very abundant in the study area but since most specimens were smaller than 20 cm, they are only a small minority in our reported observations. One other large sponge species, *Aphrocallistes vastus*, was observed in the study area in limited numbers.

3. Results

3.1. Strip Transects

A total of 13,049 m^2 of seafloor was observed on strip transects in trawled areas and 13,538 m^2 was observed in reference areas. A total of 393 sponges larger than 20 cm were observed in trawled areas compared to 591 in reference areas. Sponge density was significantly higher ($P = 0.031$) on each reference transect than its paired trawl transect based on the permutation test. The mean density of sponges in reference transects was 4.67 individuals 100 m^{-2}, while the mean density in trawl transects was 3.19 individuals 100 m^{-2} (Table 3). Averaged over all transects, the density of sponges was 31.7% lower in trawled transects compared to reference transects. The percent difference in sponge density between reference and trawled transects was highly variable ranging from 1.5 to 53.0%.

The most abundant sponge species in both trawl and reference strip transects was *Rhabdocalyptus dawsoni*. This species accounted for 47% of all trawl area sponges and 62% of all reference area sponges. Mean density of *Rhabdocalyptus dawsoni* was 1.57 individuals 100 m^{-2} in trawl transects compared to 2.91 individuals 100 m^{-2} in reference transects (Table 4). *Mycale loveni* and *Poecillastra tenuilaminaris* were the next most abundant sponge species; the average density of these 2 species was nearly equal in trawl and reference transects. The mean density of *Farea occa* was 0.22 individuals 100 m^{-2} in reference areas and 0.17 individuals 100 m^{-2} in trawl areas and the mean densities of three less commonly observed sponge species, *Axinella rugosa, Isodictya quatsinoensis*, and *Acanthascus koltuni* were slightly higher in trawl areas.

Thirteen years after trawling occurred, trawl evidence, including seafloor gouging, boulder displacement, and damaged sponges, was still readily apparent on some trawl transects. Damaged sponges were also observed in reference areas. However, the percent frequency of damaged sponges differed significantly (permutation test; $P < 0.035$) between trawl and reference strip transects. For all sponges combined, the mean percentage of damaged sponges (categories 2 and 3) was 6.3% for reference areas and 15.3% for trawled areas (Table 4). The mean percentage of damaged sponges that were erect (category 2) was 1.1% in reference areas and 6.5% in trawled areas for all sponge species combined. The mean percentage of prone sponges (category 3) was 5.2% in reference areas and 8.8% in trawled areas.

The mean percentage of damage among *Mycale loveni* specimens was about 6 times higher within trawled transects than in reference transects. On the trawl transects, the mean rate of tissue damage (category 2) for *Mycale loveni* was 31.4% and the mean rate of prone individuals was 5.6% (category 3). On reference transects, the mean rate of tissue damage was 5.7% for *Mycale loveni* and none were prone. The mean rates of damage of *Rhabdocalyptus dawsoni* (8.2%) and *Poecillastra tenuilaminaris* (19.3%) in trawl transects were about two times the rates in reference transects. All of the damaged *Rhabdocalyptus dawsoni* specimens observed were prone. The mean rate of damage observed for *Isodictya quatsinoensis* was 26.7% in trawl transects and 6.7% in reference transects. However, the number of individuals observed was rather low. Of the 11 *Isodictya quatsinoensis* specimens observed on strip transects (reference and trawl areas combined), 5 individuals were damaged, 4 of which were prone and 1 had torn tissues. This vase-shaped species is supple and quite fragile and was mostly observed attached to small rocks by a short holdfast. These characteristics may combine to make the species extremely vulnerable to both anthropogenic and natural disturbances alike, as the relatively large vase creates a disproportionate drag on the sponge’s small anchor, which may result in the sponge tipping over even in moderate currents. The only sponge species that had a higher average rate of damage in reference strip transects than in trawl transects was *Farea occa*. However, the rate of damage was very low (1.1%) and only one specimen, of the 31 observed in the reference area, had damaged tissue; none of the 18 specimens in the trawled area was damaged.

3.2. Close-up Observations

During close-up observations, 265 individual sponges were observed in the five reference areas and 256 in the paired trawled areas (Table 5). The mean percentage of damaged individuals (categories 2 and 3) for all sponge species combined was significantly greater in trawled areas than in reference areas ($P < 0.031$). In the five trawled areas, an average of 40.1% of all sponges were damaged (range 31.0%-46.9%). In the five reference areas, an average of 11.0% of sponges were damaged (range 4.4%-18.0%). The average percentage of damage for all sponge species, except for *Aphrocalistes vastus*, was higher within trawled areas (Table 6).

The incidence of flesh damage on erect sponges (category 2) was significantly greater within trawled areas than within reference areas ($P < 0.032$). The average percentage of sponges in category 2 was 15.6% in trawled areas and 3.9% in reference areas for all species combined (Table 6). The average percentage of missing tissue for all sponges combined was 3.8% for trawl areas versus 1.0% for reference areas. The mean percentage of necrotic tissue among trawl area sponges was 2.1% while the percentage among reference area sponges was 1.5%. Within the trawled areas, *Poecillastra* *tenuilaminaris* (7.7%) had the highest mean percentage of missing tissue and *Mycale Loveni* (3.5%) had the highest mean percentage of necrotic tissue. The rate of prone sponges (category 3) was higher in the trawled areas ($P < 0.028$). Mean percentage of prone individuals was 24.6% in trawled areas compared to 7.1% in reference areas. Average sponge size, for all species combined, was not significantly different ($P = 0.224$) between the reference and trawl areas (Table 6). The largest sponge specimen observed was an *Acanthascus koltuni* that was slightly taller than 100 cm and was observed in a reference area. Several *Mycale loveni* and one *Rhabdocalyptus dawsoni* had axes longer than 80 cm.

4. Discussion

4.1. Sponge Density and Damage

We found the effects of bottom trawling on large erect sponges in the Gulf of Alaska to be persistent and perhaps compounding. Our results suggest that sponges damaged by trawls suffer lingering damage and may experience delayed mortality over the course of many years. Immediate observations following disturbance may not characterize the full effect of trawling on deepwater sponges. Immediately after trawling occurred, Freese et al. (1999) found the density of sponges (Fig. 4) was 15.5% lower in trawled areas than in reference areas (3.15 sponges 100 m^{-2} vs. 3.73 sponges100 m^{-2}). About 1 yr later, the difference between trawled and reference areas had increased such that sponge density in trawled areas was 21.1% lower (2.76 sponges 100 m^{-2} vs. 3.50 sponges 100 m^{-2}; Freese 2001). In 2009, 13 yr post-trawling, we found the disparity between trawled and reference sites had increased further and the mean density of sponges at trawled sites was 31.7% less than in reference areas (3.19 sponges 100 m^{-2} vs. 4.67 sponges 100 m^{-2}).

