Evaluation of Benthic Habitats
in Bering Sea Submarine Canyons

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Executive Summary

The goal of this report is to evaluate existing data from benthic habitat studies conducted in submarine canyons in the Bering Sea. The primary objective is to evaluate data from the studies conducted by Brodeur (2001) at Pribilof Canyon and the study by Miller et al. (2012) at Pribilof and Zhemchug canyons to provide a context to evaluate the importance of structure-forming invertebrates in these areas as potential habitat for fishes.

Submarine canyons are prominent geomorphic features that can have a major influence on local and regional oceanographic conditions and flow patterns that can greatly enhance the primary production within the canyon and on the surrounding continental shelves. Local concentrations of plankton, fish and structure-forming invertebrates such as corals and sponges may be enhanced in and around shelf-break canyons. However, the distribution of corals and sponges is often limited to high-productivity areas along the shelf-slope break where current patterns are stable and expose underlying hard substrates such as rocky outcrops, boulders, and pebble/gravel habitats.

Analysis of the video from Brodeur's (2001) study at the NW head of Pribilof Canyon showed that overall coral and sponge densities were low but aggregations of sea pens (*Halipteris willemoesi*) inhabited by skates, Pacific cod (*Gadus macrocephalus*), and schools of Pacific ocean perch (*Sebastes alutus*) were observed. Occasional high sponge densities were also observed in mud/pebble habits. However, these sponges were generally small in size and simply branched in form, providing low structural relief.

Evaluation of a subset of the imagery used in the Miller et al. (2012) study was completed with the goal of conducting an independent evaluation of the experimental design, image quality, analysis, and applicability of the results presented in the study and to reveal any additional information not evident in the published paper. Our analyses found several important shortcomings in the study which had a major effect on the interpretation of the results. Specifically these included: 1) poor and variable image quality; 2) reduced ability to accurately classify habitats and identify and count corals and sponges; 3) bias in habitat analyses towards hard substrates; 4) bias in estimates of coral and sponge abundances; 5) overemphasis of the abundance and distribution of corals and sponges; and 6) overestimation of the extent of fish use of corals and sponges. Together, these issues indicate that their study has serious shortcomings which undermine both the results and the interpretation of the results as presented in the published paper. Of greatest importance is the limits placed on the statistical inferences of the study based on their experimental design due to: 1) non-random sampling; 2) inadequate sampling effort; and 3) unbalanced (or no) replication of dive sites. Combined these factors indicate that the study cannot be used to draw broad and general conclusions regarding the abundance and distribution of structure-forming invertebrates and benthic habitats in Pribilof and Zhemchug canyons.

Comparisons with similar studies of submarine canyons and shelf-slope breaks in Alaska and along the US west coast indicate that the only notable observation from these comparisons is the relatively high density estimates we found for gorgonians in

the Miller et al. (2012) study. As such, this result has the potential to be an important observation. However, when compared to other high coral areas such as the Aleutian Islands "coral gardens" the coral data collected at Pribilof and Zhemchug canyons had significantly lower average and maximum abundance, smaller size, greatly reduced coverage on the seafloor, including a narrower depth range, and lower species diversity. Thus, data from the corals in these two areas show strikingly different ecological patterns and should not be considered similar in any meaningful way. Moreover, given the extensive problems found in experimental design, image quality, methodology, and estimates of distribution and abundance, the validity of the gorgonian abundance estimates is highly suspect and thus not useful as a scientifically based estimate or for use in comparisons to other scientific studies or extrapolations to areas not sampled.

Future studies that use robust experimental designs based on the principles of randomization, replication, independence, and statistical power, along with greater sampling effort would provide important information that could address the distribution of corals and sponges in Pribilof and Zhemchug canyons.

Introduction

The goal of this report is to evaluate existing data from benthic habitat studies conducted in submarine canyons in the Bering Sea using submersibles with a focus on structure-forming invertebrates, primarily deep-sea corals and sponges. The primary objective is to evaluate data from the studies conducted by Brodeur (2001) at Pribilof Canyon and the study by Miller et al. (2012) at Pribilof and Zhemchug canyons to provide a context for the importance of structure-forming invertebrates in these areas as potential essential fish habitat (EFH) for fishes. This objective will be accomplished by a critical review of these studies, both in terms of their experimental design, methodology and conclusions, and a comparison of the data from these studies relative to other studies of submarine canyons and continental shelf-slope breaks in Alaska and along the US west coast.

The review is organized into several components. First, the literature on submarine canyons is reviewed to provide a context for their ecology and ecological importance. Next, we review the studies by Brodeur (2001) and Miller et al. (2012) with a particular focus on the latter as it comprises the first study of corals and sponges in Pribilof and Zhemchug canyons. These reviews include an examination of the original Brodeur (2001) video and a subset of images used in the Miller et al. (2012) study including the metadata made available to the public from that project. In the latter study we also present an evaluation of the results and methodology relative to other US West Coast submersible studies and an analysis of the sampling design and methodology and the adequacy of the design to provide representative samples that can be used to draw general conclusions on the distribution of EFH in Pribilof and Zhemchug canyons.

Overview of Submarine Canyon Ecosystems

Submarine canyons are prominent geomorphic features consisting of a steep-sided valley cut into the seafloor. They are ubiquitous along continental and oceanic island margins and they help connect continental shelves to deep ocean basins

(Shepard & Dill 1966). Canyons can also provide important sources of heterogeneity with their often steep or rugged topography and exposure of multiple types of hard and soft substrates (Levin & Sibuet 2012). Previous research has shown that abundance and distribution of demersal invertebrate and fish species strongly correlated with depth as well as habitat patch types, position and configuration of these patches within the broader-scale landscape (Oliver & Slattery 1976; Yoklavich et al. 2000; Bianchi 2011).

Most organisms observed in canyons are not unique to canyon systems and are commonly found at similar depths outsides canyons (Allen & Pondella 2006). However, because submarine canyons extend from shallow waters to the deep sea, they contain an incredible diversity of organisms. Mobile fishes and invertebrates, such as rockfish and seastars, have been found to aggregate in canyon heads and along canyon walls. Rocky outcrops along canyon walls are colonized by sedentary and sessile invertebrates such as feather stars, corals and sponges and may provide shelter for a variety of fishes (Yoklavich et al. 2000; Bianchi 2011). Sea cucumbers and worms burrow into canyon walls (Oliver & Slattery 1976). The soft sediments on the canyon floor support a diverse and highly abundant community of invertebrates such as sea pens, sea cucumbers, brittle stars, sea stars and fishes such as flatfishes, ratfishes, whiptails, grenadiers, sablefish, hake, thornyheads. (Brown et al. 2012)

Submarine canyons can also have a major influence on local and regional oceanographic conditions and flow patterns. Canyons can enhance the cross-shore (along-canyon) flow by an order of magnitude (Allen 1996), but also generate and trap internal tidal energy such that the related mixing inside the canyon is orders of magnitude higher than in the open ocean. This greatly enhances the primary production within the canyon and on the surrounding shelves (Shea & Broenkow 1982; Kunze et al. 2002). Enhanced upwelling can occur within canyons (Hickey 1997; Martín et al. 2006), producing local vertical displacements of various water property isoclines (e.g., temperature, salinity, density, oxygen, nutrient concentration). Local concentrations of plankton and fish are also often enhanced in and around shelf-break canyons (Pereyra et al. 1969; Macquart-Moulin & Patriti 1996). Flow dynamics within canyons may also focus and amplify internal waves (Allen & De Madron, 2009) or create patches that vary in sedimentation, larval recruitment, and flow related disturbance (Allen et al. 2001, Kuhnze et al. 2002).

Submarine canyons also serve as two-way exchange, or flux of matter, between the benthos and the overlying water body, which is important for both benthic and pelagic compartments. Organic materials are transported from the continental shelf into deeper waters during form erosion and sediment slides on steep canyon slopes, as well as during periodic turbidity flows. These events create disturbance regimes which can regulate biological communities within submarine canyons (McClain & Barry 2010). Organic flux can also enter canyons as non-living organic matter (e.g., falling plankton, fecal pellets, and animal carcasses) as well as from terrigenous sources such as entrained marsh or seagrasses, kelps, and terrestrial plant materials (Vetter & Dayton 1999). In addition many marine organisms (including infaunal and epifaunal invertebrates and demersal fish) release eggs and/or larvae that are pelagic are advected and entrained in submarine canyons. Enriched food supplies can result in elevated concentrations of organisms ranging from planktonic species (Palanques et al.

2005), benthic meiofauna (De Leo et al. 2010), megafaunal taxa (including deep-sea corals; Mortensen & Buhl-Mortensen 2005; Vetter et al. 2010), and fishes (Stefanescu et al. 1994; Yoklavich et al. 2000). Aggregations can occur for a variety of reasons including enhanced food availably, higher production associated with upwelling, local topography preventing diel migratory planktonic organisms from returning to depth, and the concentration of plankton along topographically generated fronts (Genin 2004).

Our understanding of the role and importance of submarine canyons in many systems remains limited. Some studies have shown little evidence of canyons as unique habitats when compared to adjacent slope areas. For example Bianchelli et al. (2010) found no significant differences in total meiofaunal abundance, biomass, or taxa richness among six submarine canyons and five adjacent open slopes off the Portuguese and Adriatic margins. Another study of oceanic island canyons in the central Pacific showed that for some species megafaunal abundance was similar or higher on the slope than in submarine canyons, and these differences were typically driven by higher slope abundance of sessile suspension feeders or animals with limited mobility, i.e. by organisms which are likely to have difficulty with high currents and sediment transport in canyons (Vetter et al. 2010). Off Australia demersal fish biomass and species richness were not found to be significantly different between canyon and the adjacent shelf and slope, despite compelling oceanographic evidence for canyon-related upwelling (Currie et al. 2012). These studies and others suggest that our understanding of the causes of variations in benthos and trophic linkages with demersal fauna remain poorly understood (Brown et al., 2012).

Role of structure-forming invertebrates in submarine canyons

Three submarine canyons along the US west coast (Ascension, Astoria and Carmel) were characterized as having distinct macrofaunal invertebrate communities (Bianchi 2011). In all three canyons two distinct habitat assemblages were found consisting of soft- and hard-substrate dominated areas. Mobile invertebrates (e.g., brittle stars, sea stars, sea cucumbers, and arthropods) were among the most abundant taxa and were broadly distributed across all habitats while structure-forming invertebrates, such as sponges and corals, were limited to hard substrates on the canyon head and walls (Bianchi 2011). Similar observations have been made in submarine canyons by Hecker and her colleagues who surveyed the deep corals of several canyons off the northeastern U.S. in the 1980s via submersible and towed camera sled (Packer et al., 2007). Corals were denser and more diverse in the canyons than the continental margins, and some species, such as those restricted to hard substrates, were found only in canyons while corals adapted to soft substrate habitats were found both in canyons and on the continental slope (Packer et al., 2007). Surveys of three submarine canyons off Newfoundland, Canada found that corals occupied a broad range of habitats within the canyons but were most common and diverse on hard substrates (Baker et al. 2012) throughout the 351-2245m depths covered by the surveys.

Differences in the macrofaunal invertebrate communities among submarine canyons studied by Bianchi (2011) indicated that canyon geomorphology may have a strong influence on their biological and physical environments. Astoria Canyon, located at the mouth of the largest river on the West Coast of North America, is exposed to high

fluctuations in currents and sediment loading; Ascension Canyon, is somewhat isolated from coastal influences, and is exposed to open-ocean currents; and Carmel Canyon is protected within Carmel Bay and positioned at the mouth of a relatively small river. Moreover, the walls of Astoria and Ascension Canyons consist of softer clays and limestones, whereas the Carmel Canyon walls are composed largely of granodiorite rock. Thus, observed differences in the topography and geology across the canyons, when combined with patterns in invertebrate abundance, indicate that a broad range of microhabitats are formed in these canyons and result in varying abundances of structure-forming invertebrates.

In general, corals and sponges in submarine canyons favor areas with high currents, steep slopes, hard substrata and areas of low disturbance from sediment flows. As submarine canyons are characterized by high sediment loading and frequent sediment flows, the distribution of long-lived structure-forming invertebrates is often limited to high-productivity (i.e., upwelling) areas along the shelf-slope break or middle- and upper-slope where currents patterns are stable and hard substrates such as rocky outcrops, boulders, and pebble/gravel habitats are found (Packer et al., 2007; Stone and Shotwell, 2007; Baker et al., 2012).

The extent to which submarine canyons support higher abundances of corals and sponges relative to the adjacent continental shelf and shelf-slope break is poorly known as very few studies have addressed this important question. In submarine canyons along the northeastern U.S. corals were denser then adjacent continental margins (Packer et al., 2007). However, it is not clear to what extent these surveys reflect only areas where studies have been conducted as opposed to real patterns (Lumsden et al., 2007). In the NE Channel in the Atlantic between Georges and Browns Banks corals were found to be more common in the outer part of the channel along the shelf break and slope than on the inner shelf (Mortensen and Mortensen, 2004). Thus, the few studies available suggest that in some cases structure-forming invertebrates like corals and sponges may be locally more abundant in submarine canyons than their adjacent habitats. However, given the paucity of studies on submarine canyons the generality of these patterns is largely unknown.

Bering Sea Canyons

Submarine canyons play an important role in the Bering Sea ecosystem. In general the Bering Sea shelf is relatively smooth and featureless and it has one of the gentlest shelf gradients in the world (0.24 m/km (Sharma 1977). In this system submarine canyons contribute an important source of habitat heterogeneity, incising over 20% of the northeast Pacific shelf (Kuhnze et al. 2002). Three of the canyons found along the Bering Sea margin are among the world's largest; with Zhemchug Canyon an order of magnitude larger than the largest canyon off the west coast of the United States (Carlson & Karl 1988). At the regional shelf break, Zhemchug cuts a gorge 100km wide and 2,600m deep, and while it is largely dominated by submarine slides and extensive areas of mobile soft sediments it also contains large scarps with relief as great as 2,500m and slopes as steep as 21° (Carlson & Karl 1988). While Pribilof Canyon is smaller than Zhemchug Canyon, it is a 45km wide and 1,600m deep steep-walled V-shaped canyon at the shelf break that transitions to a U-shaped deep-sea fan channel at deeper depths. It also contains extensive areas of coarse grained

materials including siltstone, sandstone, and pebble deposits left from debris flows as well as the more dominant mud and sand sediments (Carlson & Karl 1988).

Primary and secondary production is also affected by submarine canyons. While tides and the Bering Slope Current predominantly flow to the northwest, paralleling the continental slope, they are complicated by countercurrents and eddies developed near the canyons (Kinder et al. 1975). The interaction of strong tidal currents with the abrupt, steep shelf break promotes upwelling at the front (Coachman, 1986), which also helps supply nutrients to the euphotic zone. As a result, primary production apparently remains elevated throughout summer, long after the termination of the spring bloom (Iverson et al. 1979; Karl & Carlson 1987). Similarly the greatest biomass of zooplankton occurs along the shelf edge or "green belt", where annual zooplankton can reach as high as 64 g C m^{-2} y^{-1} (Cooney 1981; Vidal & Smith 1986).

The Bering Sea supports an invertebrate community dominated by polychaetes and bivalves as infauna while crabs and sea stars dominate the benthic epifauna (Yeung and McConnaughey, 2006). Although the coral fauna of this region has not been well documented it does not appear to be particularly diverse (Stone & Shotwell 2007). Sixteen species or subspecies of coral are known from the Bering Sea, largely from trawl surveys, and many of these species habitats are limited to the broad, shallow continental shelf and along the narrow continental slope (Yeung and McConnaughey, 2006). Of these, gorgonian corals are known from these areas but are further restricted to habitats containing exposed hard substratum (Stone & Shotwell 2007). Soft corals (mostly *Gersemia rubiformis*) are the most common coral in the Bering Sea and can form dense aggregations on soft unconsolidated sediments of the continental shelf but they are not structure forming (Heifetz, 2002). Other corals include sea pens, which are uncommon (< 2% of all hauls) and have patchy distributions on the edge of the continental shelf (Malecha et al. 2005) and have been observed at the head of Pribilof Canyon (Brodeur 2001). Sponges account for 16% of living substrate observations in the Bering Sea, which is less than that which occurs in the Aleutians (67% of all hauls) and the Gulf of Alaska (43%) (Malecha et al. 2005).

