Patterns of benthic mega-invertebrate habitat associations in the Pacific Northwest continental shelf waters

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TITLE: Patterns of benthic mega-invertebrate habitat associations in the Pacific Northwest continental shelf waters

RUNNING HEAD: Benthic mega-invertebrate assemblages

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ABSTRACT:

As human impacts and demands for ocean space increase (fisheries, aquaculture, marine reserves, renewable energy), identification of marine habitats hosting sensitive biological assemblages has become a priority. Epifaunal invertebrates, especially the structure-forming species, are an increasing conservation concern as many traditional (bottom-contact fishing) and novel (marine renewable energy) ocean uses have the potential to displace or otherwise impact these slow-growing organisms. The differences in mega-invertebrate species assemblages between high-relief rocks and low-relief sediments are well documented and likely hold for most marine environments. In anticipation of potential development of marine renewable energy faculties off Oregon and Washington (USA), a survey of the benthic invertebrate assemblages and habitats was conducted on the continental shelf of the Pacific Northwest, using video footage collected by ROV, to more finely characterize these assemblage-habitat associations. Four main associations were found: pure mud/sand dominated by sea whips and burrowing brittle stars; mixed mud-rock (which may be further divided based on size of mixed-in rocks) characterized by various taxa at small densities; consolidated rocks characterized by high diversity and density of sessile or motile mega-invertebrates; and rubble rocks showing less diversity and density than the consolidated rocks, possibly due to the disturbance generated by movement of the unconsolidated rocks. The results of this study will help classify and map the seafloor in a way that represents benthic habitats reflective of biological species assemblage distributions, rather than solely geological features, and support conservation and management planning.

KEY WORDS: Benthic assemblage; epifauna; rocky reef; soft sediment; underwater video

1. INTRODUCTION

Although the oceans provide a variety of valuable goods and services, societies sometimes fail to consider the damage that resource exploitation may cause to marine ecosystems over time (Jackson et al. 2001). Examples of anthropogenic impacts and over-exploitations of these ecosystems are numerous, and hard continental shelves and rocky reefs are among those most impacted (Lotze et al. 2006; Halpern et al. 2008). Fisheries using bottom gear such as trawls and dredges are by far the most damaging for the seafloor, acting like forest clear-cutting (Watling and Norse 1998). Due to technological improvements during the last decades, bottom-fishing gears are now used from polar to tropical waters on every type of seafloor; few places on the world's continental shelves remaining non-affected (Watling and Norse 1998; Halpern et al. 2008). Other human uses of the oceans like aquaculture, mining or tourism activities threaten continental shelf ecosystems (Rossi 2013) and their effects, both direct and indirect, can be synergistic (Jackson et al. 2001; Kaplan et al. 2013). Human use changes such as marine protected areas (MPAs) and marine renewable energy developments (MREs), like wave energy or offshore wind farms, both may have some benefits for ecosystems by closing some areas to fisheries (Sheehan et al. 2013). However, potential negative effects of marine renewable energy developments arise from introducing hard structure to sedimentary seafloor habitats as well as changing current and sediment flow patterns. The intensity and extent of such effects on seafloor assemblages by MRE installations are as yet poorly characterized, mostly hypothesized from studies of artificial reefs and oil platforms (see reviews in Boehlert and Gill 2010, Henkel et al. 2013, 2014). However, some hard-bottom (Keenan et al. 2011) and structure colonization studies (Leonhard and Pendersen 2006, Wilhelmsson and Malm 2008, Langhamer et al. 2009) have been conducted in relation to MRE installations in Europe (see also review by Leeney et al. 2014).

One of the major threats of seafloor exploitation to continental shelf ecosystems is a reduction of habitat complexity and heterogeneity by damage to or smothering of slow-growing structure-building organisms like sponges or gorgonians, which may create biogenic habitat (Watling and Norse 1998; Kaiser et al. 2006; Sheehan et al. 2013) as well as damage to or sedimentation of rocky outcrop or reefs themselves. Habitat heterogeneity can be a major driver of variability in the abundance and diversity of marine species (Benedetti-Cecchi and Cinelli 1995; García-Charton et al. 2004), supporting global species diversity by increasing niche availability and community complexity and facilitating the formation of distinct species assemblages (Cerame-Vivas and Gray 1966; García-Charton et al. 2004; McClain and Barry 2010).

The Pacific Northwest (PNW) continental shelf, especially in its northern part (i.e. off Oregon and Washington), is mostly characterized by mud and gravel habitats, but rocky outcrops and reefs occur in several areas (Romsos et al. 2007), supporting structure-building invertebrates that increase the habitat complexity of the seafloor (Strom 2006). This region has a long history of intense fisheries with a variety of fleets using bottom gears dedicated to benthic and / or demersal species: groundfishes, demersal rockfishes, crabs and shrimps. Moreover, it is becoming a focus for offshore wave and wind energy installations on the continental shelf and slope, with an estimate of about 1000 TWh of just wave energy resource available per year for the PNW continental shelf (EPRI 2011). However, despite the abundance (and some documentation of) of invertebrate bycatch, little is known about mega-invertebrate assemblages on this part of the continental shelf. Hixon and Tissot (2007) and Hannah et al. (2010, 2013) compared trawled versus untrawled mud assemblages at two locations on the Oregon continental shelf, and Tissot et al. (2007) described the invertebrate and fish assemblages at a single outer continental shelf reef off Oregon. Only Strom (2006) has summarized the distribution of structure-forming invertebrates at multiple sites along the continental margin off Oregon. On the southern part of the eastern Pacific continental shelf (i.e. southern California), different invertebrate assemblages have been distinguished based on the physical structure of the habitats: habitats composed of high-relief rocks were associated with sessile and structure-forming mega-invertebrates including sponges and gorgonians, while low-relief habitats composed of fine sediments were associated with motile mega-invertebrates including sea stars, crustaceans, bivalves, and sea cucumbers (Allen and Moore 1996; Allen et al. 1997; Stull et al. 1999; Tissot et al. 2006). Large structure-forming mega-invertebrates such as sponges, corals, crinoids and basket stars have been suggested to provide shelter and additional resources for fish and other invertebrates by increasing the availability of microhabitats through their large surface area (Tissot et al. 2006).