Despite best intentions to collect data in an identical manner as previous studies, the different density observed in reference areas could be attributed to subtle differences in data collection protocols or video interpretation. However, if methodological differences were to blame for the increase over time, one would expect the effect to be manifested in a like manner in both reference and trawl observations, i.e. sponge densities in trawled areas would also be higher than previous observations. Because we did not see an appreciable increase in trawled areas, it is possible that the increased density we observed in reference areas may be a result of higher sponge recruitment and/or growth in those areas, or random sampling variation. A comment about the original study was that comparison of the trawled areas before and after trawling may have provided a more precise assessment of sponge densities and damage than comparing trawled areas to reference areas. Unfortunately, this method could not be done because it was not possible to place the trawl on a predetermined transect path with the required precision. Thus for this study and the previous studies it must be assumed that the reference areas observed were not inherently different from the trawled transects prior to trawling. The present study duplicated the previous studies in most regards. Most importantly, the trawl transects observed in this study followed the same paths as those observed previously, i.e., they started and ended at physical markers placed on the seafloor in 1996. Therefore, we are certain that our trawl observations occurred in the path of the trawl. However, different reference transects were observed in our study than those used in the previous studies. Unlike the original trawl transects that were marked on the seafloor, the original reference transects were not marked because of logistical constraints. Therefore, it was impossible to return to the previous reference transects with absolute confidence. Although there is likely natural variation within the study area, the depths, slopes, and substrates of the trawled and paired reference transects were nearly identical. It should also be noted that the number of transects observed varied between the two earlier studies and the present one. Eight paired transects were observed in 1996, 3 in 1997, and 5 in 2009. Variation among the transects could have contributed to the density differences we observed between years. Unfortunately, the previous publications report results in pooled form rather than by transect, so direct comparisons between transects was not possible.

Damaged sponges that initially survive trawling may suffer secondary effects manifested in ways more difficult to observe. For instance, damaged sponges have less ability to defend themselves from predators and compete for resources (Henry and Hart 2005). Regeneration in sponges may occur by reorganization of cells rather than growth of new tissues (Korotkova 1963, Reiswig 1973). In tropical waters, this *modus operandi* allows rapid repair and helps deter overgrowth and fouling and may prevent a total disruption of the physiological processes necessary for a sponge's survival (Hoppe 1988). Damaged sponges in tropical (Duckworth 2003, Hoppe 1988) and temperate (Hovmann et al. 2003) waters can be resilient and survive significant injuries but the physiological cost of tissue regeneration often comes at the expense of somatic growth and reproduction which can ultimately lead to reductions in biomass, fecundity, and recruitment (Henry & Hart 2005). This mechanism provides a hypothesis for explaining the increasing difference in sponge density we observed between trawled and reference areas, as reproduction and growth may have been depressed in the trawled areas as a result of past injuries. We did not observe a significant difference in sponge size between the trawled and reference areas but given the extremely slow growth rates that are assumed for these species, it may take a very long time to see large differences.

The densities of sponges we observed in trawled areas in 2009 (13 years post-trawling) were comparable in magnitude to the densities observed in 1996 (immediately post-trawling; Freese et al. 1999) and 1997 (1 yr post-trawling; Freese 2001). Sponge density in reference areas was higher in 2009 than in 1996 and 1997 and this contributed to a greater relative difference between trawled and reference area densities than previously observed. The sponge species with the largest density difference between trawled and reference areas was *Rhabdocalyptus dawsoni*; this species provided much of the overall difference in density between the two areas. Our results contrast with those of Van Dolah et al. (1987), who found immediate reductions in sponge density on hard-bottom areas following trawling off the southeastern U.S. but, 1 yr later, sponge densities had returned to pre-trawl levels or greater. Differences in recovery rates between the two studies may be because the sponges in the Van Dolah et al. (1987) study are generally smaller than those in the present study and the study sites occur at vastly different depths (20 m vs. >200 m) and latitudes (31.6° N vs. 57.4° N).

Immediately post-trawling, 67% of “vase” sponges (originally identified as *Mycale* sp., *Geodia* sp., and *Esperiopsis* sp.; see the sponge identification section above for our species interpretations) in trawl transects were damaged (Freese et al. 1999); 1 yr later, the percentage of damaged sponges decreased to 47% (Freese 2001). The mean rate of damage we observed among sponges on strip transects in the trawled areas (15.3%) was considerably less than the earlier observations. Taken alone, the decreasing percentage of damaged sponges observed over time could indicate significant recovery processes occurred. However, because the difference in overall sponge density between trawl and reference sites has increased over time (Fig. 4), it is possible that damaged sponges have simply been lost from the population through delayed mortality.

The incidence of missing and necrotic tissues (category 2) and the number of prone sponges (category 3) was higher within trawled areas than reference areas. However, we did observe a higher rate of damage (both category 2 and 3) in reference areas than previous studies did. Immediately after trawling, 2% of reference area sponges were damaged (Freese et al. 1999) while one year later, 1% of reference area sponges were damaged (Freese 2001). In the present study, we observed damage among 6.3% of the reference area sponges on strip transects. It is unknown if there is a higher amount of background disturbance in the area or if our criteria and judgment regarding damage differed from the previous studies. Trawling was prohibited in the area in 1998 but longlining and pot fishing are legal and could have had an adverse effect on sponges. For reference, in the central Aleutian Islands 21% of sponges were estimated to be damaged (Heifetz et al. 2009). However, bottom trawling is allowed in that area and the intensity of fishing activity is considerably greater than in our study area. Although we did not observe active predators on the sponges in this study, nudibranchs, sea stars, and fish are known to cause tissue damage to some temperate sponges (Sheild & Witman 1993; Knowlton and Highsmith 2000; Wulff 2006). Regardless of what caused damage to reference area sponges, fishing activities and predation would likely impact the trawl and reference areas equally.

Freese (2001) noted that no new colonization or evidence of repair or regrowth of sponges had occurred after 1 year. In that study, sponges observed with damaged tissue all had jagged wounds and there was no evidence of rounding or smoothing of damaged tissues that would have indicated healing. We observed many sponges with necrotic and/or missing tissues. Some of the specimens with missing tissues appeared to have smooth edges where it is possible that tissue may have been removed at an earlier point and then subsequently, jagged edges had "healed" (Fig. 3). However, we feel it speculative to acknowledge or quantify repair or regrowth without confirmed observations of individual specimens over multiple occasions. Van Dolah et al. (1987) observed many sponges (mainly *Cliona* sp.) with damaged tissues immediately after trawling. However, 1 year later, the damage was not readily apparent since divers could not distinguish between damaged and undamaged specimens. The authors cautioned that although the *Cliona* sp. in that study were able to regenerate damaged tissues, it may take several years for the damaged specimens to recover to their original size given the slow inherent growth rate of the species. In a manipulative study in British Columbia, *Rhabdocalyptus dawsoni* demonstrated rapid tissue regeneration (Leys and Lauzon (1998). In that study, tissues removed with a coring device were replaced at 0.05±0.03 cm^2 day^{-1}, a rate 40% faster than the average growth rate they calculated for whole sponges (Leys and Lauzon 1998). Given this rapid rate of regeneration, it would have been unlikely to observe tissue damage among *Rhabdocalyptus dawsoni* caused by trawling 13 years previous because the wounds would presumably be healed and not particularly obvious. Indeed, out of the 726 *Rhabdocalyptus dawsoni* we observed in all transects combined, only 2 specimens displayed tissue damage. Likewise, Freese (2001) did not observe tissue injuries among *Rhabdocalyptus dawsoni* one year after trawling.