Until relatively recently there were no fine-scale submersible studies in submarine canyons in the Bering Sea and thus no data were available to evaluate the role of structure forming invertebrates in submarine canyon ecosystems. However, observations by Brodeur (2001) in 1995 and 1997 at Pribilof canyon and Miller et al. (2012) in 2007 at Pribilof and Zhemchug canyons obtained data at a sufficiently fine spatial scale to provide useful information towards such an evaluation.

Evaluation of Brodeur (2001) study

Our evaluation focused on an independent analysis of the video used in the Brodeur (2001) paper with the goal of collecting information for an overall analysis of the role of structure-forming invertebrates as benthic habitats for fishes in Pribilof Canyon. We obtained copies of the original ROV video from Morgan Busby (NOAA Fisheries, AFSC). The reviewed imagery consisted of eight video dive transects collected between 1995 and 1997 using a Deep Ocean Engineering Super Phantom II ROV. The overall quality of the imagery used in the analyses was generally poor due to the lower quality video recording device used (color CCD video camera [Hitachi HV-C20], lighting

configuration [two 250W tungsten-halogen lights], and the reduced visibility due to high plankton concentrations). The video quality reduced the ability to identify small and cryptic organisms and to make species level identifications on some individuals; however, the video was of sufficient quality to give a general overview of the habitat, invertebrates, and fishes present.

Habitat distributions

In general the dive sites examined by Brodeur (2001) were shallow (184-243 m) and restricted to the upper (northwest) head of Pribilof canyon (Figure 1). The dives were almost exclusively conducted in muddy-sand habitats with occasional isolated boulders or cobbles. The video showed some areas of boulder-cobble habitat which were structurally complex but infrequent in their extent with a majority of the boulder-cobble habitat occurring during a ≈10 minute period at station 29 and a 2 minute period at stations 60 and 61 where mud-cobble was encountered, followed by an additional ≈8 minute period of less complex mud-pebble habitat.

Corals and Sponges

Overall coral and sponge densities were low and no gorgonian corals were observed within any of the videos. However, there were a significant number of pennatulacean sea pens (*Halipteris willemoesi*) in some of the areas (two of seven dives) surveyed by Brodeur which occurred in aggregations that were frequently inhabited by a variety of fishes, including rays, Pacific Cod (*Gadus macrocephalus*), and most notably large schools of Pacific ocean perch (*Sebastes alutus* or POP) (Figure 2). In addition to standing sea pens the video also showed a number of axial rods of sea pens scattered across the sea floor, including areas where there were no standing sea pens. Although Brodeur (2001) suggested that fishing activities may have been responsible for these observations, according to Gary Williams, an octocoral expert at the California Academy of Sciences, sea pens can be knocked over naturally if the bottom currents are strong and tall colonies are imbedded shallowly in the substrata (personal communication, 2/6/2013).

Sponge densities were generally low in mud dominated habitats but two of the dives at station 29 contained ≈10 minute period of boulder-cobble habitat as well as several small rock outcrops. Within these habitats larger sponges were encountered, as well as structurally complex aggregations of hydroids and plumose anemones (*Metridium giganteum*). High plankton concentrations and video technical problems reduced video image quality during this period which made it difficult to assess true invertebrate densities. However, areas of high sponge densities were observed during portions of the dives at station 60 and 61 in mud-pebble habits. The observed sponges were generally small in size and simply branched in form (Figure 2), providing low structural relief.

Fish-Coral/Sponge Associations

The fish species observed during the surveys were dominated by rockfishes, primarily POP, with some flatfish, eelpouts, poachers, Pacific cod, and sculpins. Fish were not commonly observed except within structurally complex habitats. The first of these habitats were aggregations of sea pens (*Halipteris willemoesi*) where

aggregations of large numbers of POP were observed, as well as occasional other species including Pacific cod, poachers, skates, and Arrowtooth flounder. While individuals and small groups of POP were observed outside of sea whip aggregations, fish abundances were generally much lower than within sea pen aggregations. All the POP appeared to be adults, and this was corroborated by bottom trawls taken at adjacent sites which found that the fish ranged in age from 8-15 years and all were classified as mature adults (Brodeur, 2001).

Overall the extent of fish invertebrate associations in Brodeur's study was low. The main exception to this pattern occurred within relatively rare structurally complex habits (sea pen "forests" and boulder-cobble substrate), where a much higher incidence of association were observed for both POP and Ronquils, respectively. While individuals of both taxa were observed outside these structurally complex habits, they were much less abundant outside these structurally complex habitats.

Evaluation of Miller et al. (2012) study

We conducted an independent analysis of a subset of the imagery data used in the Miller et al. (2012) study with the goal of collecting information for an overall analysis of the role of structure-forming invertebrates as benthic habitats for fishes in Pribilof and Zhemchug Canyons. Relative to many of the studies on structure-forming invertebrates along the US west coast and Alaska, the analytical methods used in the Miller et al. (2012) study were new and potentially problematic to compare with other studies. Therefore, an additional goal of this analysis was to examine their study using methods more commonly used along the US west coast and Alaska to examine the abundance and distribution of corals, sponges and fishes in relation to habitat and to conduct an analysis of fish-coral/sponge associations. In addition, another goal of the analyses was to reveal additional information not evident in the published paper and thus serve as an independent evaluation of the quality, design, analysis, and interpretation of the results presented in the published paper.

Materials and Methods

We obtained imagery from the study from a publically available Bisque Database (http://bisque.ece.ucsb.edu/client_service/view?resource =http://bisque.ece.ucsb.edu/data_service/dataset/1580770) maintained by the Center for Bio-Image Informatics at UC Santa Barbara. Images for the entire project were available online along with the associated metadata which included all habitat and organism data, laser sizing distances, and image area. We also obtained a complete dataset and navigation data for our analyses from John Hocevar, one of the co-PIs on the Miller et al. (2012) study. The navigation data were comprised of start and end locations of dive transect conducted from the surface vessel during surveys and as such these navigational fixes represented approximate locations.

For the analysis we randomly sampled ≈10% of the original images which comprised n=267 images from their original data set of 2,753 frames. This subsampling included 10% of the images from each of the 16 dive transects (n = 7 for Pribilof and n= 9 for Zhemchug) from the study. As the number of images per transect varied our samples ranged from n=8-27 per transect. The images were analyzed for habitat and

organism abundance using the methodology commonly used on the US west coast as described in Stein et al. (1992), Tissot et al. (2006), Tissot et al. (2007) and Tissot (2008), and Tissot et al. (2008). For examples and variations on these methods see Anderson and Yoklavich (2007), Love and Yoklavich (2008), and Wakefield et al. (2005).

We used the method of Stein et al. (1992) to classify physical habitats using a combination of nine different categories of substrata and standard geological definitions (e.g., Greene et al. 1999). In order of increasing particle size or relief, these substrata were: mud (code M), sand (S), gravel (G), pebble (P), cobble (C), boulder (B), continuous flat rock (F), rock ridge (R), and pinnacles (T). A two-character code was assigned each time a distinct change in substratum type was noted between images, thus delineating habitat patches of uniform type. The first character in the code represents the substratum that accounted for at least 50% of the patch, and the second character represents the substratum accounting for at least 20% of the patch (e.g.,"RM" represents a patch with at least 50% cover by rock ridge and at least 20% cover by mud) (see Tissot et al., 2007 for details and rationale). Because habitat classification generally varied with image quality, the confidence of classification was scored using a quality indicator where: 1=high, 2=moderate, 3=low quality of habitat classification.

Fishes and structure-forming invertebrates (corals and sponges) were analyzed by identifying and counting the number of distinct individuals in each frame. Corals and sponges were limited to individuals > 5cm in diameter (the same criteria used in Miller et al., 2012) and organism identification was made to the lowest possible taxonomic level. Because identification varied with image quality, the confidence of identification was scored using a quality indicator where: 1=high, 2=moderate,3=low quality of organism identification. For invertebrates maximum size was estimated using the maximum dimension of either height or width relative to a reference laser present in each frame which had been calibrated in the original metadata by Miller et al. (2012). For fish we measured the total length relative to reference lasers. For both habitat classification and organism identification we made observations on the quality of the imagery, height of the vehicle, and general conditions.

The level of ecological association between fishes and invertebrates (corals and sponges) were recorded as either direct physical contact or proximity from invertebrates, resting within a distance of one fish body length, and were categorized by activity codes similar to Stone (2006). In order of increasing association we coded the data as: 0 = no close association; 1= at rest at a distance $\leq$ 1 fish body length; 3 = physical contact between fish and invertebrate.

Results of Analyses

The overall quality of the imagery used in the analyses was generally poor and had a significant negative effect on the quality of the habitat and invertebrate analyses. A total of 58% (154 of 267) of the images analyzed were unclear. As a result habitat classifications were 41% of high quality and 59% of moderate quality and coral and sponge identification were classified as high quality on 35% of the observations, 63% as moderate and 2% as poor quality (Appendix Figure 1). Although several taxa were identified to the species and/or genus levels, a fairly large portion of invertebrate identifications were limited to general categories such as "sponges" (48% of all sponge

identifications) or "gorgonians" (25% of all coral identifications). Similarly for fishes, identifications were classified as 72% high and 28% moderate quality and 58% of all identifications were limited to general taxonomic categories (i.e., rockfish, poachers, etc.). Moreover, there were significant differences among canyons in image quality and subsequent analyses. Thus, 77% (74/96) of the images from Pribilof canyon were of poor quality compared to 45% (78/171) of the images from Zhemchug canyon.

The area sampled by individual images varied both within and among dives (Table 1), indicating that images were captured from the submersible at varying heights above the seafloor. At Pribilof canyon there was an eight-fold difference in areas among dives, indicating considerable variation in submersible height above the seafloor. Image area also varied within dives but was relatively more consistent. For Zhemchug canyon there was a seven-fold difference in area sizes among dives, also indicating considerable variation in submersible height above the seafloor. Image area variation within dives was also high and thus may have affected relative sampling effort (Table 1).

Experimental design

Both canyons were sampled with a relatively small number of dives (n = 7 for Pribilof and n= 9 for Zhemchug) at a limited number of areas and narrow range of depths, 168-419m at Pribilof (Figure 1) and 351-525 m at Zhemchug (Figure 3). Both canyons are very large and would require large sampling efforts to be adequately characterized: Pribilof Canyon is 45km wide by 145 km long, encompasses 5,930 km^2 in area and ranges in depth from 130-2100m; Zhemchug Canyon, the largest submarine canyon in the world, is 100km wide and 168 km long, encompasses 11,350 km^2 and ranges in depth from 120-3200m in (Carlson and Karl, 1988).

However, the sampling effort of the Miller et al. (2012) study comprised a total of 1528m^2 (0.15 km^2) in Pribilof and 2674m^2 (0.27km^2) in Zhemchug canyon, so only a very small proportion (< 0.0026% in both cases) of these canyons was sampled, severely limiting the broad-scale applicability of the data. Although dive sites were appropriately spread across each canyon area, individual sites, which were not consistently replicated, varied by depth (Table 1) resulting in non-random sampling which confounded depth and location. Moreover, several sets of dives occurred in close proximity to each other: dives 5 & 6 at Pribilof and dives 16-17, 18-19, 23-24 and 25-26 at Zhemchug (Figures 1 and 3). Although these paired dives could in theory provide sample replication, in practice they were unbalanced, as they did not occur at all sampling locations, and thus they further increased the potential for bias and reduced the general representation of the areas sampled. Thus, based on the experimental design it is difficult to make broad inferences about the habitats and biota of these canyons based on a small, unbalanced, and depth-limited sampled effort.

Habitat distributions

Ignoring for the moment the non-randomness of sampling, the small number of areas sampled and the very low sampling fraction for both canyons, from our analysis of the Miller et al. images the overall habitats at these sites appear to be largely composed of mud dominated habitats (94%) with the remaining 16% dominated by pebble habitats (Table 2). Among mud-dominated habitats 14% occurred with pebble, gravel, cobble and boulders as secondary habitats (> 20% of image cover). Overall the

areas sampled at Zhemchug canyon had a high abundance of mud dominated habitats (99%) and 1% of pebble dominated habitats. Within mud-dominated habitats, 16% were composed of mud mixed with gravel, cobbles, pebbles and boulders. In contrast, in the small number of areas sampled at Pribilof canyon habitats were primarily dominated by mud (85%) and pebble dominated habitats (15%). Within mud dominated habitats 11% occurred with mixtures of mud with gravel, cobbles, pebbles and boulders (Table 2).

Among the seven dives conducted at Pribilof canyon, three of these dives had hard substrates and were found adjacent to the continental shelf-slope break in the canyon. Two of these dives (5 and 6) occurred close together (within 100m of each other) on the NE wall of the canyon at 275-300m depths, the third (dive 15) occurred on the NW wall of the canyon at 253 m depth, within 5-10 km from Brodeur's dive sites, and the last (dive 8) occurred on the western wall at 379 m (Figure 1). Similarly, only two of nine dives at Zhemchug canyon had pebble habitats with mixed mud and secondary rocky substrates (dives 23 and 24). These dives were located next to each other on the northern wall of the canyon at 462-529m depths (Figure 3).

Corals and Sponges

A total of 219 corals and sponges from 11 different taxa were enumerated in the subsampled images from dive transects. Both groups occurred more frequently at some of the sites sampled at Pribilof than at the sites sampled in Zhemchug canyon (Table 3). At three of the seven sites sampled in Pribilof canyon (Figure 4) corals were found: primnoid corals in the genus *Plumarella* (*P. echinata and P.* spp.) were found followed by unidentifiable "gorgonians", bamboo corals (Isididae) and sea pens (*Halipteris willemoesi* and unidentifiable "sea pens." In contrast, at two of the sites sampled at Zhemchug canyon (Figure 5) bamboo corals were present, followed by the paramuriceid coral *Swiftia* spp., "gorgonians" and a "sea pen" Similarly, sponges were present at four sites at Pribilof canyon and at two sites in Zhemchug canyon. At the four sites where sponges were found at Pribilof canyon (Figure 4), glass sponges (Hexactinellida) were present followed by unidentifiable "sponges." At the two sites where sponges were found at Zhemchug canyon (Figure 5), most sponges were unidentifiable or glass sponges (Table 3).

The distribution of corals and sponges showed unique habitat affinities among dives sites conducted at each canyon (Figures 6 and 7). At the Pribilof canyon sites, primnoid corals (*Plumarella* spp.) were found primarily on habitats with some rocky structure, particularly mud-gravel, pebbles, pebbles and mud, and some pure mud habitats at 240-311m depths. (Pure mud habitats are classified based on > 70% mud cover but may additionally have some rocky substratum <20% that allow corals to attach to the seafloor) (Appendix Figure 2). Glass sponges occurred primarily on pebble, pebble-mud and mud-boulder habitats at 257-307m depths while bamboo corals were found exclusively on mud habitats at 253 m depth. At the sites surveyed in Zhemchug canyon paramuriceid corals (*Swifta* spp.) occurred on mud-cobble, mud-gravel and pure mud habitats at 466-533 m depths and bamboo corals and glass sponges on pure mud, mud-pebble, mud-cobble and mud-gravel habitats at 466-533 depths (Figure 6)(Appendix Figure 3).

Overall the spatial distribution of corals and sponges was very patchy with most observations occurring at a few of the sites surveyed in each canyon: three of seven dives at Pribilof canyon (Figure 4); and two of the nines sites surveyed at Zhemchug canyon (Figure 5). For example, 66% of glass sponges and 44% of gorgonians were observed in a single dive (5) at 300m depth on the NE wall of Pribilof canyon (Figure 4). Most of remaining coral and sponge observations occurred on dive 6 (275m) which had a start point only 100m away from dive 5 (Figures 4 and 10) and on dive 15 (253m) on the NW wall of the canyon. At the sites surveyed in Zhemchug canyon, 71% of glass sponges and 67% of the gorgonian were observed in a single dive (23) at 529m depth on the NE wall of the canyon with the remainder of the corals and sponges occurred on dive 24 (462m) which had a start point of 1.3 km away from dive 23 (Figure 5)

Fishes

A total of 59 demersal fishes were observed from 14 different taxa (Table 4). In general fish were not common on any dive transects although they were more than twice as abundant at the sites surveyed at Pribilof then at those sampled at Zhemchug canyon. Pribilof canyon sites were dominated by rockfishes, primarily Pacific ocean perch with some flatfish, eelpouts, poachers and sculpins. In contrast, at the sites surveyed at Zhemchug canyon the dominate fishes were unidentifiable flatfish, followed by poachers and thornyheads (*Sebastolobus* spp.). Many of the POP were observed in a few isolated large schools.