The differences in mega-invertebrate species assemblages between high-relief rocks and low-relief unconsolidated sediment as described above likely hold for most marine environments. However, the diversity of assemblage-habitat associations on the seafloor is more complicated than this dual opposition and management decisions regarding protection or development of seafloor habitats require a more detailed understanding of associated affected species. Thus the objectives of this study were to distinguish finer differences in habitats based on substrata (and depth if significant in the study range) and to characterize the diversity and composition of mega-invertebrate assemblages in those habitats. The following substratum differentiations were investigated. How mega-invertebrate assemblages found on pure sediment differ from assemblages found on mud mixed with unconsolidated rocks (hereafter called mixed mud-rock), which in turn differ from assemblages living in rocky habitats. Within rocky habitats, if the slope of the rocks (i.e. flat rocks versus ridge rocks) and the cover of the rocks (i.e. a large consolidated outcrop with a cover of unconsolidated smaller rocks, hereafter called rubble rocks; rocks with a veneer of sediment; or bare rocks) affect the diversity and density of associated epifauna. To test these hypotheses, underwater video footage from three different sampling sites along the Washington (Grays Bank) and Oregon (Siltcoos Reef and Bandon-Arago outcrop) coast were analyzed, to identify and enumerate the sessile and motile mega-invertebrates from the images, and characterize the substrata encountered. These three sites were selected for this study because they are located in areas of potential interest for the development of different MRE projects and have been mapped with high-resolution multi-beam sonar.

2. MATERIALS AND METHODS

2.1 Study sites

In late August 2011 and September 2012, we used the remotely operated vehicle (ROV), *Hammerhead*, a modified Deep-Ocean Engineering *Phantom* ROV customized and implemented by Marine Applied Research & Exploration (http://www.maregroup.org/the-hammerhead-rov.html), to survey habitats and mega-invertebrates at three sites on the Pacific Northwest continental shelf (Fig. 1): Grays Bank (GB, 14 stations, off Grays Harbor, Washington) and Siltcoos Reef (SC, 10 stations, off Charleston, Oregon) in 2011 and Bandon-Arago (BA, 12 stations, off Bandon, Oregon) in 2012. Each site was composed of several stations, themselves composed of three transects, each approximately 250 meters long each separated by 250 meters (Fig. 2). The ROV was kept at a regular speed (~0.5 m.s^{-1}) and a regular height from the bottom (~1 m) to provide images of good quality to identify and enumerate the mega-invertebrates. This sampling plan was designed to maximize the number of bottom types surveyed at each study site. The ROV *Hammerhead* was equipped with two color HD video cameras attached at the front of the ROV: one facing downward and perpendicular to the sea surface, and the other facing outward, angled roughly 30 degrees from the dorsal surface of the ROV. The ROV *Hammerhead* was equipped with sizing lasers for each camera, a CTD that measured depth (meters), temperature (Celsius), and salinity (PSU) continuously, and was integrated with a navigation system that measured latitude and longitude every second.

2.2 Video analyses

Each video was watched a minimum of three times: one for substratum identification, one for sessile mega-invertebrate identification and enumeration, one for motile mega-invertebrate identification and enumeration. While two observers were used for classifying substrata, a single observer identified all organisms to reduce potential observer-related differences in organism detection or classification. Only benthic epifauna and some endofauna taxa showing recognizable body parts above the sediment were recorded. Both the outward and downward facing cameras were used to identify substratum patches and invertebrates. Since one camera faced downward at a fixed angle from the vehicle, all footage viewed by the downward-facing camera was considered "on-transect" and this view was used to count the invertebrates. Generally, video analysis followed guidelines established by Tissot (2008). Each invertebrate entry was accompanied with a time code that was used to determine in which substratum patch a particular invertebrate was found.

Substratum: Substratum patches were identified based on the grain size class estimated from the video footage and, for consolidated rocks, relief angle, with the start and end times of each substratum patch recorded. Each substratum patch was coded with two letters; the first letter indicated the primary substratum (comprising 50-80% of the duration of the patch) and the second letter indicated the secondary substratum (comprising 20-50% of the duration of the patch): R for ridge rock (angle >30°), F for flat rock (angle <30°), B for boulder (> 25.5 cm), C for cobble (6.5 – 25.5 cm), P for pebble (2 – 6.5 cm), G for gravel (4 mm - 2 cm), and M for mud (not distinguished from sand), refined from Stein et al. (1992). If a substratum patch was comprised of two substrata in equal proportions, the patch was coded with the first letter indicating the substratum with larger grain size. If a patch comprised over 80% of a single substratum, the patch was coded with the same two letters (e.g. MM).

Sessile mega-invertebrates: Only sessile invertebrates taller than 5 cm were identified and enumerated, as recommended by Riedl (1971) and Tissot et al. (2006) because smaller individuals were difficult to see and identify on the images. Sponges and gorgonians, difficult to identify on video, were characterized based on their morphology and sometimes color (e.g., branching sponge, shelf sponge, branching red gorgonian). Encrusting ascidians and bryozoans, impossible to distinguish on video from encrusting sponges, were all gathered under the name shelf sponge, while possible branching bryozoans were counted as branching sponges. These two names thus describe a life form more than a systematic group and patches (shelf sponges) or tufts (branching sponges) were counted as individuals.

Motile mega-invertebrates: Motile invertebrates taller than 5 cm were identified to the lowest possible taxonomic level and enumerated. Some taxa were only identified to the family or genus level, since many species in these families / genera have overlapping morphological features and are difficult to distinguish without specimens to analyze. When the abundance of motile invertebrates was high, one to three additional viewings were needed to identify and enumerate all the individuals. In the Bandon-Arago footage, small orange brittle stars were too numerous to be counted all along each transect and were only enumerated every 30 seconds.

2.3 Substratum patch area and species density

The ROV *Hammerhead* was equipped with a navigator beam that was used to calculate the transect width and the approximate distance traveled every second. The area covered per second was calculated based on the transect width and the distance the ROV traveled from the previous second. Thus, the area of each different patch was calculated by adding all area entries from one second after the start time of the patch to the end time of the patch. The density (individuals.m^{-2}) of each taxon for each patch was calculated by dividing the count for that taxon by the total area of that patch covered by the ROV.