Prone sponges were observed in both the reference and trawled areas; however, the percentage of prone sponges was significantly higher in the trawled areas. Although few tissue injuries of *Rhabdocalyptus dawsoni* were observed, many specimens in both the trawl and reference areas were prone. Several of the prone *Rhabdocalyptus dawsoni* were attached to small diameter (<10 cm) rocks that were unconsolidated with other seafloor substrates. These relatively small rocks may not provide a strong anchor against horizontal forces. Therefore, it is possible that many of the prone *Rhabdocalyptus dawsoni* were displaced by natural phenomenon such as strong currents or interactions with mobile organisms such as basket stars. Furthermore, undisturbed *Rhabdocalyptus dawsoni* do not necessarily orient themselves with their osculum facing upward. Leys and Lauzon (1998) observed *Rhabdocalyptus dawsoni* specimens that had naturally grown with their osculum oriented down. Therefore, it is possible that some of the *Rhabdocalyptus dawsoni* we categorized as prone may have naturally initiated their growth parallel to the seafloor rather than in the typical vertical orientation. Although some displaced sponge species may alter their growth forms in order to maximize planktonic food intake (ICES 2009), we did not observe any prone *Rhabdocalyptus* *dawsoni* with obvious growth form changes.

The rate of damage observed in both reference and trawl areas during close-up observations was generally higher than that observed during strip transects. The percentage of damaged sponges observed in trawled areas was 15.3% on strip transects and 40.1% on close-up observations. This result is not surprising given the more thorough observations we were able to complete during close-up observations. A full 360° revolution around individual specimens, compared with a passing observation at items up to 5 m distant on strip transects, provided more opportunity to identify partially damaged biota. Close-up observations are a superior method for identifying less obvious damage and probably provide the most accurate characterization of sponge condition. However, it is more appropriate to use the results from our strip transect observations for comparison with previous studies since those methods closely replicated earlier protocols.

4.2. Sponge Vulnerability

The nature and extent of sponge damage from trawling is influenced by the size and shape of individual specimens. Sponges that extend upward from the seafloor are more vulnerable to damage than low-lying encrusting type sponges (Wassenberg et al. 2002, Jørgensen et al. 2016). Also, the skeletal structure of sponges, their attachments to seafloor substrates, and the type of substrate they are attached to vary by species. These differences make some species more vulnerable to trawl disturbances and incur different types of injuries. For instance, the rigid and friable nature of *Farrea occa* makes them unable to absorb impact or bend under the force of mobile fishing gear. Therefore, a sponge of this type could be reduced to rubble when impacted by trawl gear and little evidence of the intact sponge may remain. Other species, such as *Mycale loveni* and *Rhabdocalyptus dawsoni* are more flexible and thus may be more resilient to disturbance. Our results indicate that *Mycale loveni* was more likely to have flesh injuries than to be prone. Conversely, the number of prone *Rhabdocalyptus dawsoni* was far greater than the number with flesh damage. The difference observed between these two species may be related to their seafloor attachments. *Mycale loveni* are usually attached to larger rocks and have a broader attachment whereas *Rhabdocalyptus dawsoni* are often attached to small rocks by a narrow attachment. Thus, a passing trawl is more likely to tear the tissue of a solidly attached *Mycale loveni* while a *Rhabdocalyptus dawsoni*, attached to a small rock, is more likely to be tipped over or perhaps even retained in the net. If the latter is true, the large density difference we observed between reference and trawl area *Rhabdocalyptus dawsoni* may be at least partially related to removals by the trawls that took place 13 years previously. In fact, Freese et al. (1999) reported that "...substantial quantities of broken sponge and other material were brought up in the trawl, but individual specimens could not be enumerated."

4.3. Management Implications

The descriptions of trawl effects detailed in this paper, as well those described in Freese et al. (1999) and Freese (2001) characterize the effect of a single trawl pass. It is common practice, however, for trawlers to repeat successful tows over roughly the same paths along the seafloor. In the Bering Sea and Gulf of Alaska, many areas were trawled more than 5 times per year and one area was trawled 17 times per year between 1997 and

2001 (Rose & Jorgensen 2005). Similar rates have been reported in heavily trawled areas on both sides of the Atlantic Ocean as well (Floderus & Pihl 1990, Auster et al. 1996). The net result of concentrated trawl effort tends to accumulate effects on benthic organisms. Moran & Stephenson (2000) estimated that a single pass of a demersal trawl "destroyed" 15.5% of benthic organisms larger than 20 cm; after 4 trawl passes the density of these organisms was reduced by about half. Over time, repeated disturbance to these long-lived organisms may alter species compositions and ultimately benthic communities. For example, in the Barents Sea, the density of some benthic organisms, especially sponges, was negatively correlated with fishing intensity whereas densities of other taxa were positively correlated (Buhl-Mortensen et al. 2016). Sainsbury et al. (1997) postulated that benthic community shifts occurred during a period of intensive trawling on the northwest Australian shelf. Epibenthic organisms, including sponges, greatly decreased concomitantly with decreases in targeted fish populations, while non-targeted, low value, fish populations increased.

The persistence of damage we observed and the potential resultant changes to benthic community structure provide rationale for cautious management of bottom trawling in areas where deepwater habitat-forming biota, such as large erect sponges, is present. Maintaining fisheries depends upon maintaining healthy ecosystems. Fishery managers must take into account the effect fishing has on the seafloor and benthic communities. In the United States, provisions in the Magnuson-Stevens Fishery Conservation and Management Act mandate that the effects of fishing on habitat should be minimized to practicable extents. Similar policies and regulations are in place in other parts of the world as well but, maintaining a balance between fishery production and habitat protection is no small challenge. In higher latitudes and deepwater, little is known about the basic life history and recovery dynamics of many benthic habitat-forming organisms. Growth, recruitment and recovery rates of these deepsea biota are essential information for quantifying impacts and determining the sustainability of anthropogenic seafloor disturbances, such as bottom trawling. Hopefully the results from this study will resolve questions about the persistence of damage in benthic ecosystems and provide managers greater insight when evaluating the effects of fisheries. Using the results from this and similar studies to parameterize fishing impact models, such as that of Fujioka (2006), will aid in decision making when contemplating conservation measures that mitigate and/or protect habitat and may ultimately facilitate marine spatial planning and ecosystem-based management (Ehler & Douvere 2009).