Fish-Coral/Sponge Associations

Overall, the extent of fish invertebrate associations was low. Of the 59 fish observed only 3 (5%) were classified as having close spatial associations with structure-forming invertebrates (< 1 fish body length). No fish were observed making physical contact with any invertebrates. Two of the three observations occurred in dives made at Pribilof and one in Zhemchug Canyon. Observed associations included a glass sponge and unidentifiable flatfish (Pleuronectidae) and a "sponge" and a bigmouth sculpin (*Hemitripterus bolini*) at Pribilof canyon; and a "sponge" and a snailfish (*Careproctus* spp.) at Zhemchug canyon.

The data were also examined for quantitative statistical associations between fishes (flatfish and POP), corals (gorgonians and sea pens) and glass sponges using correlation analysis (Figure 8). For the Pribilof canyon data, there were statistically significant associations (P < 0.05) between flatfish, glass sponges and gorgonians but the patterns of distribution suggest the overall levels of associations were not strong (Figure 8). In contrast, there were no significant associations between corals or sponges with POP in the Pribilof canyon data. The Zhemchug canyon data showed no statistically significant associations among any invertebrate taxa and fish examined (all P > 0.05).

Comparisons of Results with Miller et al. (2012)

Overall, a comparison of our analyses with those published in the Miller et al. (2012) paper reveal several important issues that indicate significant areas of concern regarding the conclusions reached in their paper. Some of these differences may be due to the methodologies used in our review relative to their analysis (see Table 5 for

summary) but we found several important substantive differences in our review that bear on the overall quality of the study and the ability of the paper to adequately characterize the abundance and distribution of corals and sponges in Pribilof and Zhemchug canyons. Below we summarize our results in reference to two questions:

Question 1: Was the Miller et al. 2012 study conducted in a manner that was statistically sound, and implemented in a way that collected representative samples from target study areas where one can draw broad and general conclusions about Pribilof and Zhemchug canyons?

Question 2: If the results are statistically biased (based on the conclusions in Q1), do the results of the Miller et al 2012 provide any valuable data? Taking that bias into consideration, how does the study compare to submersible studies conducted at other sites in other submarine canyon and shelf/slope habitats along the west coast?

Major conclusions:

- Poor and variable image quality: the imagery derived from the submersible used in the study, perhaps in combination with bottom conditions and/or other physical limitations, exhibited significant variability in height about the seafloor and in the quality of the images extracted from the video and subsequent analyses.

- Significantly reduced ability to accurately classify habitats and identify and count corals, sponges and fishes: the combination of poor, variable image quality and varying submersible height made it difficult to identify, count biota and classify habitats. This image quality issue was not discussed in their paper although they "*checked for overall scene quality.*" Our analyses indicated that about half of the images were compromised to some degree and had a significant negative effect on our analyses.

- Bias in habitat classification methods towards hard substrates: their method of classifying habitats was different than ours and they reported higher frequencies of hard substrates relative to our study in most, but not all, cases. Although their paper states that "*dominant (>50% cover) substrate type was scored in each frame*" the metadata associated with their images indicate that more weight was applied to rocky substrates in their methods relative to our review. Thus, we classified 73% of images as pure mud habitats compared to their 66% for Pribilof canyon. In contrast, we found 84% of pure mud habitats at Zhemchug compared to their 85%.

- Bias in estimates of coral and sponge abundances: analysis of invertebrates found significant differences in mean densities reported in their paper relative to our analysis. In general, *we found fewer corals and more sponges than they reported*. Overall, our study found significantly lower densities of corals at Pribilof canyon dive sites then reported in their study (56 vs.97/100m[1]) and higher densities of sponges (64 vs.41/100m[1]). At the sites surveyed in Zhemchug canyon we found lower densities of corals then reported in their study (15 vs.18/100m[1]) but higher densities of sponges (12 vs. 2.0/100m[1]). We believe these differences are primarily due to misidentified objects and

undercounting of some taxa in their image analysis. Moreover, in several cases replicate dives were conducted in areas of high coral/sponge abundances without corresponding replicate dives in other non-coral areas, which further contributed to bias in overall abundance estimates.

- <u>The abundance and distribution of corals and sponges were overemphasized</u>: we found that habitats that supported corals and sponges were uncommon and occurred at relative few dive sites (5 of 16 dives) and in relatively few frames (2-19%). This highly patchy distribution combined with the highly positive skewed distribution of coral and sponge abundances indicates that high coral abundances at a few sites, and a few images at those sites, had a disproportionally strong influence on average abundance estimates. Thus although the overall conclusions of the study stated that:

    Thus, based on the survey data reported here, Pribilof and Zhemchug Canyons can be regarded as harboring areas of high densities of slow-growing corals ...(p. 8).

    Our results indicate that structure-forming invertebrates were very patchy and localized in distribution, absent from the majority of the areas surveyed (Figures 4, 5 and 6), and highly skewed in distribution (Figure 9). These patterns are given a cursory mention in the discussion of their paper but they overlook this issue and fail to give it adequate consideration in their conclusions regarding overall coral and sponge abundance estimates reported in their paper.

- <u>Extent of fish use of corals and sponges was over estimated</u>: using our method of defining fish-invertebrate associations we found low levels of association and few statistically significant trends. Thus our conclusions are in contrast to Miller et al. (2012) Table 3 which found multiple statistically significant associations in both canyons between fishes, gorgonians, sponges and sea pens. This difference is likely due to the different methods they used, which is based on the presence/absence of fish and corals/sponges, when compared to the more quantitative approaches we used (Table 5). Our methods, however, are similar to that used in many US West Coast submersible studies (e.g., Pirtle, 2005; Tissot et al., 2006; Bright, 2007; Graiff, 2008; Bianchi 2011) while their methods has not been previously used in these types of studies, to our knowledge.

Discussion

Our analyses revealed several important problems with the Miller et al. (2012) study with respect to the experimental design, image quality, data analysis, and interpretation of results. Together, these issues indicate that <u>their study has serious flaws which undermine both the results and the interpretation of the results as presented in the published paper</u>. Perhaps of greatest importance is the limits placed on the statistical inferences of the study based on their experimental design. First we discuss the major conclusions of our analyses with a focus on the implications of the shortcomings of the paper. We then conduct comparisons of the abundance estimates collected by the Miller et al. (2012) study relative to other studies in submarine canyons

and continental shelf-slope breaks and conclude with summary of our findings relative to the design of a more rigorous submersible survey of Pribilof and Zhemchug canyons.

Experimental design and sampling effort

The studies' ability to draw broad and general conclusions about Pribilof and Zhemchug canyons depends principally on experimental design and sampling effort. To adequately sample a given study area requires surveys to collect random (or representative) samples stratified by target depths and habitats with individual samples (dive transects or collections of images) serving as replicates at a given dive site (Tissot 2008). Submersible studies in general are very challenging as sampling effort is limited relative to the scale of the study area and logistical challenges can limit or prohibit using a randomized approach (Tissot et al., 2008). These limitations include depth and time limitations of the submersible, lack of detailed maps of the seafloor on which to select sampling sites, as well as the extent of currents, visibility on the seafloor, and the goal of trying to locate areas that contain the study organisms of interest. However, given these limitations studies that do not meet the basic principles of experimental design should restrict their inferences to the specific areas sampled and avoid any broad generalizations based on limited and potentially biased data, especially when the data have important policy implications.

According to Miller et al. (2012) the objective of their study was

> *...to evaluate density of structure-forming corals and sponges in Zhemchug and Pribilof Canyons, Bering Sea .... and evaluate the use of corals, sponges, and boulders as habitat in the canyons. ...* (p. 2)

Thus, their target study areas were defined as the entire area of the two canyons with a focus on sponges, coral and benthic habitats. To accomplish these goals their experimental design was based on the following experimental design:

> *Transects were located to cover the geographical extent of the canyons and were located approximately equidistantly apart* (p. 2)

This statement implies that dive transects were evenly distributed across the study areas, which would include a range of depths from the head of each canyon at the shelf-slope break to the base of the canyons near the end of the continental slope. Their design was clarified by additional conversations with John Hocevar:

> *...logistics (weather, available dive days, and equipment functionality) impacted site selection considerably. We started with a rough map of transects spread equidistantly across both canyons, and modified that based on logistical factors. Groundfish surveys and observer data were consulted, as they were some of the only existing sources of relevant information available, but given the geographic scale and taxonomic generalizations used in those data sets, they didn't really affect our site selection...* (personal communication, Dec. 20, 2012)..

Thus, as in many submersible studies, their actual sampling effort was non-random and guided by ancillary information that assisted in targeting key organisms. Moreover, when examining their sampling effort (Figures 1 and 3; Table 1) it is clear that dive sites were focused primarily adjacent to the shelf-slope break and a few slope areas at 237-

412m depths at Pribilof and 351-529m depths at Zhemchug canyon. Limitations in sampling across depths can introduce additional bias. The Miller et al. (2012) sampling effort at Pribilof canyon was biased in the depth range 200-400m water depth. In the Aleutian Islands, the shallower 200-300m depths range was were coral abundance was the highest, and included up to 50% greater coral densities in shallower relative to deeper depths (Stone 2006, p. 233). In addition, as previously mentioned, in several cases multiple dives were conducted in close proximity to each other: dives 5 & 6 at Pribilof, both of which had relatively high abundances of corals and sponges (Figure 7), and dives 16-17, 18-19, 23-24 and 25-26 at Zhemchug, none of which had coral and sponges, which would necessarily significantly bias estimates of coral/sponge encounters and estimates of densities..

The principle problems with their experimental design include: 1) non-random sampling; 2) sampling bias in a limited number of areas and narrow range of depths; 3) inadequate effort: a small number of dives relative to the size of the areas of study; 4) unbalanced (or no) replication of dive sites; and 5) repeated surveys at multiple sites in close proximity to each other (100m-2 km) with high coral/sponge abundances. Combined these factors indicate that <u>the study cannot be used to draw broad and general conclusions regarding the abundance and distribution of structure-forming invertebrates and benthic habitats in Pribilof and Zhemchug canyons</u>.

Image Quality

A combination of variable image quality combined with varying submersible height above the seafloor had a significant effect on our ability to accurately classify habitats and identify corals, sponges and fishes with taxonomic precision. Although the Miller et al. (2012) study collected voucher specimens, which can greatly improve taxonomic classification, using known coral and sponge identifications from collected specimens in image interpretation is still problematic. Although all submersible studies are challenged with these issues to various degrees the high frequency of unclear images combined with varying distance from the seafloor was higher than previous submersible studies on the US West coast that we have been involved in (e.g., Stein et al., 1992; Tissot et al., 2006; Tissot et al., 2007; Tissot et al. 2008).

In most studies these image quality issues are addressed by maintaining the height of the submersible above the seafloor at a constant level. For example, mean transect width (a proxy for area) varied between 1.3 and 1.9 m using the submersible ROPOS at Heceta Bank, Oregon (Tissot and Wakefield, unpublished data), significantly less than the 7-8 fold variation in image area observed in this study. Moreover, in a recent benthic habitat study conducted by a SeaBed AUV at the Olympic Coast National Marine Sanctuary our analysis of image quality found 99.9% of the images to be of high quality and <0.1% of poor quality (Clarke and Tissot, unpublished data). Poor image quality can result from several factors but likely resulted from frames being captured while the submersible was changing direction and/or speed. Variation in height from the seafloor generally is due to variability in habitat type, strength of currents, and or maneuverability of the submersible. Regardless, poor image quality had a significant impact on our ability to accurately classify habitats and identify and count biota and it likely had a significant effect on the Miller et al. (2012) data analysis as well.

Abundance and distribution of coral, sponges and habitat

Based on our analysis of the Miller et al. (2012) images the sites surveyed in Pribilof and Zhemchug canyons were predominantly mud-dominated (94% overall, or 251 of 267 images) with highly patchy areas of pebble and mud with secondary substrates of boulder, cobble, gravel and pebbles. Pebble-dominated habitats occurred on 19% (3 of the 16) of the dives and mud with secondary rocky substrates occurred on 44% (7 of the 16) of the dives and were generally located on the canyon walls adjacent to the shelf-slope break (Figure 6). However, we found 10% less non-mud habitats in our analyses relative to their published results indicating that there may have been a bias in their methodology towards higher abundances of hard substrates. Although their methodology stated that:

> Dominant (>50% cover) substrate type was scored in each frame following a generalized version of the Wentworth scale ... with fine sediment categories grouped as soft sediment, and pebble categories grouped as pebbles. (p.2)

We found some habitats classified as "cobble-boulder" based on a single cobble or boulder in the image which clearly consisted of less than 50% cover. Thus, errors in overestimating percent cover of hard substrates were evident and may have contributed to biased habitat estimates. However, given the limitations of their experimental design and these methodological errors the extent to which their reported habitat composition is reflective of the actual habitat distributions in these canyons is problematic.

Based on our analysis of the images collected at Pribilof canyon the average density of corals and sponges across all sites was 56/100m^2 and 64/100m^2, respectively. Across the Zhemchug Canyon sites we calculated averages of 15/100m^2 for corals and 11.5/100m^2 for sponges. The extent to which these average densities are representative of actual population densities, however, is questionable for several reasons. The major problems we encountered in our review resulted from errors in their methodology, an inadequate experimental design which lacked balanced replication of dive sites, non-random sampling which may have favored shallower, coral/sponge areas and the difficulty with estimating density based on the highly patchy and non-normal distribution of coral and sponge.

With respect to methodology, our analyses found 73% fewer corals and 56% more sponges at their dives sites in Pribilof canyon and 20% fewer corals but 475% more sponges at their dives sites in Zhemchug canyon then reported in their study (compare our Table 3 with their Table 1). We believe these differences are primarily due to mistakes in their image annotation process which resulted in misidentified objects and undercounting of some taxa. When comparing the metadata from their study, which listed tagged objects on each image with a point and identifying label, with the data from the images we analyzed we found:

1) Many non-coral objects (e.g., sponges and sometimes boulders/cobbles) were identified and counted as corals, particularly for the gorgonian *Plumarella* where our density estimates were 177% less than theirs; and

2) Many sponges were missed in their analyses and not counted.

Thus, our finding of 73% fewer corals and 56% more sponges at Pribilof canyon is consistent with some sponges being counted as corals. These mistakes were likely due to poor image quality (poor image quality occurred more frequently at images collected at Pribilof compared to Zhemchug canyon, 77% vs. 45%, respectively) and image annotation may have been conducted by individuals lacking the expertise for the proper identification of target organisms, which requires specialized training, protocols and quality assurance (Tissot 2008).

Another important issue affecting abundance estimates was the lack of balanced site replication. In a well-designed study (see below) areas for study would be randomly selected based on target depths and habitats and replicate dives and/or dive transects would be conducted in targeted area. This design would allow an assessment of overall abundance both within and among study areas and address small- (100m-1k) and larger-scale (10-100km) spatial variability. In contrast, the sampling conducted in the Miller at al. (2012) study had five pairs of dives that could be considered replicates (start points were located 100m-1.3k apart) but an additional six dives with no corresponding replication. This unbalanced design would have a strong effect on overall abundance estimates at Pribilof canyon: where transects were closely spaced (Figure 10) density estimates for corals were 160/100m^2 (dive 5) and 95/100m^2 (dive station 6). If dive replication was balanced at Pribilof canyon dive 6 would not be an issue but as it stands an additional dive in one of the two high coral/sponge areas adds significant bias to the results. Thus, If dive 6 was removed from our abundance estimates overall density for corals would be reduced from 56/100m^2 (already 73% less than their reported 97/100m^2) to 50/100m^2 (93% less). Thus, poor image quality combined with methodological problems and unbalanced replication raise significant issues on the reliability of their density estimates of corals and sponges.