2.4 Statistical analyses

The sample units considered here were the different patch types in a whole site: data from all the same substratum patches were pooled at the site level. Only patch types observed longer than one minute in total for a site were kept in the analyses. A matrix of Bray-Curtis similarities between patch types was calculated on log-transformed density data. Nonmetric multidimensional scaling (nMDS), analyses of similarities (ANOSIM), SIMPER, and DIVERSE were performed using PRIMER 6th Edition (Clarke and Gorley 2006). The nMDS analysis plotted sample units (patch types) on a two-dimensional ordination plane based on taxa composition similarities and dissimilarities. Groups of patch types (hereafter ‘habitat types’) were discerned from the nMDS plot and an ANOSIM was performed to test the strengths of similarities within and differences between these habitat type groups, using permutation and randomization methods on the resemblance matrix. SIMPER (Similarity of Percentage) was used to determine which taxa and their densities contributed to defining each group and the percent contribution of each defining taxon. DIVERSE was used to calculate the diversity indices (average number of taxa S, average density N, Pielou's evenness J') on the untransformed abundances for each habitat group, and a series of ANOVAs and Tukey HSD tests was performed in the open-source software R (R Development Core Team 2013) to test whether or not the indices were significantly different among habitat type groups. To test for a possible bathymetric structuring of the organisms, a second set of nMDS was performed at the transect level on the density of taxa within a patch, coded by the habitat type defined at the first round of analyses, using depth bin (sections 10 meters deep) as a factor. For this second set of nMDS, the sample units were the patch types within a transect, that is all the patches of a same substratum type pooled at the transect level because the depth range varied within a site but not so much along a transect. An ANOSIM was also performed on the seven depth bins.

3. RESULTS

3.1 Site characteristics

The three sites showed slightly different physical characteristics (Table 1). Bandon-Arago (BA) and Grays Bank (GB) were shallower than Siltcoos Reef (SC). The temperature was the coldest at the northern stations (GB) and up to one degree Celsius warmer in 2012 at BA as compared to SC in 2011. No bathymetric or latitudinal variation in salinity was noticed among the three sites. A total of 28 different substrata (two-letter code combinations) were identified in the transects: 16 at SC, 20 at BA as well as GB. Eight substrata were discarded at GB, seven at SC, and two at BA because of durations shorter than a minute, resulting in a grand total of 22 different substrata (Fig. 3) that were analyzed and are discussed further. Substrata found in large proportion across all sites were flat rock-mud (average = 23%), mud-mud (average = 20%), ridge rock-ridge rock (average = 19%) and ridge rock-mud (average = 18%). A total of 85 taxa representing eight phyla were found across all three sites (Table 2, Online Resource 1). The phyla Echinodermata, Porifera and Cnidaria together comprised over 91% of all the invertebrates encountered in the survey (Table 2). Porifera and Echinodermata were the most abundant at BA whereas Cnidaria were the most abundant at GB and Echinodermata at SC (Fig. 4).

3.2. Assemblage composition

Six habitats (groups of patches hosting similar invertebrate taxa) were identified from the nMDS ordination (Fig. 5). The habitat groups were mostly organized by substratum characteristics (e.g. pure mud, mixed mud-rock, rock) and subsequently by sites. Unconsolidated sediment patches from the sites split into three groups: group MM-GBSC consisted of pure mud patches from GB and SC; group Mx-GBSC was made of mixed mud-rock patches from GB and SC; and group Mx-BA gathered pure and mixed mud-rock patches from BA only. Rock-based patches clustered into two main groups: cR made of consolidated rocks, both bare and covered with a veneer of mud (BM, FM, RM, RR), from the three sites; and group rR made of rubble rocks (e.g. BC, FB, RG) from the three sites. No distinction was observed between ridge rocks and flat rocks meaning that the slope does not seem to matter. Group PG (pebble-gravel), was a patch type found only at BA in a single transect and will not be discussed further. The ANOSIM performed on the five remaining groups (MM-GBSC, Mx-GBSC, Mx-BA, cR and rR) demonstrated significant overall differences in the compositions of assemblages between the habitats (Global R statistic = 0.700, $p<0.01$). In the pairwise test, comparisons were considered reliable when more than ten permutations were possible. Nine of the ten possible pairwise comparisons showed significant differences between groups (Table 3). The only non-significant pairwise comparison was MM-GBSC vs. Mx-GBSC (p=0.067). This was not surprising because of the low number of permutations possible for this pairwise comparison. The SIMPER analysis showed large dissimilarities for each pairwise comparison, ranging from 70.81% to 99.47% of difference in the taxonomic composition of the groups (Table 4). Differences also were found among habitats based on the univariate analyses of number of taxa S, density N and evenness J' (Fig. 6).

Pure mud at GB and SC (33 % similar) showed a medium number of taxa and a high density of individuals with a significantly lower Pielou's evenness than all other habitats. Pure mud habitat at these sites was characterized by high density of burrowing brittle stars and Subselliflorae (sea whips) (Table 5). Mixed mud-rock habitats at GB and SC were characterized by medium to high density of anemones and low density of sponges with the lowest within group similarity (16 %; Table 5); they also showed lower number of taxa and density of individuals than the same habitats at BA. Mixed mud-rock habitats at BA (which included pure mud at this site; patches 46 % similar) showed a medium number of taxa, a low density of individuals and were characterized by many of the same taxa as the consolidated rocks (minus the anemones and squat lobsters) but in much lower densities (Table 5). What made the two mixed mud-rock groups 93.18% dissimilar was the higher density of several echinoderm species (brittle stars, sea stars and sea cucumbers), sponges, branching gorgonians and tunicates at BA than GB and SC, and a higher density of sea anemones at GB and SC than BA (Online Resource 2).

Consolidated rocks showed 37 % within-group similarity, supported the highest number of taxa and density of individuals (Fig. 6), and were characterized by high density of sponges, branching gorgonians, giant plumose anemones, echinoderms (brittle stars, sea cucumbers and sea stars) and squat lobsters (Table 5). In contrast, rubble rocks supported significantly fewer taxa (three-fold) and much smaller densities of individuals (88-fold) and were characterized by low density of sponges and sea cucumbers with nearly 36 % within-group similarity (Table 5). What made the consolidated rock group 90.47 % different than the rubble rock group was higher density and diversity of sponges, gorgonians, echinoderms (brittle stars, basket stars, sea stars, sea cucumbers), anemones, squat lobsters and tunicates on the consolidated rock (Online Resource 2).

There appeared to be some distinction of groups by depth; however separation on the ordination plane was dominated by habitat (Fig. 7) and the ANOSIM performed on the seven depth bins did not demonstrate significant overall differences in the compositions of assemblages between depth (Global R statistic = 0.193, $p<0.01$). Based on taxa densities pure mud transects at GB and SC clustered together in the top right section of the graph with further separation by depth bin; mixed mud-rock transects at GB and SC (50-79 m) clustered in the bottom right. Mixed mud-rock at BA (50-69 m) and consolidated rocks (50-119 m) from the three sites mixed together on the left side of the two-dimensional plot with rubble rocks (50-119 m) in the lower left. Clearer distinctions among the three habitat groups appeared on the three-dimensional plot (results not shown).