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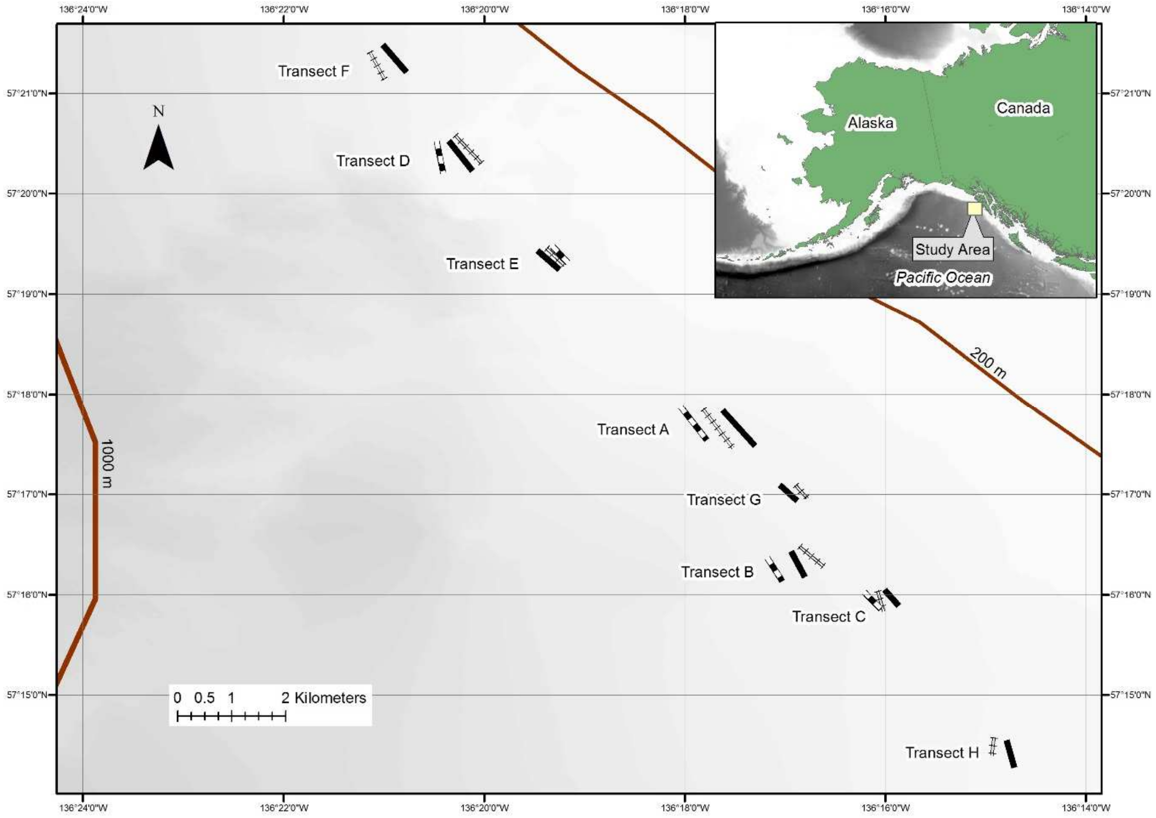

Fig. 1. Map of study area including eight trawl transects (solid black lines) and paired reference transects from 1996 (railroad tracks) and 2009 (dashed lines). In 1996, all trawl transects were observed. In 1997, transects A, D, and E were observed. In 2009, strip transects A, B, C, D, and E were observed. Locations of the paired reference transects observed in 1997 are not available.

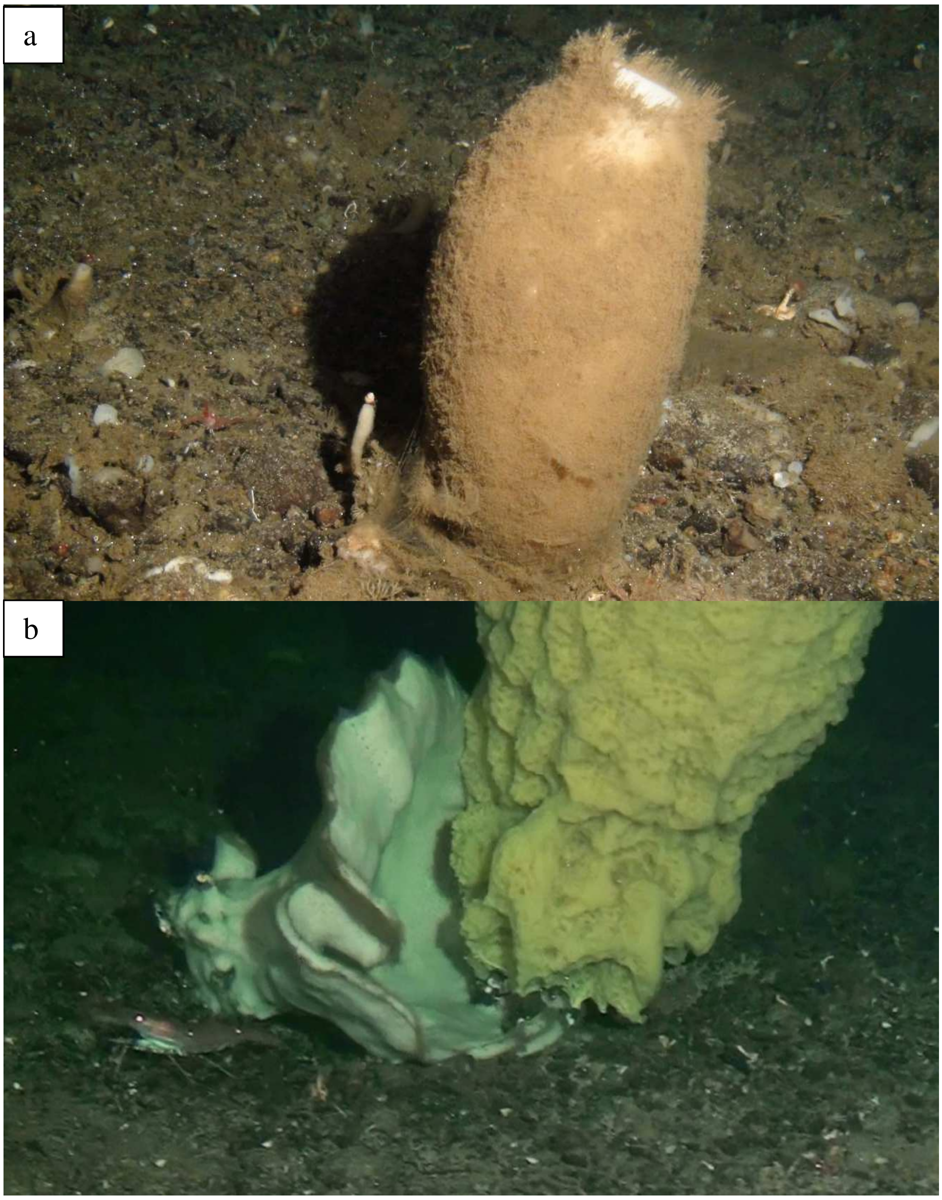

Fig. 2. a) An undisturbed *Rhabdocalyptus dawsoni*, the most commonly observed sponge in the study area. b) A basket-shaped *Poecillastra tenuilaminaris* (left) lying prone at the base of a *Mycale loveni* specimen (right).