In addition to these issues, the overall densities we estimated for each canyon were not representative of broad scale abundances as corals and sponges were very patchy in distribution with the vast majority of areas having no individuals. Most sponges and gorgonian corals require some hard substrate for attachment to the seafloor and were limited to areas that contained these habitats (Figures 6 and 7). Thus, gorgonians occurred only on 19%, and sponges on 12%, of all images at Pribilof canyon and corals and sponges occurred only on 2% of images at Zhemchug canyon. As a result, mean density values were primarily influenced by a relatively small number ($\geq$10%) of images from locations with high densities (e.g., up to 200/100m^2 in gorgonian corals and 100/100m^2 in sponges) (Figure 9). To illustrate this effect, if we eliminated 5% of the highest observed abundances overall mean densities would be reduced by 461% (from 64/100m^2 to 11/100m^2) in gorgonians and 395% in sponges (from 69/100m^2 to 14/100m^2). Therefore, overall density estimates from the Miller et al. (2012) need to be carefully interpreted in the context of which they were collected: they were derived from a small number of high density observations at relatively few dive sites and are thus not broadly representative of abundances across the two canyons.

Fish-Invertebrate associations

We found few observed associations between corals, sponges and fishes which contrasted with the results in Miller et al. (2012) who found multiple statistically significant associations in both canyons between fishes, gorgonians, sponges and sea

pens. Part of the differences between our results was likely due to the different methodology used and different sample sizes. Miller et al. (2012) used a logistic regression (generalized linear model [GLM], binomial distribution) on presence/absence frame-specific data. Thus, their focus was to detect the frequency of the presence of fish and corals/sponges in the same frame. Our methods, which are more commonly employed in the peer-reviewed literature (e.g., Tissot et al., 2006; Stone 2006), uses two independent metrics: 1) a numerical response: the correlation between the density of fish and corals/sponges among frames; and 2) a behavioral response: the frequency of direct physical contact or an activity (resting) within one fish body length from corals/sponges. Thus, our methodology requires "associations" to exhibit stronger evidence when compared to the logistic regression approached of Miller et al. (2012). The differences in our results could also be due to the reduced statistical power in our tests relative to theirs as we analyzed a subset (10%) of the data used in their analyses. However, the conclusions of our analyses indicate that the overall level of fish invertebrate associations were low.

Value of data

Given the paucity of studies on submarine canyons in general, and the Bering Sea in particular, the Miller et al. (2012) study provides valuable data on habitat, fishes and invertebrates in Pribilof and Zhemchug canyons and is very useful in terms of what habitats and species are present in these areas. However, given the problems oulined with respect to experimental design, image quality, methodology, and estimates of distribution and abundance, the study has important limitations which undermine both the results and the interpretation of the results as presented in the published paper.

Comparisons with other studies

Despite the limitations found in the Miller et al. (2012) study it is useful to conduct a comparison between the results of our analyses of their data relative to other submersible studies conducted in submarine canyons and adjacent to the shelf-slope break on the US west coast and Alaska. Many of these studies suffer from limitations in experimental design and making broad comparisons among studies should be undertaken with caution. Most importantly, abundance and size estimates derived from the small, non-random sampling efforts in some of these studies should not be used to draw general conclusions regarding the abundance and distribution of corals and sponges in these study areas. However, these comparisons are useful to examine the general range of abundances and sizes that have been observed in these systems which can provide a context for the data collected by Miller et al. (2012) relative to their conclusion that "*Pribilof and Zhemchug Canyons can be regarded as harboring areas of high densities of slow-growing corals* ...(p. 8).

In order to make these comparisons we summarized (or extracted) data from eight studies in Alaska and along the U.S. west coast. The studies we selected included all known studies that collected data on structure-forming invertebrates with a submersible using similar methodology to that used here. These studies included one study of three submarine canyons on the U.S. west coast by Bianchi (2011) and seven studies of sites adjacent to the shelf-slope break in Alaska, Washington, Oregon and California conducted by Krieger and Wing (2002), Tissot et al. (2004), Stone (2006), Tissot et al. (2006), Pirtle (2005), Bright (2007) and Wrubel (unpublished data).

Because of the serious issues we identified in the published Miller et al. (2012) study, all data from Pribilof and Zhemchug canyons used in these comparisons were derived from the results of our analyses (not from the original paper) and correcting for errors in estimating abundance and bias due to non-random sampling (e.g., we removed dive 6 from the abundance estimates for Pribilof Canyon as described above). These comparisons are summarized in Tables 6-8.

One key issue that emerges from these comparisons is the large disparity between the sampling effort among studies. The 4202m^2 sampled in Pribilof and Zhemchug canyons by Miller at al. (2012) is <u>one-three orders of magnitude less</u> than the other studies examined, which ranged from the 26,597m^2 sampled by Stone (2006) in the Aleutian Islands to the 260,000m^2 sampled by Tissot et al. (2006) in southern California (Tables 6 and 7). Given the large size of the Bering Sea canyons this small sampling effort adds significant additional concern with respect to the ability of the Miller et al. (2012) study to derive meaningful inferences on the abundance and distribution of corals and sponges from their surveys and additional caution regarding the interpretation of the comparisons described below.

Bianchi (2011) is the only study to examine the abundance of structure-forming invertebrates in submarine canyons along the U.S. west coast. She examined three canyons: Astoria Canyon in Oregon/ Washington (7 dives using the ROPOS ROV); Carmel canyon in California (12 dives using the occupied submersible Delta); and Ascension canyon (12 Delta dives) in California. In general, our estimated abundances of gorgonians at Pribilof and Zhemchug canyons were higher than estimates reported from Astoria, Carmel and Ascension canyons (Table 6). With respect to sea pens, our estimates at Pribilof canyon were also higher than other west coast canyon sites but abundances at Zhemchug canyon were not significantly different from other west coast canyon sites. In contrast, stony corals (Scleractina) were found at Astoria canyon and soft corals (Alcyonarians) were found at both Astoria and Carmel canyons, neither of which were found in our analyses or reported in the Miller et al. (2012) study. In addition, sponge abundances at Astoria canyon were higher than our estimates for sponges Pribilof canyon and those reported at Carmel, Zhemchug and Ascension canyons (Table 6).

The abundance and distribution of corals and sponges along the continental shelf-slope break in studies conducted in Alaska and the U.S. west coast varied significantly among sites (Table 7). With the exception of the Aleutian Island "coral gardens" studied by Stone (2006), our estimated abundances of gorgonians at Pribilof and Zhemchug canyon were higher than estimates from the other sites studied. In contrast, sea pen densities were higher at the southern California rocky banks studied by Tissot et al. (2006) relative to our estimates at these canyons. With respect to sponges, our abundance estimates for Pribilof canyon were higher than other shelf-slope sites but not significantly greater than those found at the Anacapa Island, California "footprint" studied by Bright (2007). With respect to sponges, our estimated abundances at Zhemchug canyon dive sites were less than the "footprint" and not significantly different than abundances found at the Olympic Coast National Marine Sanctuary sites studied by Wrubel (unpublished data) and the Cordell Bank, California sites studied by Pirtle (2005).

Based on the coral and sponge size comparisons from these studies, none of the data collected from Pribilof or Zhemchug canyons showed uniquely large structure-forming invertebrates as both the maximum and average size observed in these taxa were within the ranges or less than that observed in other studies (Tables 6 and 7). For example, gorgonian corals in the three submarine canyons studied by Bianchi (2011) had a maximum size ranging from 5-60 cm and an average size from 5-42 cm. In contrast, the gorgonian corals we observed at Pribilof and Zhemchug canyons ranged from 14-36 cm in maximum size with an average size from 7-20 cm (Table 6). Similarly, maximum and average observed coral and sponge sizes in the Bering sea canyon survey sites were within the ranges observed in continental shelf-slope break study areas and significantly smaller than those observed in the Gulf of Alaska (Table 7), which may range up to 7m in height (Krieger, 2001), and those observed in the Aleutian Island "coral gardens" which are generally greater than 1m in height (Stone and Shotwell, 2007).

Comparisons of Bering sea submarine canyons with the Aleutian island "coral gardens" studied by Stone (2006) are problematic as the Aleutian islands represent a very unique environment not likely to be found anywhere else. However, these comparisons reveal multiple major differences in the abundance, distribution, size and diversity of corals between these two areas (summarized in Table 8). With respect to abundance and distribution, corals in the Aleutian islands had significantly higher average and maximum densities, greater maximum percent coverage on the seafloor, greater frequency of occurrence in sampled locations, occupied a greater range of depths, and had lower variability in abundance relative to Pribilof and Zhemchug canyon data. With respect to size, corals in the Aleutians were significantly larger on average and had a significantly larger maximum size than those found in the dives at the Bering Sea canyons. Finally, the species diversity or corals found in the Aleutians was 2.7 times higher than found during the Pribilof and Zhemchug canyon surveys (Table 8). In summary, the "gardens" are characterized by consistently large (≥ 1m), very dense coral colonies that occupy a broad range of depths and habitats while corals in Pribilof and Zhemchug canyons from our analyses are described as small (20-30cm), moderately dense colonies that occupy a narrow range of depths and habitats and are highly variable in distribution. Thus, data from the corals in these two areas show strikingly different ecological patterns and should not be considered similar in any meaningful way.

With respect to the frequency of fish-invertebrate associations, based on our analyses from both the Pribilof and Zhemchug canyon dive sites, we calculated lower frequencies of observed associations, both in terms of physical contact and with respect to a spatial metric (within fish body length) relative to the three canyons studied by Bianchi (2011). Similarly, the frequency of fish-invertebrate associations were low at study sites in Pribilof and Zhemchug canyons relative to continental shelf-slope break study areas, particularly in the Aleutian Islands "coral gardens" where the frequency of associations were as high as 20% showing physical contact and 85% overall (within one body length while at rest, or within 1 m while swimming or hovering), and in the Gulf of Alaska where overall associations (< 1m) ranged from 15-85% (Table 7).

Brodeur (2001) observed associations between Pacific Ocean perch and sea pens at night at the NW head of Pribilof canyon, however the extent of these associations were not quantified and our review showed these incidences to be relatively uncommon across the sites he surveyed. Moreover, all other studies were conducted during the daytime while Broduer's observations of POP-sea pen associations were made at night and time of day is likely have an effect of the extent of fish-invertebrate interactions considering the diel migratory behavior of Pacific Ocean Perch and many groundfish (Hart et al., 2010).

Because POP were observed to be less abundant outside these sea pen habitats Brodeur (2001) suggested these observations could indicate a preference for high relief substrates and that sea pens may provide important structural habitat for POP in an otherwise featureless environment. However, the observation that fishes and invertebrates are present in the same types of habitats does not necessarily imply a functional relationship between these two groups of organisms (Tissot et al., 2006). Parrish (2004) reached similar conclusions on studies of black coral in Hawaii. Although fish densities were higher in areas that included corals, when bottom relief and depth were accounted for these densities were not higher than those for surrounding areas without corals. Thus, there was no clear evidence that corals served to aggregate fish. Rather, fishes and corals co-occurred in areas with similar physical relief and unique flow regime (Parrish, 2004). Auster (2005) also reached similar conclusions by finding no significant difference in the density of a common rockfish species (*Sebastes fasiatus*) between areas of rock and boulders with high coral cover and similar areas having high epifaunal cover (i.e., without coral). Auster concluded that although dense coral and dense epifaunal habitats were functionally equivalent, the epifaunal habitat was more widespread in his study area, making that habitat perhaps more important to the fish populations. Finally, Syms and Jones (2001) demonstrated that removal of high densities of soft corals caused no significant changes in the associated fish communities and that the heterogeneity of habitat generated by soft corals was indistinguishable from equivalent habitat formed by rock alone. Thus, fish-invertebrate associations, by themselves, do not necessarily demonstrate the functional importance of invertebrates as habitat to benthic fishes and the actual ecological significance of these associations has yet to be experimentally tested.

In summary, comparisons with other similar studies of submarine canyons and shelf-slope breaks in Alaska and along the U.S. west coast indicate the following with respect to our analysis of the Miller et al. (2012) study:

- Low sampling effort: effort is 1-3 orders of magnitude less than other similar studies and is thus significantly low;
- Moderate gorgonian density: overall density estimates of gorgonians at Pribilof canyon, and to a much lesser extent, Zhemchug canyon, are in the middle range;
- No similarity to Aleutians Islands "coral gardens": there are multiple major differences when compared to the "gardens" such that there is no valid similarity between these two areas;

- <u>Small coral sizes</u>: none of the data showed uniquely large structure-forming corals or sponges as both the maximum and average size observed were within or below the size ranges observed in other studies;
- <u>Low fish habitat associations</u>: we found lower frequencies of observed associations, both in terms of physical contact and with respect to a spatial metric, relative to other studies.

Thus, the only notable observation from these comparisons is the moderately high density estimates we found for gorgonians in the Miller et al. (2012) study. As such, this result has the potential to be an important observation. <u>However, given the extensive problems discussed with respect to experimental design, image quality, methodology, and estimates of distribution and abundance, the validity of this result is highly suspect and thus not useful as a scientifically based estimates for use in comparisons to other scientific studies or extrapolations to areas not sampled.</u>

Assessing Benthic Habitats in Bering Sea Canyons

Given the shortcomings in the experimental design in the Miller et al. (2012) study and the subsequent limitations imposed on the interpretation of their results, how could benthic habitats in Bering Sea submarine canyons, including their structure-forming invertebrates, be adequately assessed?

The major elements of experimental design of submersible studies include randomization, replication, independence, and statistical power (Tissot, 2008). If sample effort is large, random selection of study sites from all possible sampling locations should be used to minimize sampling bias. Most sampling strategies use a stratified design to focus on particular depths and/or habitat types and use appropriately sized grids overlaid on maps of the study area to randomly select areas of the grid to sample (e.g., Jagielo et al. 2003, Tissot et al. 2006; Yoklavich et al. 2007). However, if the number of possible grids is small relative to those being sampled, it is better to systematically select sites to be sampled to ensure appropriate interdispersion over the study area (Hurlbert 1984).

Replication should occur both within and among strata (e.g., depth, habitat) to minimize confounding of spatial variation and should be balanced (all sampled grids should be replicated) to avoid creating a biased sampling effort. If the study area has significant small-scale (100m-1 km) variation in habitat, the area should be stratified and subsampled using nested replicates to further account for spatial variation (Underwood 1997). Finally, but importantly, the power of the statistical design to reject the null hypotheses of the study should be examined if the study is focused on developing baselines, detecting change over time, or for control-impact studies (Mapstone 1996). To address this important design issue, power analyses should be conducted. Power analysis requires some measure of the variability in the measured traits, which can be derived from pilot studies or related studies, and the amount of change to be detected, or the "effect size" (example in Tissot et al. 2007).

The major critiques of the Miller et al. (2012) were: 1) non-random sampling; 2) sampling bias in a limited number of areas and depths; 3) low effort; and 4) unbalanced replication of dive sites. Given the limited number of dives in the study, which precluded

random sampling, their approach to locate transects approximately equidistantly apart and cover the extent of the canyons was reasonable but was not followed through in their field surveys. However, sampling sites at different locations varied by depth and therefore locations and depth were confounded resulting in non-random and potentially biased samples. The lack of a high-resolution multibeam map at the time of their study likely contributed to this problem as did their non-random choice of dive locations.

A well-designed study would be based on a sampling grid overlaid on a multibeam map which included bathymetry and backscatter to identify depths and habitats. To illustrate this approach we created a grid for Pribilof canyon using a multibeam map which including bathymetry (Figure 11) (backscatter is currently unavailable). Given the large size of the canyon we superimposed a 5 x 5km sampling grid over the map which resulted in 132 sampling blocks ranging in depth from 141-1878m and covering 3,300 km^2 or 56% of the 5,930 km^2 area of Pribilof Canyon. Sampling stations would be selected by randomly allocating effort across the grid stratified by depth. Balanced stratified sampling would be achieved by allocating effort relative to the depth distribution across the grid (Figure 12). Thus, based on the distribution of depths in the sampling grid, ~25% effort would be allocated to surveys at 150-350 m, ~25% at 350-550 m, ~15% at 550-750 m, etc. Overall sampling effort would ideally be calculated from a power analysis based on hypotheses developed for the study, although in practice effort is often limited by costs, weather and/or other logistical constraints. Within each sampling block multiple transects, spaced sufficiently apart, would be completed to provide independent replication. The extent of sampling effort allocated to within- vs. among-sampling blocks would be based on the amount of spatial variability at these two scales. A study designed along these principles would fulfill the experimental design criteria of randomization, replication, independence, and statistical power.