4. DISCUSSION

This study aimed to distinguish finer resolution in benthic habitats that support distinct epifaunal invertebrate assemblages on temperate continental shelves. Specifically, groups of benthic mega-invertebrate epifauna were described from three rocky reefs and the surrounding soft sediments off the Oregon and Washington coast and associated with the substrata on which they were observed. In addition to building an understanding of the diversity, density, and taxa various habitats support, this study provides data on benthic mega-invertebrate abundances and distributions on the Pacific Northwest continental shelf at a specific time point, which may be compared to future similar surveys for assessments of the effects of global warming, fisheries management and marine renewable energy development on the distribution of such taxa. Hundreds of thousands of sessile and motile individuals were identified and enumerated, as well as the characteristics of the substratum. However, several identifications were not able to reach the species level without actual specimens to check and dissect for diagnostic morphological characters. For example, the different species of the sea star genera *Henricia* and *Solaster* are impossible to differentiate without a check of the aboral plates, the adambulacral spines and the pedicellariae (Lambert 2000; C. Mah, pers. comm.); similarly, species identification via images is nearly impossible for organisms like sponges, which are usually identified on the structure of their spicules. All branching and encrusting organisms (trickier to enumerate and discriminate) were gathered as functional groups under the names "branching sponge" and "shelf sponges" respectively, even if these groups included more than just sponge taxa (e.g. bryozoans or colonial ascidians). Since different species use different ecological niches and suitable habitats, a full understanding of which taxa might be most susceptible to small habitat changes would require sampling these organisms, particularly the sessile invertebrates, and identifying them to species. Despite these taxonomic limitations, the review of the video footage and the statistical analyses performed on taxa densities allowed the discrimination of different assemblages on particular substrata based on their taxonomic composition. Like previous studies (Allen and Moore 1996; Allen et al. 1997; Stull et al. 1999; Tissot et al. 2006), differences were observed between habitats composed of higher-relief rocks (greater densities of sessile and structure-forming mega-invertebrates and greater diversity) versus low-relief habitats composed of fine sediments (more motile mega-invertebrates). However, finer distinction was also characterized within both low-relief (between pure mud and mixed mud-rock) and higher-relief (among rock types) habitats as described in the following sections. Although the goal was to describe habitats that were generalizable across sites, some differences among sites were observed. However, this did not seem to be driven by latitudinal or depth differences, which might be suspected to affect species distributions. Siltcoos Reef was more similar to Grays Bank, which is ~500 km north, than to Bandon-Arago, which is only 50 km south (Fig. 1), and Grays Bank and Bandon-Arago had overlapping depth ranges, while Siltcoos was deeper. Thus, observed differences likely stem from differences in the geologic history of the sites such that the assemblage-habitat associations are not unique to a site *per se* but rather are based on characteristics of the substratum. The major habitat types discerned across this ROV survey are described here below.

Pure mud

Not surprisingly, the assemblages found along patches of pure mud (not distinguished from sand) were very different from the assemblages found in other types of habitats. The diversity and evenness of taxa living on the mud or partially burrowed in it were quite low while the abundance of some of these taxa numbered in the hundreds. The pure mud community was thus largely dominated by a very few taxa, like Subselliflorae sea whips and burrowing brittle stars with occasional sea anemones and sponges. This dominance of sea whips on mud communities previously has been noted along the Oregon coast (Hixon and Tissot 2007; Hannah et al. 2010, 2013), as well as on the southern California shelf (Tissot et al. 2006; de Marignac et al. 2009), the Gulf of Alaska and the Bering Sea (Malecha and Stone 2009). This type of mega-invertebrate can live in dense populations and provides structure and habitat heterogeneity for other invertebrates in this otherwise non-complex environment (Tissot et al. 2006; Malecha and Stone

2009). However, Subselliflorae are adapted to life in very homogeneous and stable habitats and are more vulnerable to habitat alteration (e.g. from bottom-fishing gears) than benthic communities found in less consolidated coarse sediments like the mixed mud-rock (Collie et al. 2000; Malecha and Stone 2009). Nonetheless, despite the high number of shrimp-trawl records in the vicinity of Siltcoos Reef (R. Hannah, pers. comm.), the observed high abundance of Subselliflorae indicates that the populations observed on the video transects might be in areas around the reef not really accessible to bottom-trawling and could act as source populations to refill the impacted ones nearby. Burrowing brittle stars were also identified in de Marignac et al. (2009) as dominant taxa along what they called the 'recovering transects' in central California. In contrast to Siltcoos Reef and Grays Bank, the pure mud patches at Bandon-Arago were not differentiated in their benthic assemblages from the mixed mud-rock patches at the same site and were comprised of very few to no Subselliflorae and burrowing brittle stars. Bandon-Arago is a large and old rock outcrop on the mid Oregon shelf (Romsos et al. 2007) and the pure mud and mixed mud-rock patches were found within the reef itself (Fig. 2). In contrast, Siltcoos Reef and Grays Bank are smaller rock outcrops and pure mud was mostly found around the reefs. The 'pure mud' at Bandon-Arago might rather be a thin layer of mud on the bedrock, not really stable and not suitable enough for the species characteristic of pure mud communities to settle in.

Mixed mud-rock

Mixed mud-rock habitats were made of mud (or sand) more or less assorted with coarser sediments like gravel, pebble, cobble or even boulder. These unconsolidated rocks act as physical supports for sessile organisms. The taxa inhabiting the mixed mud-rock at Bandon-Arago were sessile organisms like sponges (both shelf and branching) and gorgonians, known as structure-forming mega-invertebrates. They add complexity and heterogeneity to this habitat and supply support, shelter, or food to motile invertebrates like sea stars, sea cucumbers and nudibranchs. However, some of the most abundant motile taxa in this habitat were partially burrowing organisms such as the sea cucumbers *Cucumaria* spp. or the small orange brittle stars that live with the body hidden in tiny cracks in the mud or between small rocks and the arms extending out. At Siltcoos Reef and Grays Bank, in addition to the structure-forming sessile organisms (gorgonians and sponges), the taxa inhabiting the mixed mud-rock habitats were mostly sea anemones and a few motile species like sea stars.