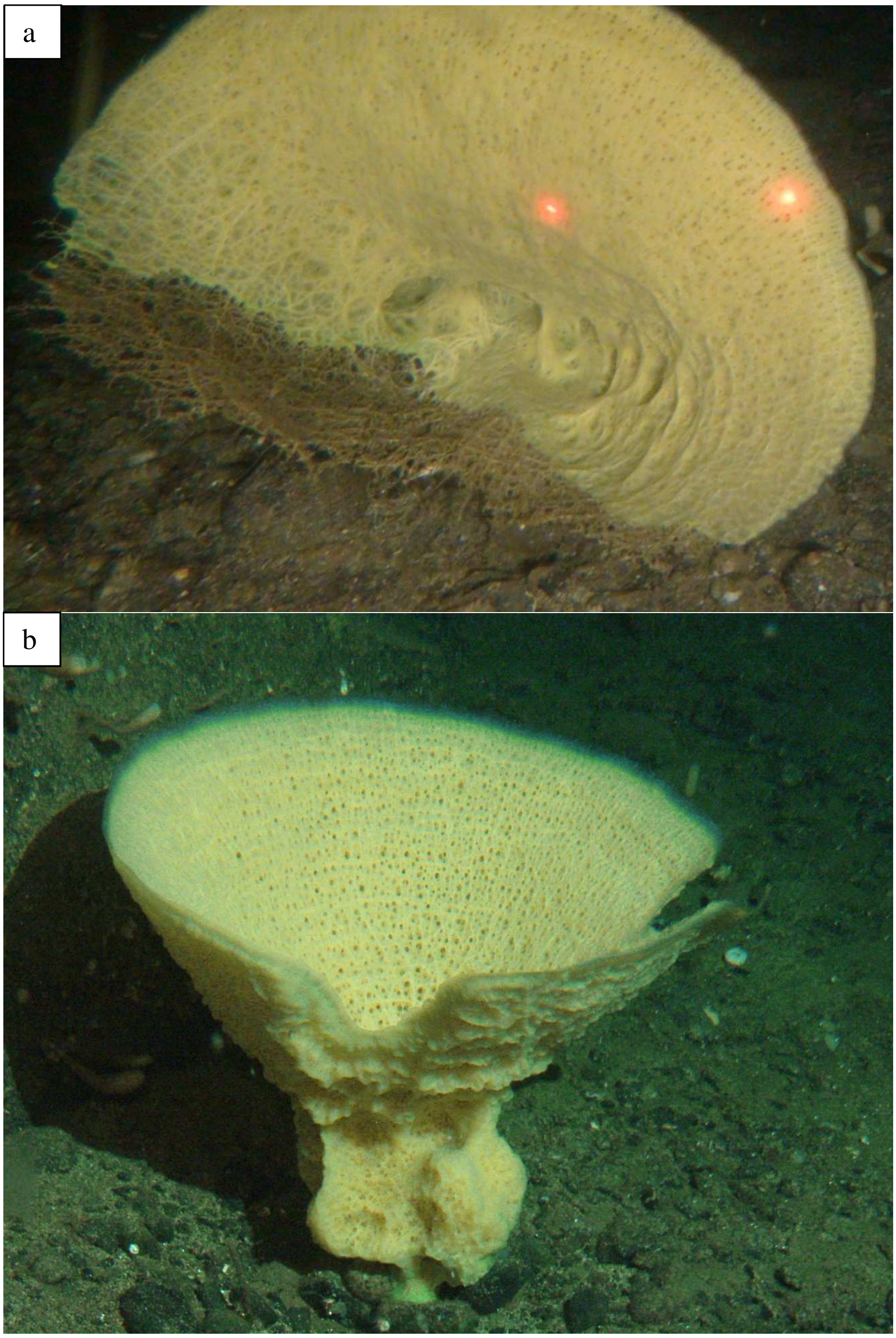

Fig. 3. Examples of tissue injuries among *Mycale loveni*. a) A partially necrotic specimen lying in a prone position. Distance between lasers is 20 cm. b) Specimen with missing tissue in two locations on upper margin. Note smooth edges of tissue where flesh is absent.

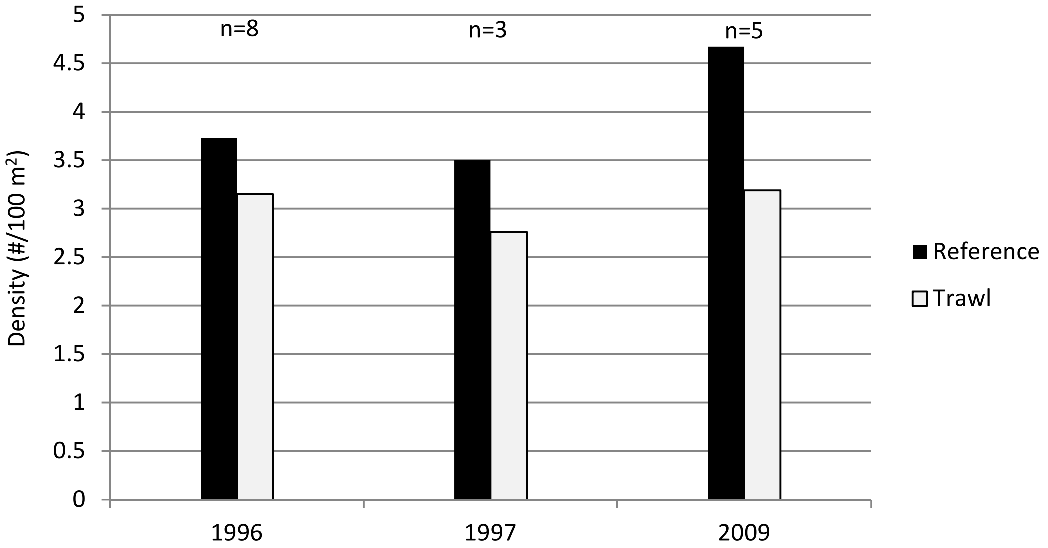

Fig. 4. Average density (number 100 m^{-2}) of sponges in reference and trawled areas near Salisbury Sound immediately after trawling (1996), 1 yr post-trawling (1997) and 13 yr post-trawling (2009). Data from 1996 is from Freese et al. (1999); data from 1997 is from Freese (2001).

Table 1. Strip transect start and end locations, depth (m), percent slope, and years observed. Trawl transects are identified by single letter designations; their paired reference transects are identified by the letter designation followed by "-Ref". Locations of reference transects observed in 1997 are not available.