A comparison between the sampling distribution of a well-designed study and the Miller et al. (2012) study at Pribilof canyon (Figure 12) shows that their sampling allocation was biased towards 200-400m depths and did not sample depths greater than 600 m, which were greater than the maximum depth of their submersible. In addition, their approach of analyzing image frames captured from HD video every 30s reduced their sampling effort significantly. A complete analysis of the entire video, although time-consuming, would have greatly increased the total areas of their samples.

Conclusions

Submarine canyons are prominent geomorphic features that can have a major influence on local and regional oceanographic conditions and flow patterns that can greatly enhance the primary production within the canyon and on the surrounding continental shelves. However, the abundance and distribution of corals and sponges in submarine canyons is not well understood and is often limited to high-productivity areas which contain hard substrates such as rocky outcrops, boulders, and pebble/gravel habitats.

Evaluation of the Miller et al. (2012) study found multiple serious issues which undermine both the results and the interpretation of the results as presented in the published paper and the study cannot be used to draw broad and general conclusions

regarding the abundance and distribution of structure-forming invertebrates and benthic habitats in Pribilof and Zhemchug canyons. Although the data from their study are useful in terms of what habitats and species are present in the dive areas they surveyed, they are not useful as scientifically based estimates for use in comparisons to other scientific studies or extrapolations to areas not sampled.

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Table 1. Descriptive statistics of image area (in m^2) among dives and canyons. The dive numbers used in the Miller et al. (2012) paper are cross-referenced with those used in the actual imagery metadata. The latter dive numbers are used throughout the paper except in Figure 1.

Canyon	Miller et al dive	Actual Dive	Mean	SD	CV	N
Pribilof	1	1	2.51	1.39	56%	15
	2	3	1.30	0.86	66%	21
	3	5	1.82	0.82	45%	11
	4	6	2.77	1.66	60%	8
	5	8	0.32	0.18	56%	8
	6	11	2.00	1.23	61%	8
	7	15	1.20	0.94	78%	24
Zhemchug	8	16	1.19	0.36	30%	23
	9	17	1.96	1.05	54%	22
	10	18	0.96	0.83	86%	20
	11	19	1.08	0.61	56%	15
	12	21	2.06	0.75	36%	11
	13	23	0.39	0.32	80%	15
	14	24	1.18	0.70	59%	14
	15	25	3.06	1.46	48%	22
	16	26	0.97	0.32	32%	27

Table 2. Distribution of habitat types in Bering Sea submarine canyons. Habitats indicated with an * were organized into structured sediment waves.

Canyon	Dive No.	Mean Depth (m)	Mud Dominated					Pebble Dominated	
			MB	MC	MG	M	MP	PM	P
Pribilof	1	237				100%			
	3	412				100%			
	5	300			18%		9%	9%	64%
	6	275					13%	50%	38%
	8	379				75%	25%		
	11	308				100%			
	15	253	4%		12%	80%	4%		
Zhemchug	16	477				100%*			
	17	489			5%	95%*			
	18	423				100%			
	19	421				100%			
	21	351				100%			
	23	529		18%	53%	12%	12%	6%	
	24	462	7%	21%	36%	21%	14%		
	25	465				100%			
	26	473				100%			
Pribilof			1%	0%	5%	73%	5%	5%	10%
Zhemchug			1%	4%	9%	84%	2%	1%	0%

Table 3. Abundance of corals and sponges in Bering Sea submarine canyons. Corals are divided into sea fans (Gorgonacea) and sea pens (Pennatulacea). Sponges are divided into glass sponges (Hexactinellida) and unidentifiable sponges (Porifera). Mean densities were calculated as averages among all dives at each site.

Phylum	Classification	Taxa	Mean Density (No./m^2)		Counts	
			Pribilof	Zhemchug	Pribilof	Zhemchug
Corals	Gorgonacea	*Plumarella* spp.	0.256	--	40	--
	Gorgonacea	*Plumarella echinata*	0.069	--	12	--
	Gorgonacea	Family Isididae (Bamboo corals)	0.058	0.068	13	6
	Gorgonacea	*Swiftia* spp.	--	0.034	--	3
	Gorgonacea	unknown gorgonian	0.141	0.041	24	3
	Pennatulacea	*Halipteris willemoesi* (sea pens)	0.027	--	6	--
	Pennatulacea	Unknown sea pens	0.009	0.007	2	1
		Total coral density	0.560	0.151		
Sponges	Hexactinellida	*Chonelasma calyx*	0.343	0.023	50	2
	Hexactinellida	Rossellidae	--	0.054	--	4
	Hexactinellida	Unknown glass sponge	--	0.015	--	1
	Porifera	Unknown sponge	0.296	0.023	49	3
		Total sponge density	0.639	0.115		
		Total Area sampled (m^2)	157.5	247.1		
		Total Counts			200	19

Table 4. Abundance of demersal fishes in Bering Sea submarine canyons. Fishes are divided into rockfishes, flatfish and other taxa.

Group	Common Name	Scientific name	Mean Density (No./m^2) Pribilof	Mean Density (No./m^2) Zhemchug	Counts Pribilof	Counts Zhemchug
Rockfish	Pacific ocean perch	*Sebastes alutus*	0.127	--	20	--
	rougheye rockfish	*Sebastes aleutianus*	--	0.004	--	1
	unknown rockfishes	*Sebastes* spp	0.013	0.004	2	1
	unknown thornyhead	*Sebastolobus* spp	--	0.012	--	3
Flatfish	arrowtooth flounder	*Atheresthes stomias*	0.006	0.008	1	2
	dover sole	*Microstomus pacificus*	0.006	--	1	--
	unid righteyed flatfish	Pleuronectidae	0.019	0.032	3	8
	Yellowfin sole	*Pleuronectes asper*	--	0.004	--	1
Other	Eelpouts	unknown Zoarcidae	0.032	0.004	5	1
	Darkfin sculpin	*Malacocottus zonurus*	--	0.004	--	1
	Poachers	unknown agonidae	0.006	0.012	1	3
	Bigmouth sculpin	*Hemitripterus bolini*	0.019	--	3	--
	Aleutian skate	*Bathyraja aleutica*	--	0.004	--	1
	Snailfishes	*Careproctus* spp	--	0.004	--	1
	Total Fish Density		0.229	0.093		
	Total Area sampled (m^2)		157.5	247.1		
	Total Counts				36	23

Table 5. Comparisons of methods used in Miller et al. (2012) relative to the current study.

Topic	Miller et al. (2012)	This study
Video quality		
Distance from seafloor	n/a	image area as proxy
Image quality	n/a	evaluated by eye
Habitat classification		
Method	Wentworth scale; dominate substrate > 50%	Stein et al. (1992); primary (> 50%) and secondary (>20) substrates
Quality indicator	n/a	evaluated by eye
Organism quantification		
Method	manual frame annotation	manually counted and sized on projected image
Quality indicator	n/a	evaluated by eye
Fish-invertebrate associations		
Degree of association	presence/absence	quantitative
Observed behavior	n/a	range of behaviors
Statistical approach	logistic regression	correlation analysis

Table 6. Comparison of structure-forming invertebrate abundance, size and degree of association with fishes among studied submarine canyons on the US West Coast and the Bering Sea. Data from Astoria, Ascension and Carmel canyons are from Bianchi (2011). All data from Pribilof and Zhemchug were derived from the results of analyses based on a subset of the Miller et al. (2012) data and corrected for errors in estimating abundance and bias due to non-random sampling (see text). *Depths deeper than 320m were excluded from this analysis as most samples in this category were taken > 1000m.

	Astoria	Ascension	Carmel	Pribilof	Zhemchug
Depths (m)	148-320*	182-253	90-182	168-419	351-533
Sampling effort (m^2)	15,000	19,000	13,000	1,528	2,674
Coral density (no./100m^2)					
Scleractinians	21.5	--	--	--	--
Antipatherians	--	--	--	--	--
Alcyonarians	1.0	--	1.3	--	--
Gorgonians	2.0	0.4	2.3	45.4	14.4
Pennatuleaceans	0.5	<0.01	0.67	4.2	0.9
Sponge density (no./100m^2)	69.3	3.5	14.7	48.2	11.5
Coral max / mean size (cm)					
Scleractinians	40 / 17.2	40 / 17.8	--	--	--
Antipatherians	--	--	--	--	--
Alcyonarians	40 / --	20 / 15.3	40 / 14.0	--	--
Gorgonians	5.0 / 5.0	60 / 42.6	50 / 13.9	14.0 / 6.7	36.0 / 19.8
Pennatuleaceans	140 / 9.0	40 / 36.4	140 / 21.2	15.4 / 15.2	--
Sponge max / mean size (cm)	160 / 22.4	140 / 32.9	140 / 16.5	28.8 / 8.8	91.7 / 41.6
Fish associations					
Percent contact	0.3	0.3	0.4	0	0
Percent other	24	23	38	5.6	4.3

Table 7. Comparison of structure-forming invertebrate abundance, size and degree of association with fishes among studied submarine canyons and shelf/slope areas on the US West Coast and the Bering Sea. *All data from Pribilof and Zhemchug were derived from the results of analyses based on a subset of the Miller et al. (2012) data and corrected for errors in estimating abundance and bias due to non-random sampling (see text). **Data from shallow depths < 150 m were eliminated from the analysis.

	Southern California Banks	Channel Islands "Footprint"	Cordell Bank	Heceta Bank	Olympic Coast	Gulf of Alaska	Aleutian Islands	Pribilof Canyon	Zhemchug Canyon
Source	Tissot et al., 2006	Bright, 2007	Pirtle, 2005	Tissot et al., 2004	Wrubel, unpublished	Krieger and Wing, 2002	Stone 2006	Tissot & Rooney, 2013*	Tissot & Rooney, 2013*
Depths (m)	32-320	97-314	55-250	68-342	44-372	151-365	150-363**	168-419	351-533
Sampling effort (m^2)	260,000	96,500	58,400	65,000	141,089	Not listed	26,597	1,528	2,674
Coral density (no./100m^2)									
Scleractinians	--	2.00	--	1.56	--	--	--	--	--
Antipatherians	0.1	4.45	--	--	--	--	--	--	--
Alcyonarians	--	--	--	<0.01	--	--	7.85	--	--
Gorgonians	0.03	7.23	0.59	0.14	7.79	--	66.8	45.4	14.4
Pennatuleaceans	8.19	2.31	0.34	1.42	--	--	1.20	4.2	0.9
Sponge density (no./100m^2)	6.71	34.5	7.41	2.54	11.2	--	--	48.2	11.5
Coral max / mean size (cm)									
Scleractinians	--		--	10 / --		--	--	--	--
Antipatherians	250 / 60	240 / 22	--	--		--	--	--	--
Alcyonarians	--	--	--	25 / --		--	--	--	--
Gorgonians	40 / 25	80 / 30	30/ 30	26 / 10		150 / --	--	14 / 7	36 / 20
Pennatuleaceans	100 /	30 /	70 / 45	40 / --				15 / 15	--
Sponge max / mean size (cm)	100 / 82	120 / 20	120 / 52	80 / 57		--	--	29 / 9	92 / 42
Fish associations									
Percent contact	1.8	0.9	0.1	1.6	--	--	20.2	0	0
Percent other	--	17.4	47.1	2.3	--	15-85%	84.7	5.6	4.3

Table 8. Comparison of structure-forming invertebrate sampling, abundance, size and species diversity among submarine canyons in the Bering Sea and the Aleutian Islands "coral gardens" described by Stone (2006) and Stone and Shotwell (2007). All data from Pribilof and Zhemchug were derived from the results of analyses based on a subset of the Miller et al. (2012) data and corrected for errors in estimating abundance and bias due to non-random sampling (see text). **Data from shallow depths < 150 m were eliminated from the analysis.

	Aleutian Islands**	Pribilof Canyon	Zhemchug Canyon
Sampling			
Sampling effort (m^2)	26,597	1,528	2,674
Depths sampled (m)	150-363	168-419	351-533
Coral depth distribution (m)	200 m (100-300)	70 m (241-311)	67 m (466-533)
Abundance			
Maximum coral density (no./100m^2)	385.0	150.0	91.0
Average coral density (no./100m2)	123.0	49.6	15.1
Maximum percent cover	100%	20%	10%
Frequency of occurrence (% of locations sampled)	68%	19%	4%
Variability in abundance (coefficient of variation)	163%	308%	629%
Size			
Maximum observed size	1.5m	23 cm	30 cm
Average Size	> 1m	9 cm	11 cm
Species Diversity			
Number of species (reported in Millet et al., 2012)	40	15	15
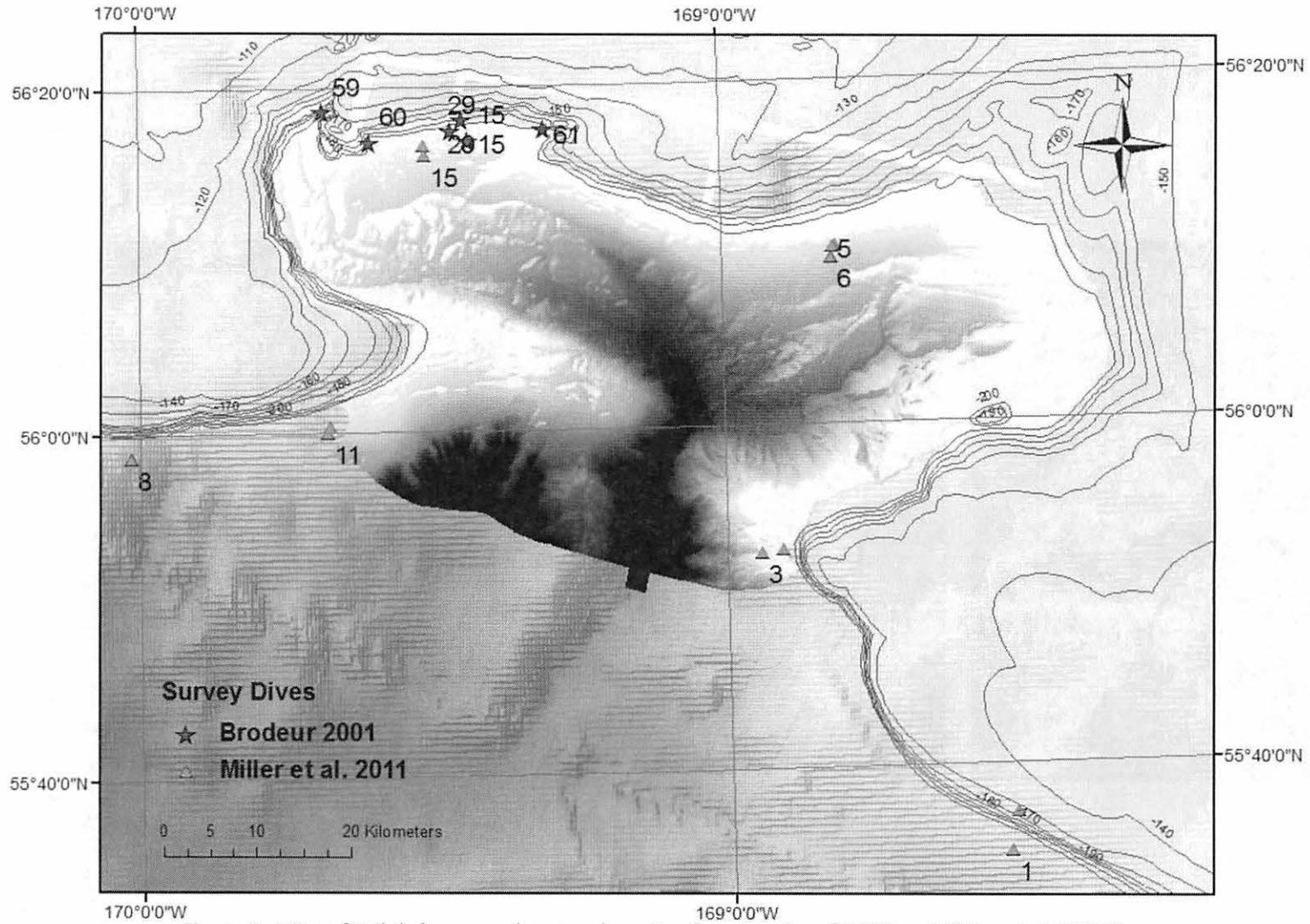
Figure 1. Map of Pribilof canyon showing dive sites from Brodeur (2001) and Miller et al. (2012).