Mixed mud-rock has not been described as a major benthic habitat type on the PNW continental shelf in previous studies. On other temperate continental shelves like the Bay of Biscay or the English Channel, mixed mud-rock habitat is described and is further divided into different categories, depending on the size and abundance of the unconsolidated rocks involved, with different assemblages (Brind'Amour et al. 2014). Within this study, the differences between mixed mud-rock at Bandon-Arago versus the other two sites similarly may be related to the difference of the size and abundance of the unconsolidated rocks. At Siltcoos Reef and Grays Bank, the mud was mixed with gravel and occasionally pebbles (small rocks). At Bandon-Arago the mixed mud also included cobbles and boulders. It is thus not certain whether the differences observed between the two mixed mud-rock assemblages here described are locally-induced differences from a general mixed mud-rock habitat, or two distinct habitats differentiated by the characteristics of the mixed-in rocks which support different assemblages. More occurrences of each substratum across sites might have helped highlight differences in benthic assemblages related to the size of the unconsolidated rocks mixed in the mud. Given these findings, 'mixed mud-rock' should be mapped as a distinct habitat characterized by low densities of a diversity of taxa, particularly sponges, gorgonians, anemones, and burrowing echinoderms. Since Brind'Amour et al. (2014) have shown that this habitat can be divided in several categories, future studies should be designed to obtain thorough coverage of transition areas between consolidated rock and mud habitats to discern whether the different sizes of the interstitial rocks in the transition zone support distinct mega-invertebrate assemblages.

Consolidated rocks

Most of the species diversity and individual densities were associated with consolidated rocks, which include boulders, flat rocks and ridge rocks with a veneer of mud as well as bare ridge rocks. Across all sites, this habitat had the highest abundance of sessile and structure-forming invertebrates such as sponges, gorgonians, giant plumose anemones, sometimes in very dense aggregations, and other sea anemones. The motile mega-invertebrates were very diverse, with an average of forty taxa, including a variety of crabs, echinoderms (basket stars, brittle stars, feather stars, sea cucumbers and sea stars), nudibranchs, octopuses, scallops and squat lobsters. This diversity can be attributed to the physical complexity of higher-relief substrata where there may be greater variation in depth, temperature, current direction and velocity, nutrient transport, and the substrata may be composed of different elements (Taylor & Wilson 2003). Furthermore, the large diversity of structure-forming sessile and motile invertebrates (e.g. basket stars and feather stars) further increases the habitat complexity and heterogeneity and provides a variety of shelters, refuges, spawning grounds and ecological niches for both invertebrates and fishes (Cerame-Vivas and Gray 1966; Benedetti-Cecchi and Cinelli 1995; Tissot et al. 2006).

Rubble rocks

On the other hand, although some of the major species were the same, the substrata composed of rubble rocks (flat or ridge rocks with a cover of unconsolidated rocks) showed very different assemblages. Despite these substrata being rock-based, they did not support the greater densities of sessile and structure-forming mega-invertebrates and greater diversity generally attributed to high-relief rocks (Allen and Moore 1996; Allen et al. 1997; Stull et al. 1999; Tissot et al. 2006). This habitat had the lowest diversity (an average of only ten different species) and densities. This difference might be due to the weak stability of the unconsolidated rocks on a high-relief substratum, probably engendered by hydrodynamic movements due to the strong currents found on the Oregon continental shelf (Kurapov et al. 2003; Osborne et al. 2014). This instability of the substratum may result in frequent disturbance not suitable for the establishment of dense populations of structure-forming organisms able to attract a variety of motile invertebrates. The role of natural disturbance in structuring marine communities has been well described in the intertidal (Dayton 1971; Lubchenco and Menge 1978; Sousa 1979, 1984; Paine and Levin 1981) and shallow subtidal, especially for algae (Airoldi et al. 1996; Airoldi 1998; Scheibling et al. 2008). Disturbance due to the movement of rubble rocks might similarly affect the recruitment and persistence of mega-invertebrates in this habitat. Mapping efforts have not yet distinguished this habitat from consolidated rocks and will be challenging to differentiate from complex, yet still consolidated rocks using sonar. However, it should be classified as a separate habitat since it certainly supports a different species assemblage and lower abundances than consolidated rocks without associated rubble.

Rocky reefs in the PNW continental shelf were highly targeted by fishing activities due to the high diversity of associated rockfish species. Repeated contacts of bottom-trawls on the reefs have damaged or even eradicated slow-growing structure-forming sessile invertebrates and the motile species they attract (Watling and Norse 1998; Kaiser et al. 2006; Sheehan et al. 2013). Nevertheless, because of the decline in rockfish stocks along the PNW coast at the end of the 20th century (see review in NRC 2002), the Pacific Fishery Management Council established in the early 2000’s new regulations leading to a drastic decrease of the fishing pressure on part of the rocky reefs particularly on the outer continental shelf (Hannah 2003; Bellman et al. 2005; Bellman and Heppell 2007). Since that time, some studies have focused on the recovery of rockfish populations on reefs (Bellman et al. 2005; Bellman and Heppell 2007) or invertebrate populations on mud substrata (de Marignac et al. 2009; Hannah et al. 2010, 2013) after fishing closures, but much remains to be done on the recovery of structure-forming invertebrate species on rocky reefs. The three reefs in our study are not included in the Essential Fish Habitat conservation areas (NMFS 2013) and are thus still open to bottom-trawling, as evidenced by fishing gear debris seen on the video footage at Grays Bank and Siltcoos Reef. Although the fishing pressure is not too high on these three inner shelf reefs (R. Hannah, W. Wakefield, pers. comm.), it is not the case for all the non-protected rocky reefs on the PNW continental shelf, and a comprehensive description of the benthic assemblages is needed to understand the effect of bottom-contact ocean-use activities (e.g. fishing, renewable energy development) and integrate this benthic component into the conservation and management plans. The present results could encourage the design of a video survey on rocky reefs now protected from fishing activities to compare the mega-invertebrate assemblages of reefs now recovering from bottom-gear disturbance to those of reefs clearly still impacted by bottom-fishing activities.