Transect	Start Latitude	Start Longitude	Start Depth	End Latitude	End Longitude	End Depth	Slope	1996	1997	2009
A	57.2914	136.2884	209	57.2973	136.2937	208	0.14%	X	X	X
A-Ref 1	57.2910	136.2920	208	57.2975	136.2970	208	0.00%	X		
A-Ref 2	57.2924	136.2964	208	57.2979	136.3007	208	0.00%			X
B	57.2739	136.2823	208	57.2696	136.2800	209	0.20%	X		X
B-Ref 1	57.2747	136.2810	210	57.2714	136.2770	209	0.23%	X		
B-Ref 2	57.2728	136.2863	210	57.2689	136.2838	211	0.22%			X
C	57.2675	136.2668	212	57.2648	136.2645	212	0.00%	X		X
C-Ref 1	57.2673	136.2680	210	57.2639	136.2670	210	0.00%	X		
C-Ref 2	57.2643	136.2674	212	57.2671	136.2701	211	0.28%			X
D	57.3371	136.3353	208	57.3421	136.3392	208	0.00%	X	X	X
D-Ref 1	57.3382	136.3340	205	57.3419	136.3390	208	0.59%	X		
D-Ref 2	57.3421	136.3413	207	57.3368	136.3401	212	0.85%			X
E	57.3207	136.3209	209	57.3239	136.3245	209	0.00%	X	X	X
E-Ref 1	57.3240	136.3230	207	57.3212	136.3200	207	0.00%	X		
E-Ref 2	57.3244	136.3224	207	57.3216	136.3199	208	0.29%			X
F	57.3540	136.3465	201	57.3579	136.3500	199	0.42%	X		
F-Ref 1	57.3525	136.3499	202	57.3568	136.3523	198	0.80%	X		
G	57.2826	136.2817	209	57.2848	136.2840	209	0.00%	X		
G-Ref 1	57.2828	136.2810	206	57.2838	136.2820	206	0.00%	X		
H	57.2427	136.2458	210	57.2382	136.2460	210	0.00%	X		
H-Ref 1	57.2426	136.2487	210	57.2406	136.2489	210	0.00%	X		

Table 2. Close-up observation transect start and end locations, depth (m), and percent slope. Trawl transects are identified by single letter designations; their paired reference transects are identified by the letter designation followed by "-Ref".

Transect	Start Latitude	Start Longitude	Start Depth	End Latitude	End Longitude	End Depth	Slope
B	57.2700	136.2806	209	57.2741	136.2828	208	0.21%
B-Ref	57.2749	136.2794	210	57.2713	136.2773	209	0.24%
C	57.2648	136.2656	212	57.2674	136.2670	212	0.00%
C-Ref	57.2679	136.2641	211	57.2653	136.2628	212	0.33%
D	57.3417	136.3391	208	57.3393	136.3374	208	0.00%
D-Ref	57.3369	136.3313	212	57.3330	136.3314	209	0.69%
E	57.3243	136.3234	209	57.3225	136.3224	209	0.00%
E-Ref	57.3220	136.3272	208	57.3205	136.3255	207	0.51%
G	57.2849	136.2838	209	57.2824	136.2814	209	0.00%
G-Ref	57.2838	136.2791	210	57.2820	136.2759	210	0.00%

Table 3. Number of sponges observed (all species combined), area observed (100 m^2), and density of sponges (number 100 m^{-2}) on paired strip transects in reference and trawl areas near Salisbury Sound 13 yr post-trawling.

	Reference			Trawl		
Transect	# Observed	Area	Density	# Observed	Area	Density
A	153	48.27	3.17	55	36.84	1.49
B	224	22.90	9.78	129	25.02	5.16
C	66	17.70	3.73	51	16.47	3.10
D	81	29.48	2.75	85	31.37	2.71
E	67	17.03	3.94	73	20.79	3.51
Mean	118.20	27.08	4.67	78.60	26.10	3.19

Table 4. Average density (number 100 m^{-2}), range of observed densities, average percentage of damaged individuals, average percentage of torn individuals, and average percentage of prone individual sponges observed by species on five paired strip transects in trawl and reference areas near Salisbury Sound, 13 yr post-trawling. Averages are based on five transects in each of the trawl and reference areas. Percent damaged is the sum of percent torn (category 2) and percent prone (category 3).

	Average density		Density range		Average % damaged		Average % torn		Average % prone	
	Ref	Trawl	Ref	Trawl	Ref	Trawl	Ref	Trawl	Ref	Trawl
Hexactinellida										
Acanthascus koltuni	0.10	0.13	0.00-0.35	0.03-0.36	0.0	3.3	0.0	3.3	0.0	0.0
Rhabdocalyptus dawsoni	2.91	1.57	0.65-8.12	0.45-3.72	4.9	8.2	0.0	0.0	4.9	8.2
Farrea occa	0.22	0.17	0.00-0.37	0.00-0.40	1.1	0.0	1.1	0.0	0.0	0.0
Demospongiae										
Axinella rugosa	0.01	0.04	0.00-0.03	0.00-0.13	0.0	0.0	0.0	0.0	0.0	0.0
Isodictya quatsinoensis	0.02	0.05	0.00-0.06	0.00-0.12	6.7	26.7	0.0	6.7	6.7	20.0
Mycale loveni	0.83	0.71	0.00-1.82	0.06-1.11	5.7	37.0	5.7	31.4	0.0	5.6
Poecillastra tenuilaminaris	0.59	0.53	0.25-1.12	0.32-1.15	8.8	19.3	1.1	9.5	7.8	9.8
All species combined	4.67	3.19	2.75-9.78	1.49-5.16	6.3	15.3	1.1	6.5	5.2	8.8

Table 5. Number of sponges observed (all species combined), percentage of damaged individuals, percentage of torn individuals, and percentage of prone individual sponges observed by transect on five paired close-up observations in trawl and reference areas near Salisbury Sound, 13 yr post-trawling. Percent damaged is the sum of percent torn (category 2) and percent prone (category 3).

	Number observed		Percent damaged		Percent torn		Percent prone	
Transect	Ref	Trawl	Ref	Trawl	Ref	Trawl	Ref	Trawl
B	45	32	4.4	46.9	4.4	12.5	0.0	34.4
C	23	54	13.0	33.3	0.0	5.6	13.0	27.8
D	26	58	11.5	31.0	0.0	12.1	11.5	19.0
E	61	59	18.0	44.1	11.5	28.8	6.6	15.3
G	110	53	8.2	45.3	3.6	18.9	4.5	26.4
Mean	53.0	51.2	11.0	40.1	3.9	15.6	7.1	24.6

Table 6. Average number of sponges observed, average percentage of damaged individuals, average percentage of torn individuals, average percentage of prone individuals, average percentage of missing tissue, average percentage of necrotic tissue, and average size of sponges observed during close-up observations in trawled and reference areas near Salisbury Sound, 13 yr post-trawling. Averages are based on five paired transects in each of the trawl and reference areas. Percent damaged is the sum of percent torn (category 2) and percent prone (category 3). Size was estimated by comparison to scaling lasers and was recorded as the longest axis of each individual.