Figure 2. Frame grabs from Brodeur (2001) video showing: Top: sea pen (*Halipteris willemoesi*) aggregation with associated Pacific ocean perch (*Sebastes alutus*); Middle: Dead sea pens lying scattered on the bottom with Pacific ocean perch; Bottom: branching demosponges on mud pebble habit. The slanting vertical lines are the center portions of sea whips which are around 2m (~6 ft) high.
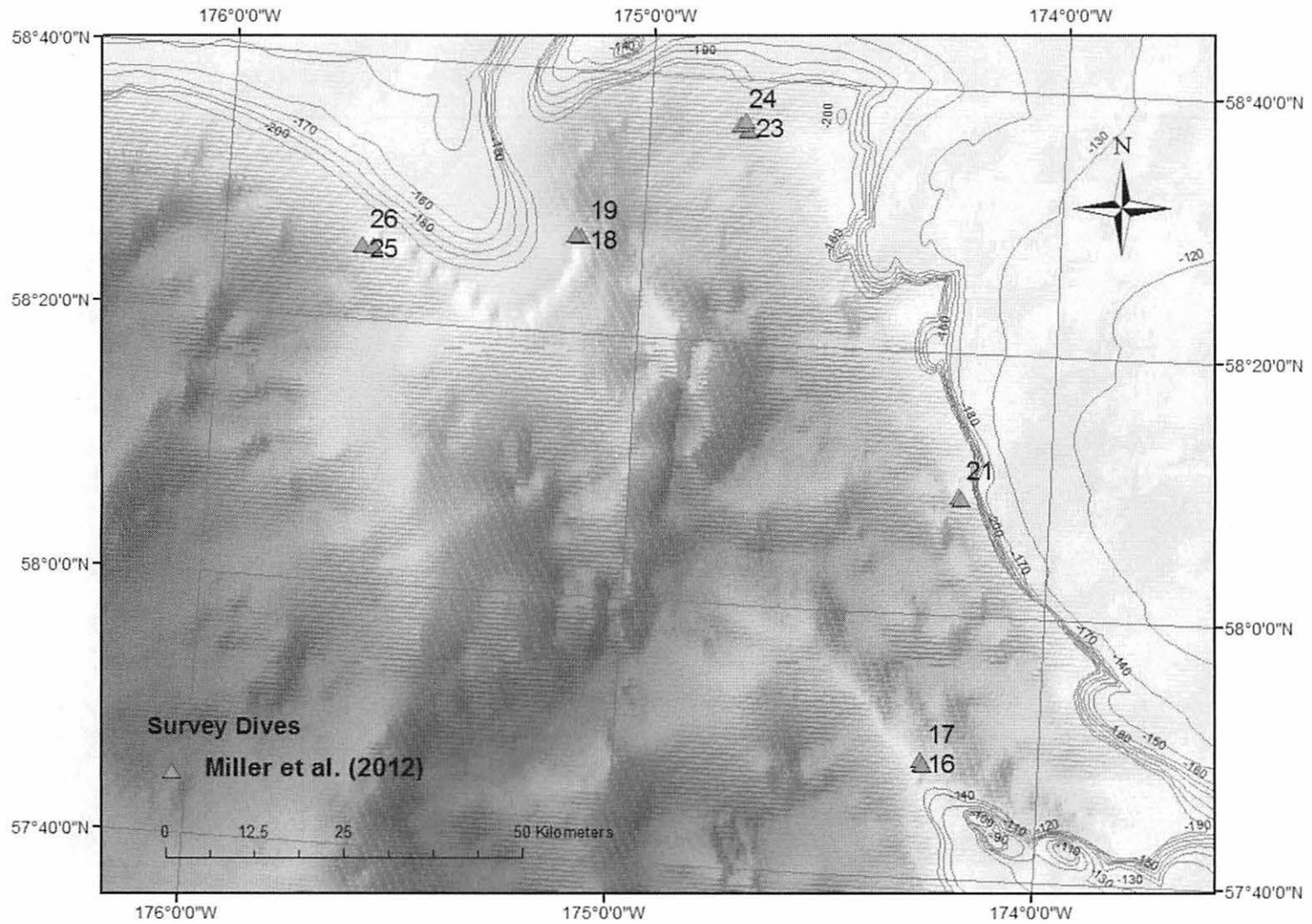
Figure 3. Map of Zhemchug canyon showing dive sites from and Miller et al. (2012).
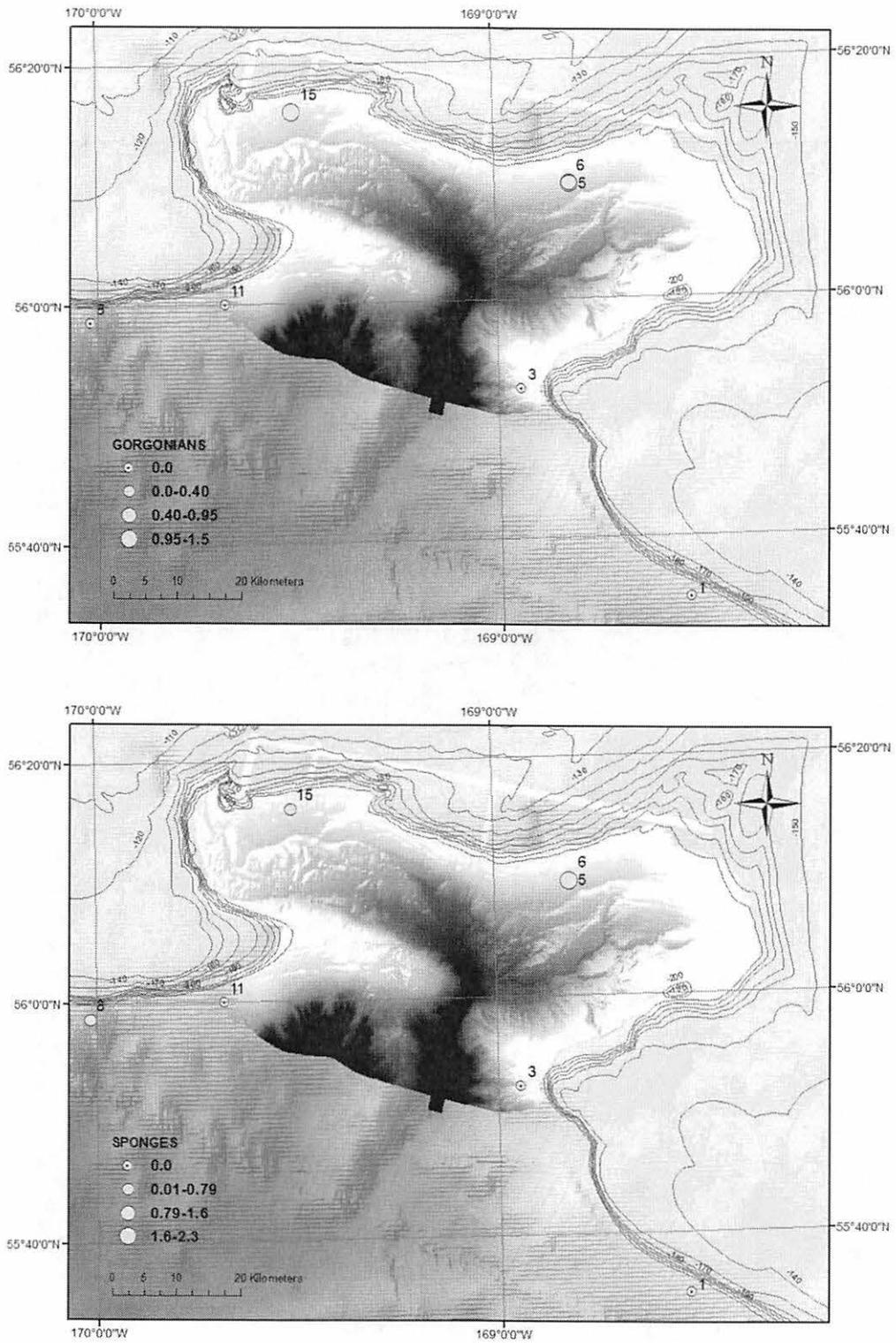
Figure 4. Abundance and distribution of gorgonians and sponges in Pribilof canyon based on analysis of full data set in Miller et al. (2012) .
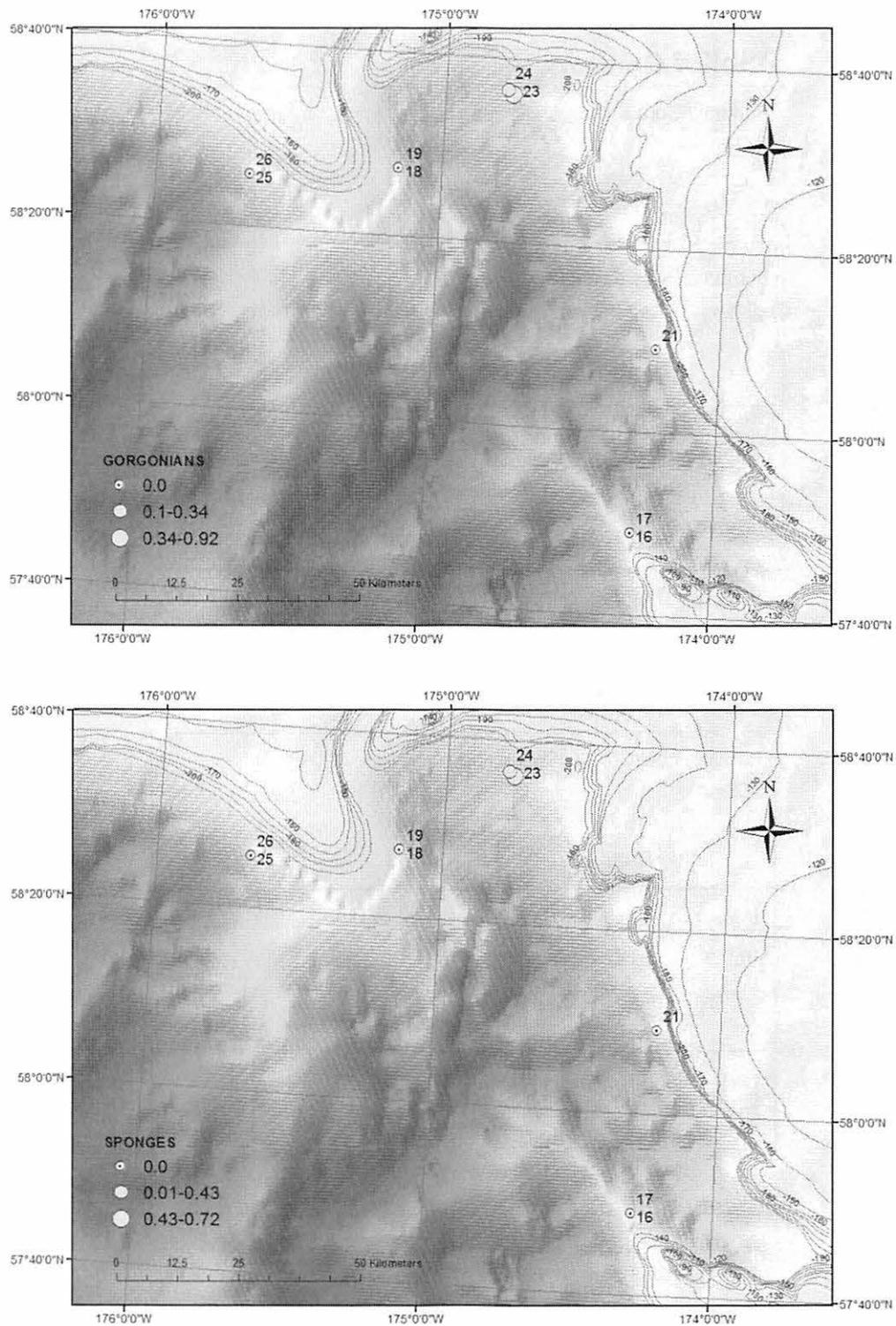
Figure 5. Abundance and distribution of gorgonians and sponges in Zhemchug canyon based on analysis of full data set in Miller et al. (2012) .
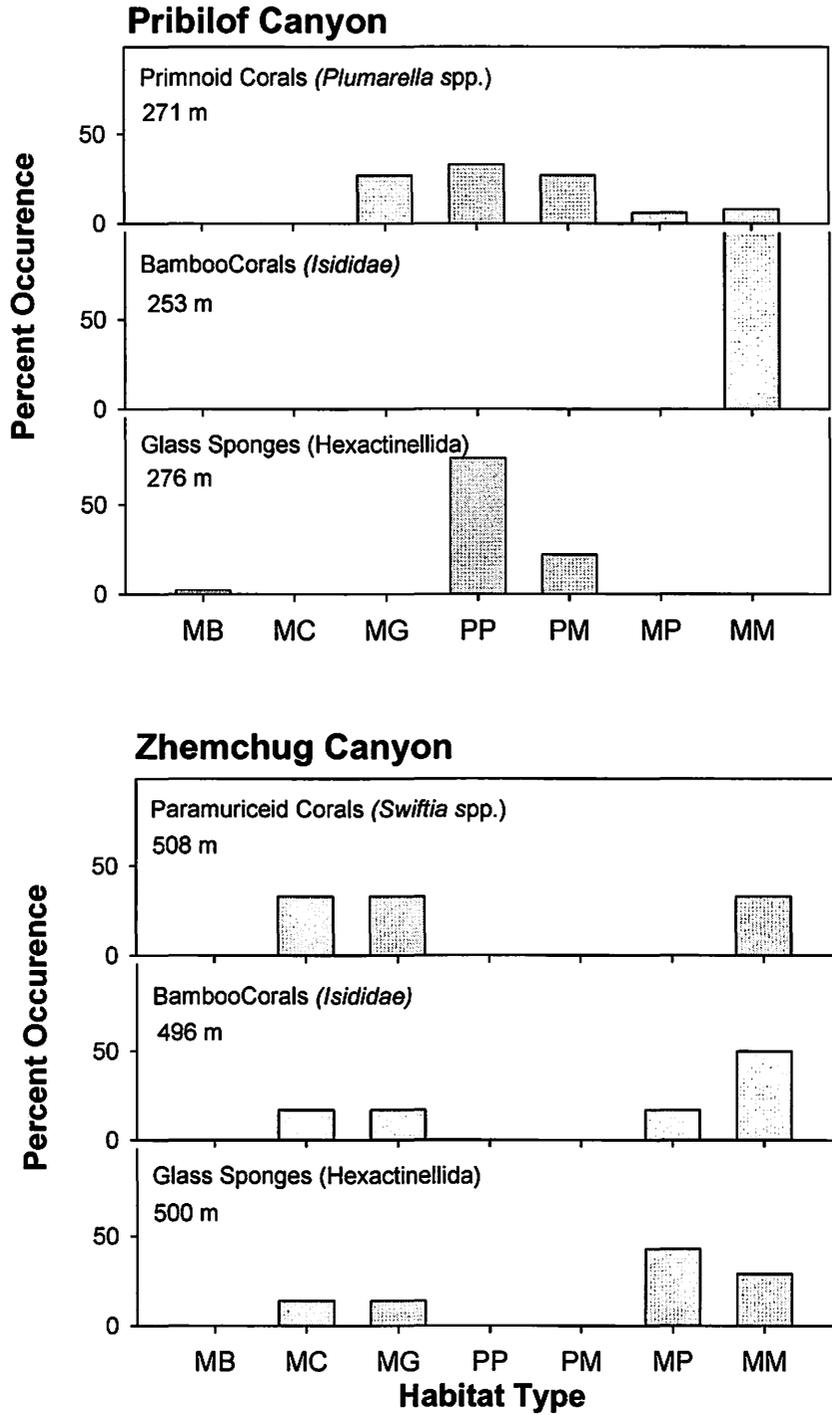
Figure 6. Distribution of structure-forming corals and sponges in Pribilof and Zhemchug canyons . Habitat coding is described in the text with MM = mud, MP = mud-pebble, etc.
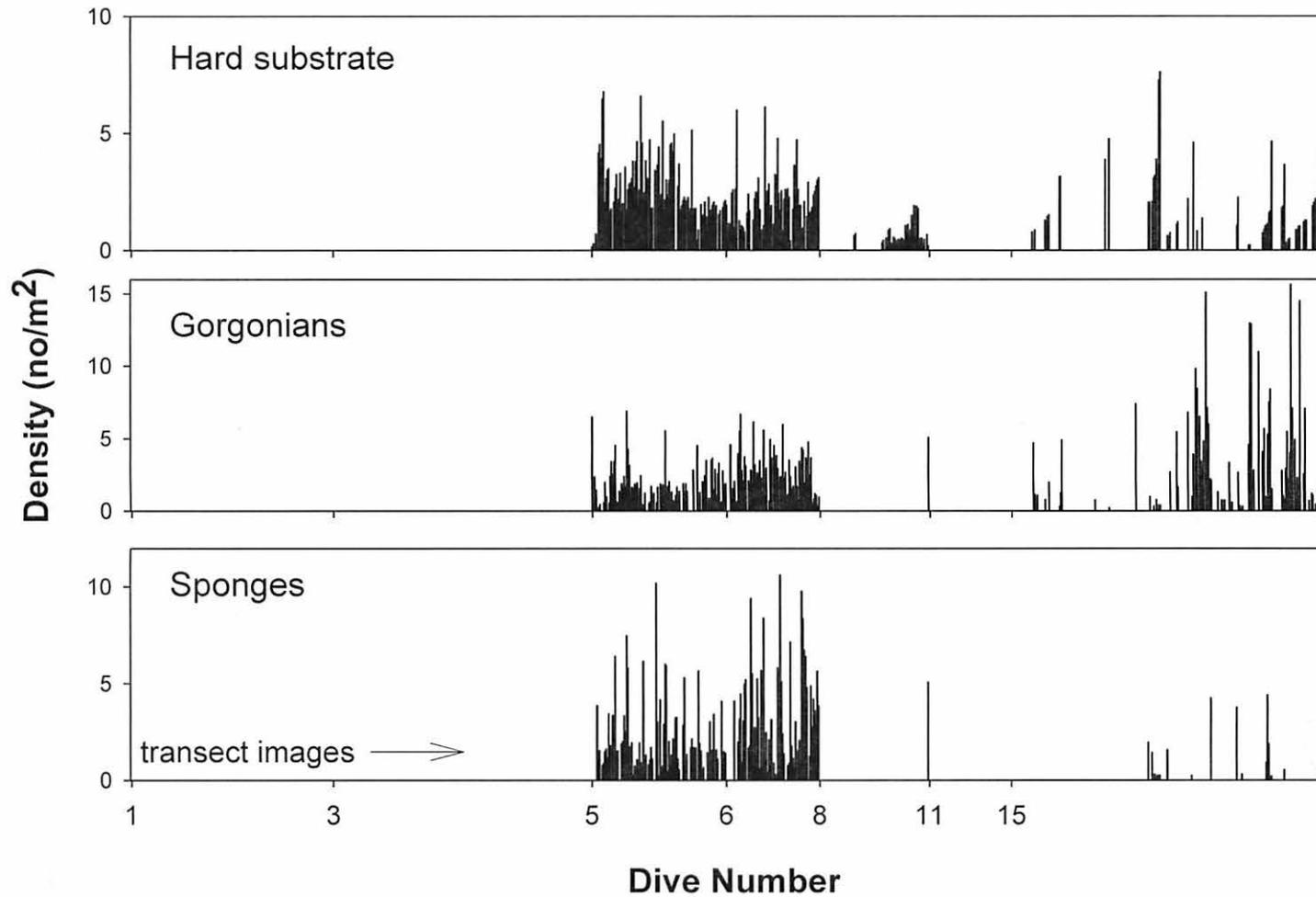
Figure 7. Relationships between the abundance of rocky substrates, gorgonians and sponges along dive transects at Pribilof canyon using data from Millet et al. (2012). Data from individual images (n= 938) were arrayed in sequence from left to right along individual dive transects which were placed end to end.