5. CONCLUSIONS

Before management decisions can be made about the ocean (for example where to close to fishing practices, where to allow renewable energy installations) it is useful to know what is being protected from potential impacts. While biological communities are shaped by a variety of bottom-up and top-down processes, and species interactions, a major driver structuring benthic mega-invertebrate communities is substratum. Thus, more precise habitat mapping is necessary. This study identified at least four habitats for mega-invertebrate assemblages: (1) Pure mud (not distinguished from sand on the video footage) dominated by sea whips and burrowing brittle stars; (2) Mixed mud-rock (which may be further divided based on size of mixed-in rocks) characterized by medium diversity of species in low density; (3) Consolidated rocks (big rocks with or without a veneer of sediment) characterized by high diversity and density of sessile and motile taxa; and (4) Rubble rocks (big rocks with a cover of unconsolidated rocks) showing less diversity and density than the consolidated rocks, probably due to the disturbance generated by the unconsolidated rocks. These four habitats were consistent across the sites, even if some differences were observed between the mixed mud-rock habitats at BA versus GB and SC, probably due to the different geologic history of the reefs. It may be possible to map mixed mud-rock separately from other unconsolidated sediment with existing data. Future survey methods should attempt to distinguish rubble-rock from consolidated rock.

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FIGURE CAPTIONS

Fig. 1 Location of the three studied sites and surficial lithologic habitats on the Pacific North-West continental shelf, with the number of ROV stations (black lines) per site

Fig. 2 Tracklines of the stations covered during the 2011 and 2012 ROV surveys at Grays Bank, Siltcoos Reef and Bandon-Arago. The background is the bathymetry shown at slightly different scales for the three maps

Fig. 3 Proportion of substratum types per study site. B = boulder, C = cobble, F = flat rock, G = gravel, M = mud, P = pebble, R = ridge rock

Fig. 4 Abundances of benthic macroinvertebrate phyla at the study sites

Fig. 5 Nonmetric multidimensional scaling (nMDS) ordination of the substratum types based on invertebrate assemblages. cR = consolidated rocks, MM-GBSC = pure mud at Grays Bank and Siltcoos Reef, Mx-BA = mixed mud-rock at Bandon-Arago, Mx-GBSC = mixed mud-rock at Grays Bank and Siltcoos Reef, PG = pebble - gravel, rR = rubble rocks

Fig. 6 Graphic representation of (A) the number of species (ANOVA p-value < 0.001), (B) the density (ANOVA p-value < 0.01), (C) the Pielou’s evenness (ANOVA p-value < 0.01) for each assemblage, their standard deviation and membership from the Tukey test (labels a and b above the bars)

Fig. 7 Nonmetric multidimensional scaling (nMDS) ordination of the habitat types regarding the depth from the ROV *Hammerhead* survey. cR = consolidated rocks, MM = pure mud at Grays Bank and Siltcoos Reef, Mx1 = mixed mud-rock at Grays Bank and Siltcoos Reef, Mx2 = mixed mud-rock at Bandon-Arago, PG = pebble - gravel, rR = rubble rocks

Figure 1

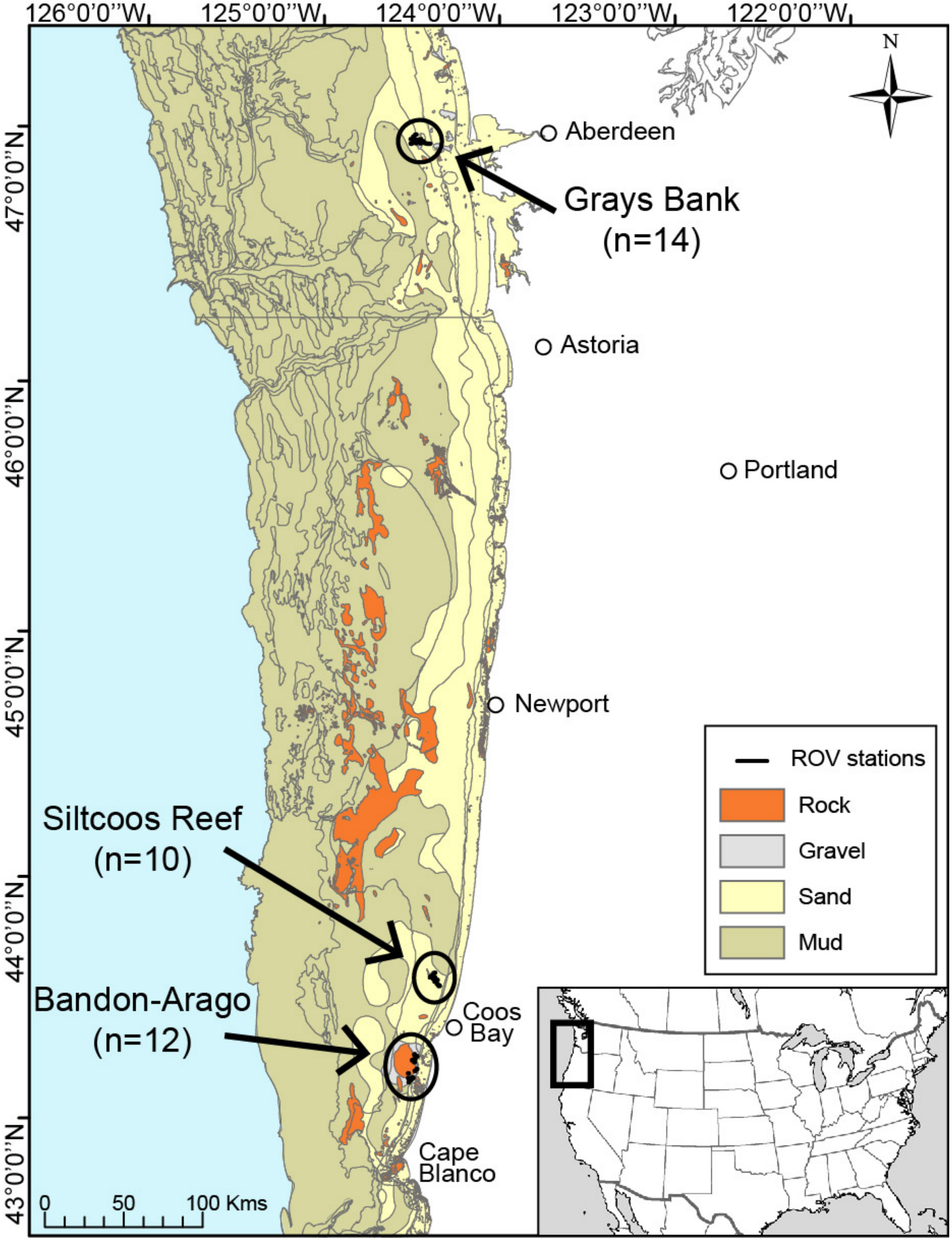

126°0'0"W
125°0'0"W
124°0'0"W
123°0'0"W
122°0'0"W
47°0'0"N
46°0'0"N
45°0'0"N
44°0'0"N
43°0'0"N
N
Aberdeen
Grays Bank
(n=14)
Astoria
Portland
Newport
Siltcoos Reef
(n=10)
Bandon-Arago
(n=12)
Coos Bay
Cape Blanco
0
50
100 Kms
ROV stations
Rock
Gravel
Sand
Mud