	Average number observed		Average percent damaged		Average percent torn		Average percent prone		Average percent missing		Average percent necrotic		Average size (cm)	
	Ref	Trawl	Ref	Trawl	Ref	Trawl	Ref	Trawl	Ref	Trawl	Ref	Trawl	Ref	Trawl
Hexactinellida														
Acanthascus koltuni	7.4	6.0	4.0	18.1	2.0	7.3	2.0	10.8	0	0.6	0.2	0.7	29.4	29.6
Rhabdocalyptus dawsoni	16.6	17.6	5.1	24.6	0.0	1.1	5.1	23.5	0.0	0.2	0.0	0.0	27.7	24.4
Aphrocalistes vastus	0.2	0.0	0.0	--	0.0	--	0.0	--	0.0	--	0.0	--	20.0	--
Farrea occa	0.6	1.2	0.0	33.3	0.0	33.3	0.0	0.0	0.0	0.0	0.0	2.3	25.0	22.9
Demospongiae														
Isodictya quatsinoensis	1.4	1.2	20.0	40.0	0.0	6.7	20.0	33.3	0.5	0.3	0.0	0.7	21.7	22.5
Mycale loveni	23.0	17.2	9.8	41.6	5.0	24.4	4.8	17.2	1.8	5.7	3.1	3.5	41.3	41.1
Poecillastra tenuilaminaris	3.8	8.0	16.7	57.1	11.7	22.5	5.0	34.6	3.4	7.7	1.5	1.3	31.1	26.7
All species combined	53.0	51.2	11.0	40.1	3.9	15.6	7.1	24.6	1.0	3.8	1.5	2.1	33.8	30.3

Supplementary Material

Table 7. Density, number observed, percentage damaged, percentage torn, and percentage of prone sponges observed on strip transects by class, species, and transect in trawled and reference areas near Salisbury Sound, 13 yr post-trawling. Percent damaged is the sum of percent torn (category 2) and percent prone (category 3). Averages by species are calculated from five transects each in trawl and reference area.

	Density		Number		Percent damaged		Percent torn		Percent prone	
	Ref	Trawl	Ref	Trawl	Ref	Trawl	Ref	Trawl	Ref	Trawl
Hexactinellida										
Acanthascus koltuni										
Transect A	0.10	0.05	5	2	0.0	0.0	0.0	0.0	0.0	0.0
Transect B	0.35	0.16	8	4	0.0	0.0	0.0	0.0	0.0	0.0
Transect C	0.00	0.36	0	6	0.0	16.7	0.0	16.7	0.0	0.0
Transect D	0.03	0.03	1	1	0.0	0.0	0.0	0.0	0.0	0.0
Transect E	0.00	0.05	0	1	0.0	0.0	0.0	0.0	0.0	0.0
Average	0.10	0.13	2.80	2.80	0.0	3.3	0.0	3.3	0.0	0.0
Rhabdocalyptus dawsoni										
Transect A	1.86	0.65	90	24	6.7	4.2	0.0	0.0	6.7	4.2
Transect B	8.12	3.72	186	93	1.6	10.8	0.0	0.0	1.6	10.8
Transect C	2.82	1.94	50	32	16.0	18.8	0.0	0.0	16.0	18.8
Transect D	1.09	0.45	32	14	0.0	7.1	0.0	0.0	0.0	7.1
Transect E	0.65	1.11	11	23	0.0	0.0	0.0	0.0	0.0	0.0
Average	2.91	1.57	73.80	37.20	4.9	8.2	0.0	0.0	4.9	8.2
Farrea occa										
Transect A	0.37	0.03	18	1	5.6	0.0	5.6	0.0	0.0	0.0
Transect B	0.09	0.40	2	10	0.0	0.0	0.0	0.0	0.0	0.0
Transect C	0.34	0.30	6	5	0.0	0.0	0.0	0.0	0.0	0.0
Transect D	0.00	0.00	0	0	0.0	0.0	0.0	0.0	0.0	0.0
Transect E	0.29	0.10	5	2	0.0	0.0	0.0	0.0	0.0	0.0
Average	0.22	0.17	6.20	3.60	1.1	0.0	1.1	0.0	0.0	0.0
Demospongiae										
Axinella rugosa										
Transect A	0.00	0.00	0	0	0.0	0.0	0.0	0.0	0.0	0.0
Transect B	0.00	0.00	0	0	0.0	0.0	0.0	0.0	0.0	0.0
Transect C	0.00	0.06	0	1	0.0	0.0	0.0	0.0	0.0	0.0
Transect D	0.03	0.13	1	4	0.0	0.0	0.0	0.0	0.0	0.0
Transect E	0.00	0.00	0	0	0.0	0.0	0.0	0.0	0.0	0.0
Average	0.01	0.04	0.20	1.00	0.0	0.0	0.0	0.0	0.0	0.0
Isodictya quatsinoensis										
Transect A	0.06	0.08	3	3	33.3	33.3	0.0	0.0	33.3	33.3
Transect B	0.00	0.12	0	3	0.0	100.0	0.0	33.3	0.0	66.7
Transect C	0.00	0.00	0	0	0.0	0.0	0.0	0.0	0.0	0.0
Transect D	0.00	0.03	0	1	0.0	0.0	0.0	0.0	0.0	0.0
Transect E	0.06	0.00	1	0	0.0	0.0	0.0	0.0	0.0	0.0
Average	0.02	0.05	0.80	1.40	6.7	26.7	0.0	6.7	6.7	20.0
Mycale loveni										
Transect A	0.52	0.30	25	11	0.0	18.2	0.0	9.1	0.0	9.1
Transect B	0.87	0.44	20	11	25.0	18.2	25.0	18.2	0.0	0.0
Transect C	0.00	0.06	0	1	0.0	100.0	0.0	100.0	0.0	0.0
Transect D	0.92	1.66	27	52	3.7	26.9	3.7	21.2	0.0	5.8
Transect E	1.82	1.11	31	23	0.0	21.7	0.0	8.7	0.0	13.0
Average	0.83	0.71	20.60	19.60	5.7	37.0	5.7	31.4	0.0	5.6
Poecillastra tenuilaminaris										
Transect A	0.25	0.38	12	14	0.0	14.3	0.0	7.1	0.0	7.1
Transect B	0.35	0.32	8	8	12.5	12.5	0.0	0.0	12.5	12.5
Transect C	0.56	0.36	10	6	0.0	33.3	0.0	16.7	0.0	16.7
Transect D	0.68	0.41	20	13	0.0	15.4	0.0	15.4	0.0	0.0
Transect E	1.12	1.15	19	24	31.6	20.8	5.3	8.3	26.3	12.5
Average	0.59	0.53	13.80	13.00	8.8	19.3	1.1	9.5	7.8	9.8

Table 8. Total number of sponges individually observed during close-up observations, percent of damaged individuals, percent of torn (category 2), percent of prone (category 3), and average percentage of missing and necrotic tissue of sponges by transect in trawled and reference areas near Salisbury Sound, 13 yr post-trawling. Percent damaged is the sum of percent torn and percent prone. Averages by species are calculated from five transects each in trawl and reference areas.