Pribilof Canyon
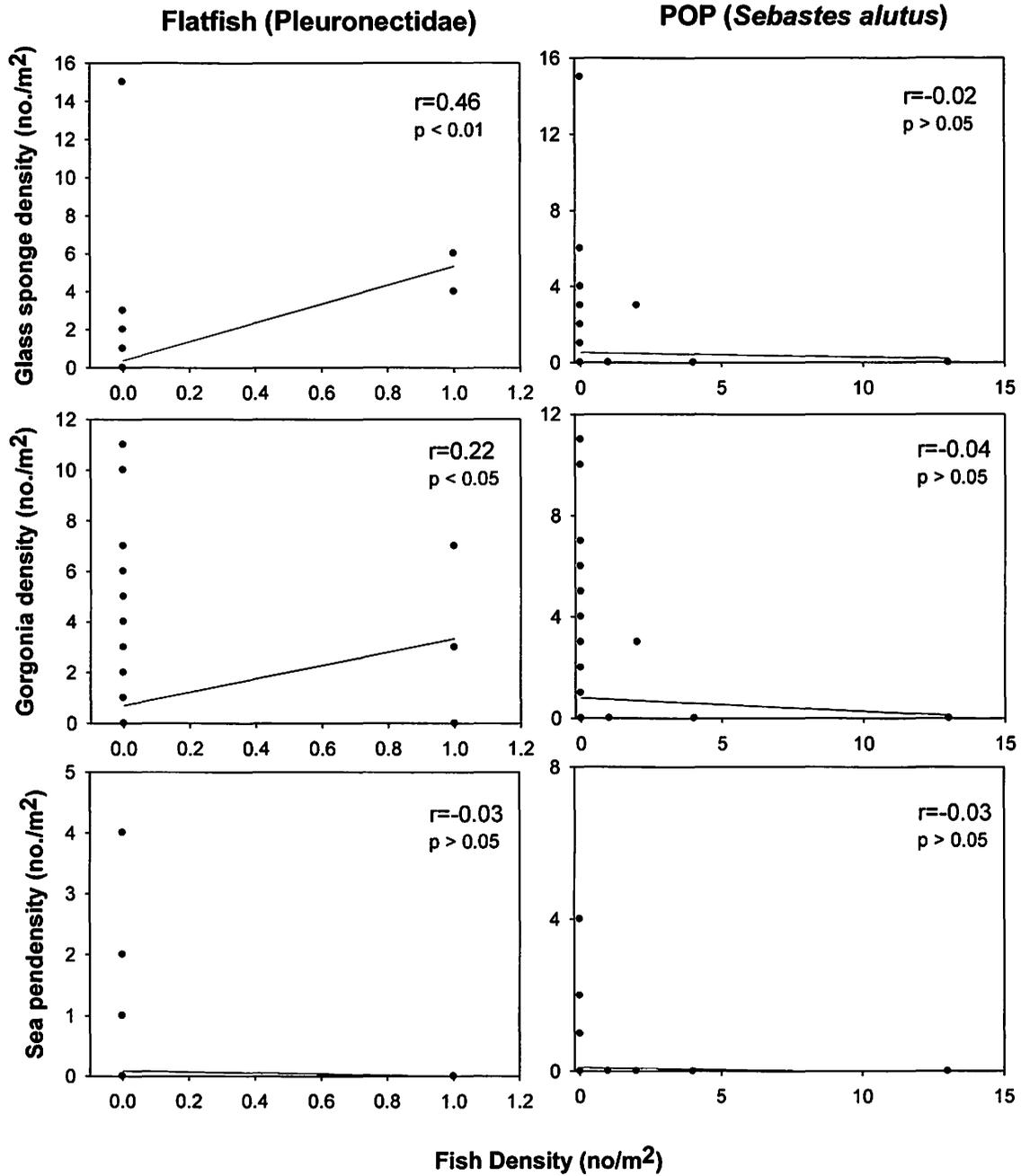
Figure 8. Correlations between fish and structure-forming invertebrate abundances in Pribilof canyon. Regression are shown to illustrate general patterns but were not used in statistical analyses.
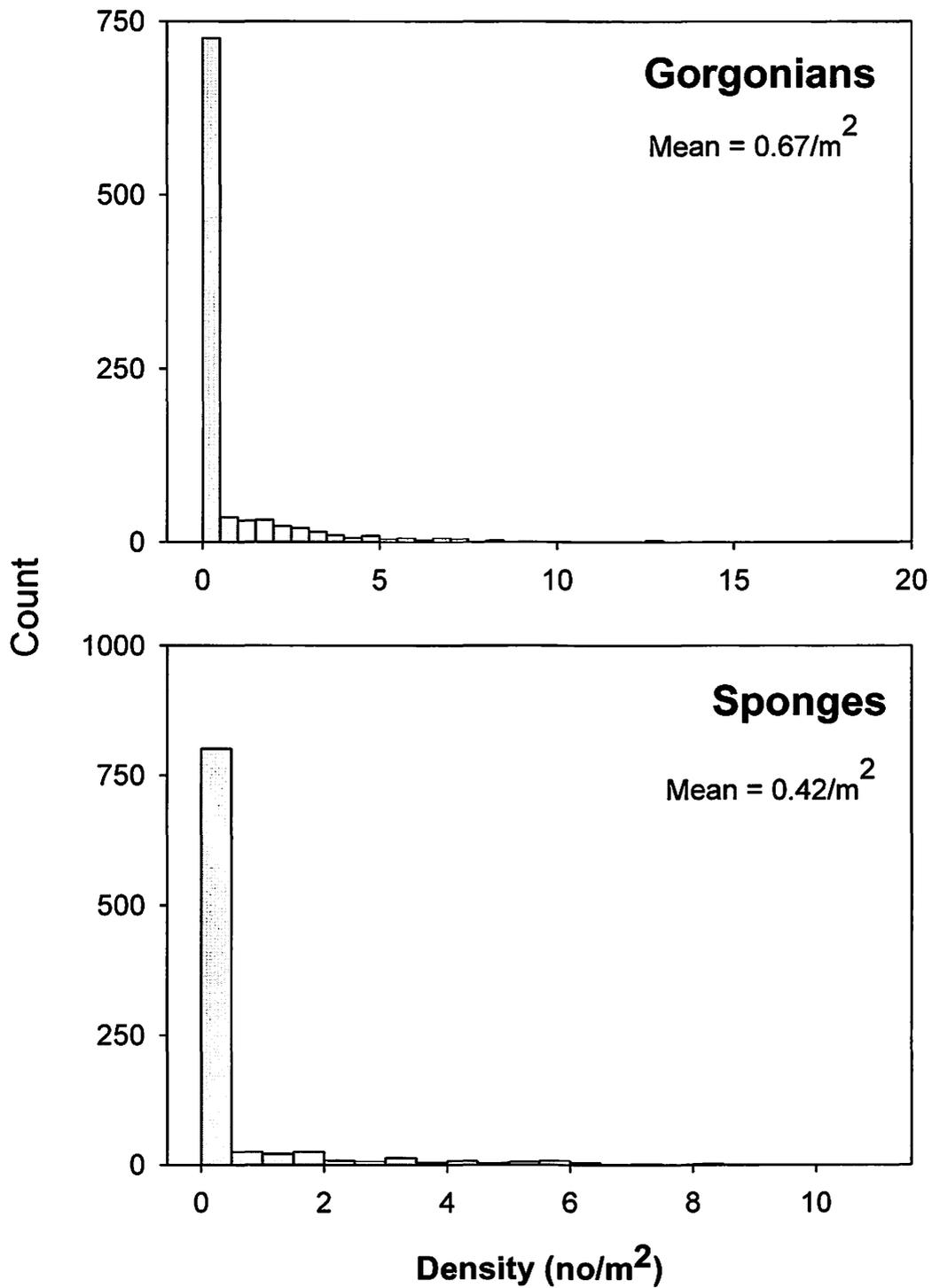
Figure 9. Frequency distribution of major structure-forming invertebrate abundances in Pribilof canyon based on complete data set in Millet et al. (2012).
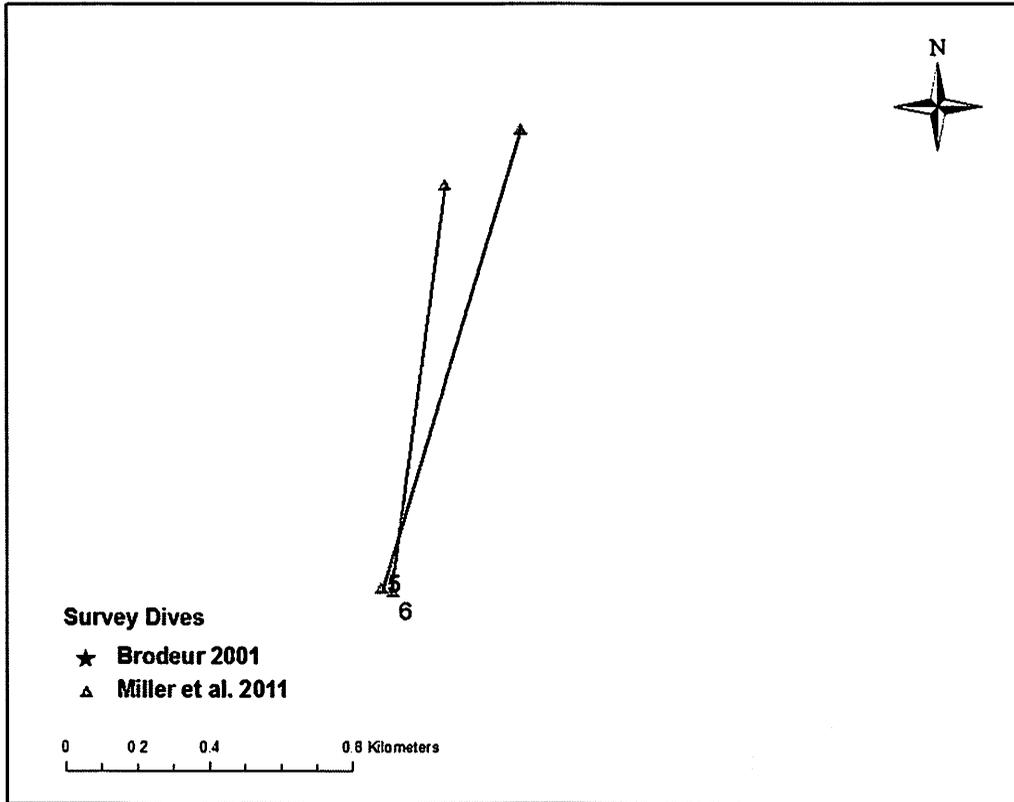
Figure 10. Start and end coordinates of dives 5 and 6 at Pribilof canyon conducted by Millet et al. (2012).
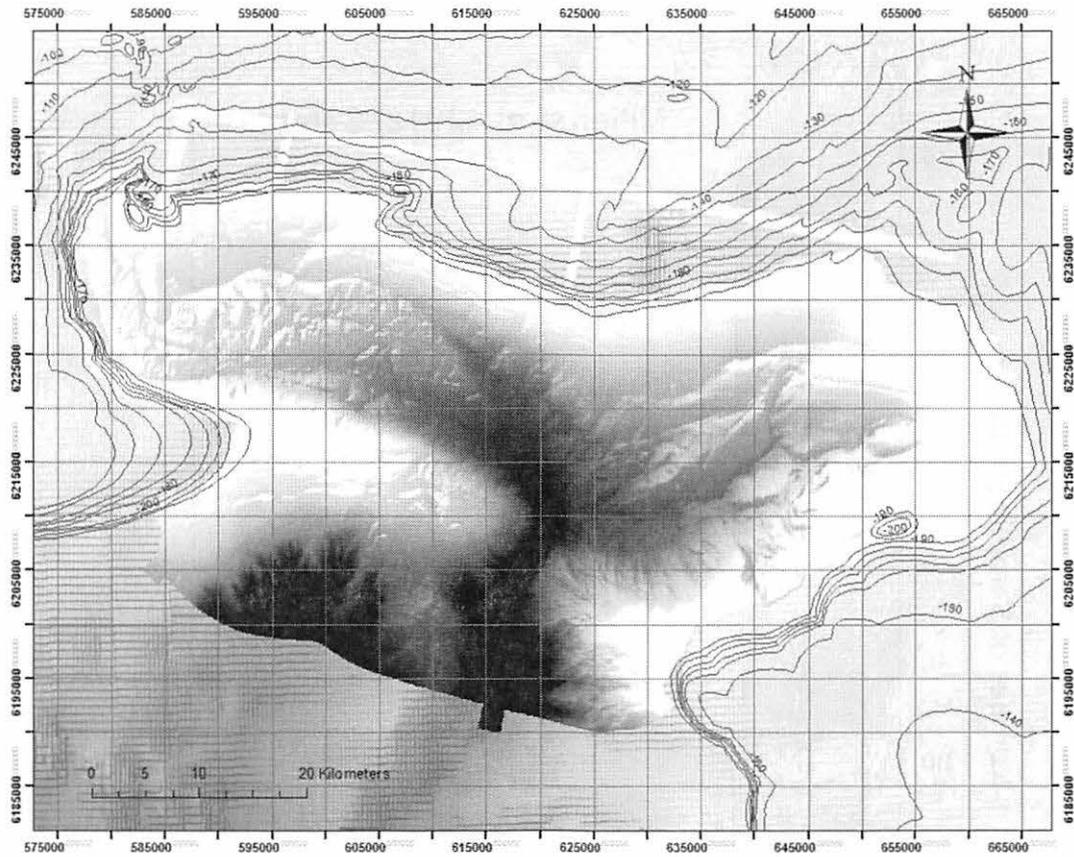
Figure 11. A 5 x 5km sampling grid of Pribilof canyon overlaid on multibeam bathymetry. The 132 grids superimposed on the canyon map range in depth from 141-1878m and cover 3,300 km^2 or 56% of the 5,930 km^2 area of Pribilof canyon.
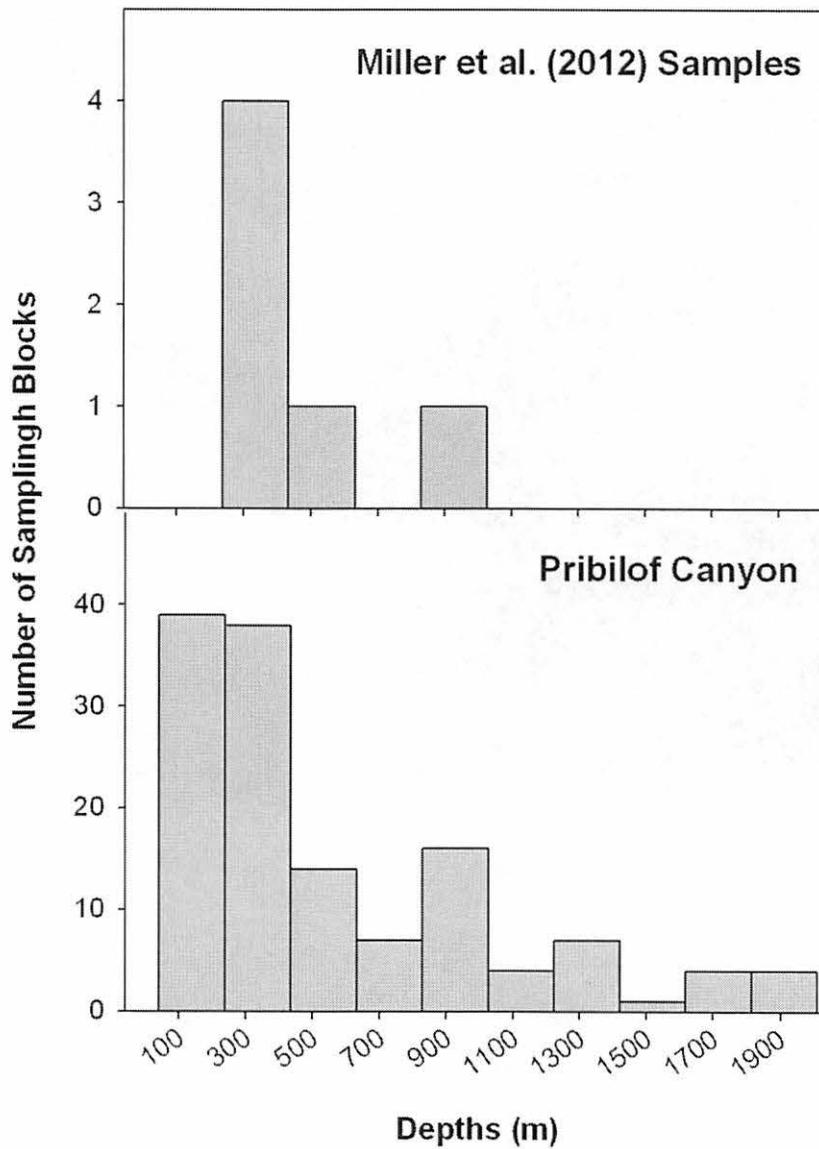
Figure 12. Sampling effort stratified by depth in the Miller et al. (2012) study relative to an ideal sampling grid for Pribilof canyon (Figure 10). Mean depth for each sampling block for the grid and the Miller study were obtained by sampling the depth in the multibeam bathymetry in the center of block using ArcGIS.