Figure 2

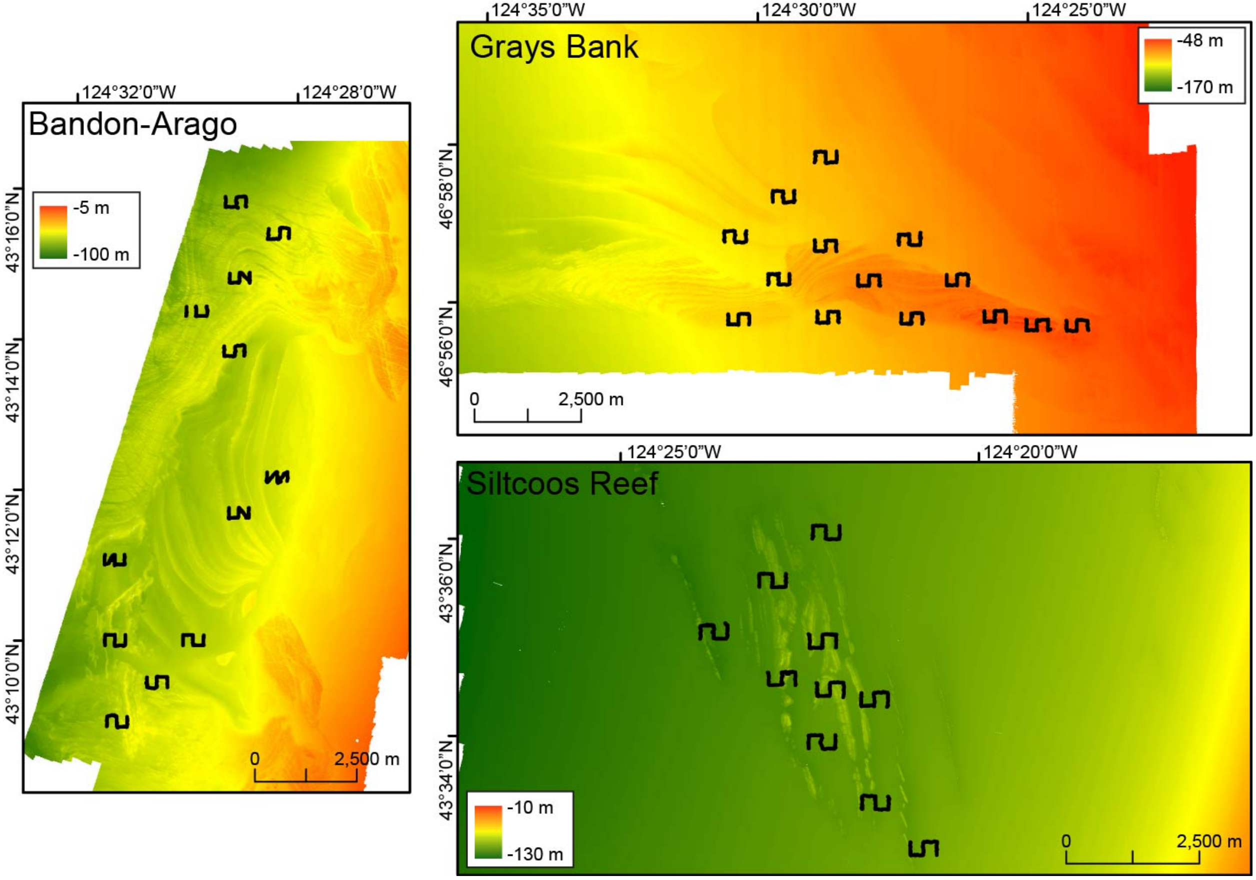

Bandon-Arago
124°32'0"W
124°28'0"W
43°16'0"N
43°14'0"N
43°12'0"N
43°10'0"N
-5 m
-100 m
0
2,500 m
Grays Bank
124°35'0"W
124°30'0"W
124°25'0"W
46°58'0"N
46°56'0"N
-48 m
-170 m
0
2,500 m
Siltcoos Reef
124°25'0"W
124°20'0"W
43°36'0"N
43°34'0"N
-10 m
-130 m
0
2,500 m