	Number		Percent damaged		Percent torn		Percent prone		Percent missing		Percent necrotic	
	Ref	Trawl	Ref	Trawl	Ref	Trawl	Ref	Trawl	Ref	Trawl	Ref	Trawl
Hexactinellida												
Acanthascus koltuni												
Transect B	1	7	0.0	42.9	0.0	14.3	0.0	28.6	0.0	1.4	0.0	0.0
Transect C	0	7	0.0	14.3	0.0	0.0	0.0	14.3	0.0	0.0	0.0	0.0
Transect D	10	2	20.0	0.0	10.0	0.0	10.0	0.0	0.0	0.0	1.0	0.0
Transect E	26	5	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Transect G	0	9	0.0	33.3	0.0	22.2	0.0	11.1	0.0	1.7	0.0	3.3
Average	7.4	6.0	4.0	18.1	2.0	7.3	2.0	10.8	0.0	0.6	0.2	0.7
Rhabdocalyptus dawsoni												
Transect B	12	31	16.7	38.7	0.0	0.0	16.7	38.7	0.0	0.0	0.0	0.0
Transect C	17	35	5.9	20.0	0.0	5.7	5.9	14.3	0.0	0.9	0.0	0.0
Transect D	6	6	0.0	16.7	0.0	0.0	0.0	16.7	0.0	0.0	0.0	0.0
Transect E	37	7	2.7	14.3	0.0	0.0	2.7	14.3	0.0	0.0	0.0	0.0
Transect G	11	9	0.0	33.3	0.0	0.0	0.0	33.3	0.0	0.0	0.0	0.0
Average	16.6	17.6	5.1	24.6	0.0	1.1	5.1	23.5	0.0	0.2	0.0	0.0
Farrea occa												
Transect B	0	1	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Transect C	2	1	0.0	100.0	0.0	100.0	0.0	0.0	0.0	0.0	0.0	0.0
Transect D	0	0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Transect E	0	3	0.0	66.7	0.0	66.7	0.0	0.0	0.0	0.0	0.0	11.7
Transect G	1	1	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Average	0.6	1.2	0.0	33.3	0.0	33.3	0.0	0.0	0.0	0.0	0.0	2.3
Aphrocalistes vastus												
Transect B	0	0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Transect C	1	0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Transect D	0	0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Transect E	0	0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Transect G	0	0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Average	0.2	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Demospongiae												
Isodictya quatsinoensis												
Transect B	1	0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Transect C	2	3	100.0	100.0	0.0	33.3	100.0	66.7	2.5	1.7	0.0	3.3
Transect D	0	0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Transect E	4	0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Transect G	0	3	0.0	100.0	0.0	0.0	0.0	100.0	0.0	0.0	0.0	0.0
Average	1.4	1.2	20.0	40.0	0.0	6.7	20.0	33.3	0.5	0.3	0.0	0.7
Mycale loveni												
Transect B	9	12	11.1	16.7	0.0	16.7	11.1	0.0	5.6	1.7	11.1	0.0
Transect C	0	3	0.0	33.3	0.0	33.3	0.0	0.0	0.0	3.3	0.0	3.3
Transect D	37	34	13.5	52.9	10.8	35.3	2.7	17.6	1.8	9.1	1.4	6.8
Transect E	40	29	17.5	55.2	7.5	24.1	10.0	31.0	1.3	7.6	2.8	3.1
Transect G	29	8	6.9	50.0	6.9	12.5	0.0	37.5	0.5	6.9	0.3	4.4
Average	23.0	17.2	9.8	41.6	5.0	24.4	4.8	17.2	1.8	5.7	3.1	3.5
Poecillastra tenuilaminaris												
Transect B	0	3	0.0	33.3	0.0	0.0	0.0	33.3	0.0	0.0	0.0	0.0
Transect C	4	9	0.0	55.6	0.0	22.2	0.0	33.3	0.0	3.3	0.0	1.7
Transect D	8	17	50.0	41.2	25.0	29.4	25.0	11.8	3.8	2.9	7.5	5.0
Transect E	3	9	33.3	55.6	33.3	11.1	0.0	44.4	13.3	22.2	0.0	0.0
Transect G	4	2	0.0	100.0	0.0	50.0	0.0	50.0	0.0	10.0	0.0	0.0
Average	3.8	8.0	16.7	57.1	11.7	22.5	5.0	34.6	3.4	7.7	1.5	1.3

Table 9. Average size (cm), range of sizes (cm), and number of sponges by transect individually observed on close-up observations in trawled and reference areas near Salisbury Sound, 13 yr post-trawling. Composite numbers are averages or ranges for all transects combined. Size was estimated by comparison to scaling lasers and was recorded as the longest axis of each individual. Only specimens larger than 20 cm, in any dimension, were observed.

	Average size (cm)		Range (cm)		Number	
	Ref	Trawl	Ref	Trawl	Ref	Trawl
Hexactinellida						
Acanthascus koltuni						
Transect B	20.0	26.4	20-20	20-50	1	7
Transect C	-	25.0	-	20-30	0	7
Transect D	37.0	25.0	20-100	20-30	10	2
Transect E	31.3	42.0	20-70	30-60	26	5
Transect G	-	29.4	-	20-40	0	9
Composite	29.4	29.6	20-100	20-60		
Rhabdocalyptus dawsoni						
Transect B	30.0	21.9	20-80	20-35	12	31
Transect C	23.5	24.4	20-50	20-60	17	35
Transect D	26.7	21.7	20-40	20-25	6	6
Transect E	22.6	27.1	20-35	20-50	37	7
Transect G	35.5	26.7	20-60	20-60	11	9
Composite	27.7	24.4	20-80	20-60		
Farrea occa						
Transect B	-	20.0	-	20-20	0	1
Transect C	20.0	25.0	20-20	25-25	2	1
Transect D	-	-	-	-	0	0
Transect E	-	26.7	-	20-40	0	3
Transect G	30.0	20.0	30-30	20-20	1	1
Composite	25.0	22.9	20-20	20-40		
Aphrocalistes vastus						
Transect B	-	-	-	-	0	0
Transect C	20.0	-	20-20	-	1	0
Transect D	-	-	-	-	0	0
Transect E	-	-	-	-	0	0
Transect G	-	-	-	-	0	0
Composite	20.0	-	20-20	-		
Demospongiae						
Isodictya quatsinoensis						
Transect B	20.0	-	20-20	-	1	0
Transect C	22.5	20.0	20-25	20-20	2	3
Transect D	-	-	-	-	0	0
Transect E	22.5	-	20-30	-	4	0
Transect G	-	25.0	-	20-30	0	3
Composite	21.7	22.5	20-30	20-30		
Mycale loveni						
Transect B	38.3	38.8	25-60	20-75	9	12
Transect C	-	50.0	-	40-60	0	3
Transect D	46.6	36.0	20-80	20-80	37	34
Transect E	35.8	43.1	20-70	20-80	40	29
Transect G	44.3	37.5	20-80	25-45	29	8
Composite	41.3	41.1	20-80	20-80		
Poecillastra tenuilaminaris						
Transect B	-	28.3	-	20-35	0	3
Transect C	32.5	26.7	25-50	20-40	4	9
Transect D	35.0	30.0	20-50	20-50	8	17
Transect E	21.7	26.1	20-25	20-35	3	9
Transect G	35.0	22.5	20-50	20-25	4	2
Composite	31.1	26.7	20-50	20-50		