Appendix
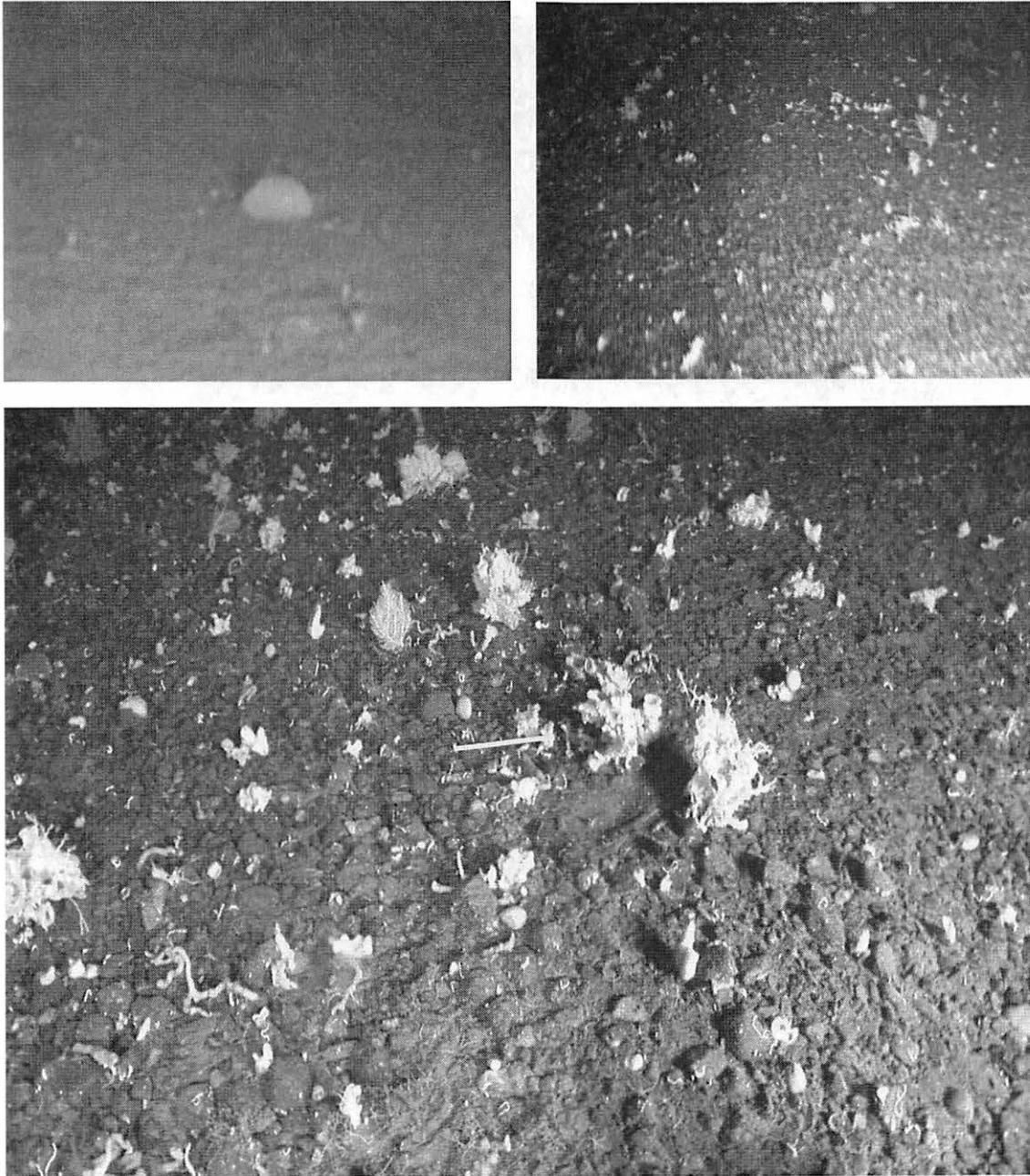
Figure 1. Illustration of poor image quality (top two frames) relative to high image quality (bottom frame) at Pribilof canyon. The bottom frame illustrates high sponge density on pebble habitat from dive 6. The reference laser scale bar in the bottom frame is 10cm (~4 inches).
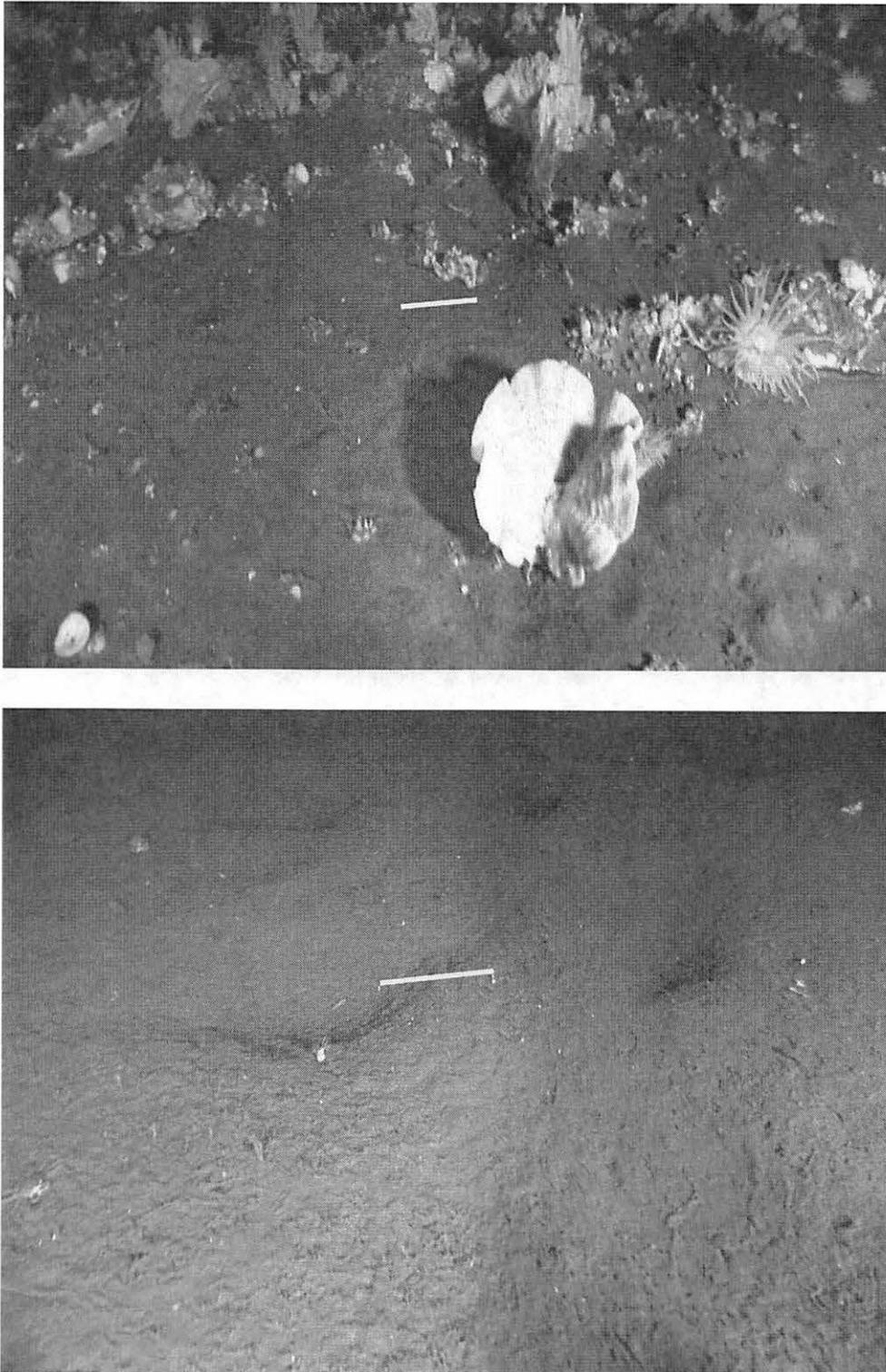
Figure 2. Sponges and Primnoid corals on mud-pebble habitats at Pribilof canyon from dive 15 (top). Mud habitats at Pribilof Canyon from dive 3 (Bottom). The reference laser scale bar in the frames is 10cm (~4 inches).
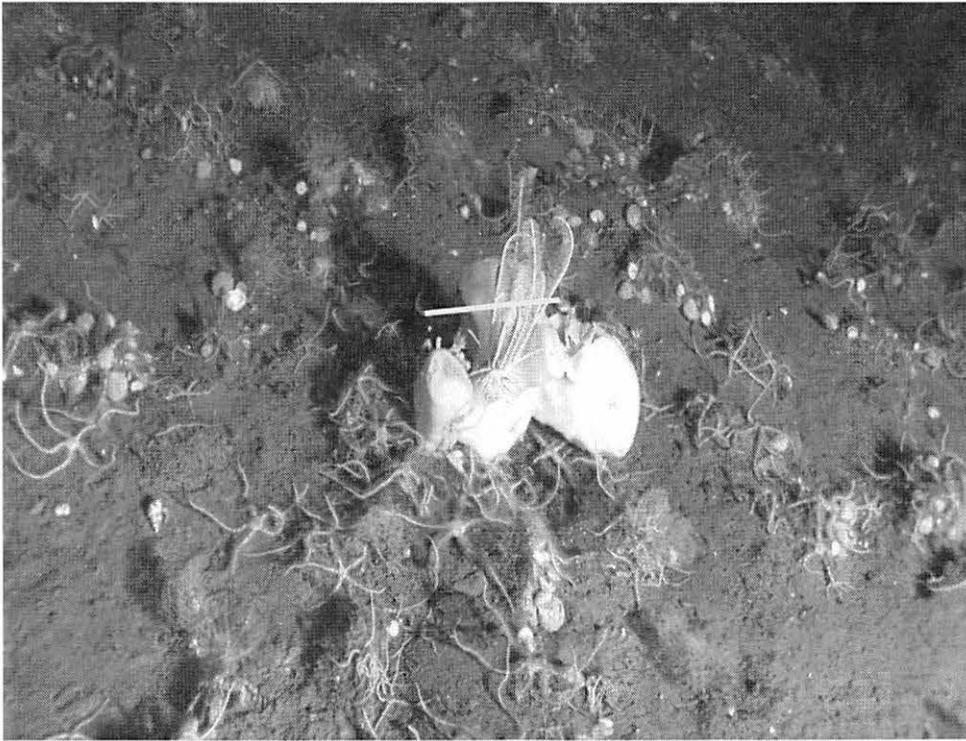
Figure 3. Sponges and Primnoid corals on mud-cobble habitats at Zhemchug canyon from dive 24 (top). Mud habitats at Zhemchug Canyon from dive 26 (Bottom). The reference laser scale bar in the frames is 10cm (~4 inches).