Figure 3

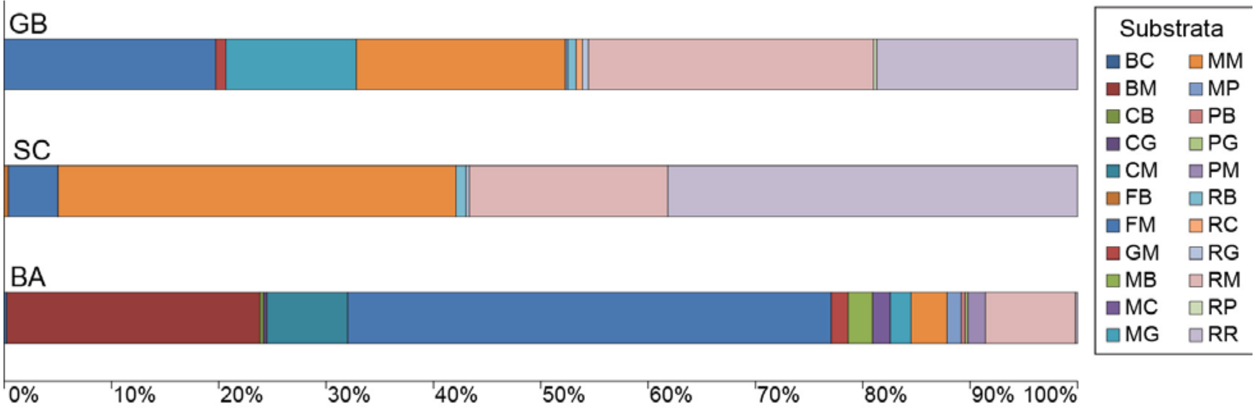


Figure 4

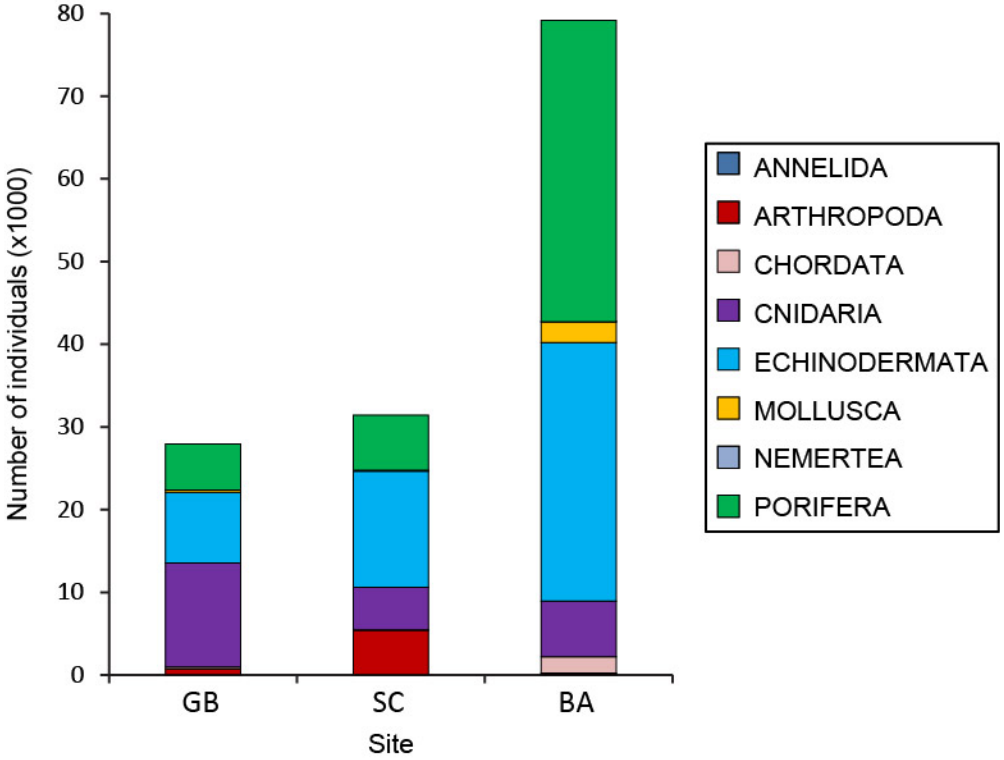


Figure 5

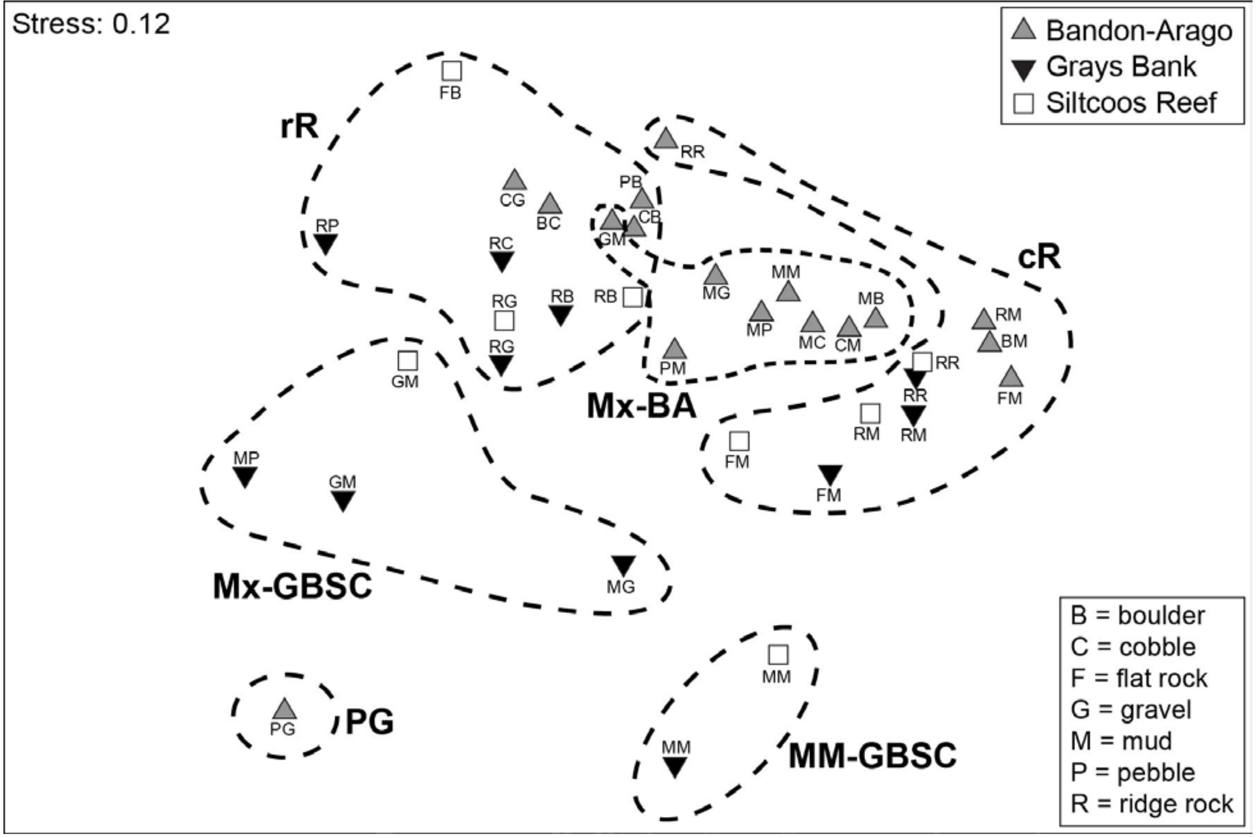

Stress: 0.12
Bandon-Arago
Grays Bank
Siltcoos Reef
rR
cR
Mx-BA
Mx-GBSC
PG
MM-GBSC
FB
RR
CG
BC
PB
CB
GM
RP
RC
RG
RB
RB
MM
MG
MB
MP
MC
CM
RM
BM
FM
PM
RR
RR
RM
RM
FM
FM
GM
MP
GM
MG
MM
MM
PG
B = boulder
C = cobble
F = flat rock
G = gravel
M = mud
P = pebble
R = ridge rock

Figure 6

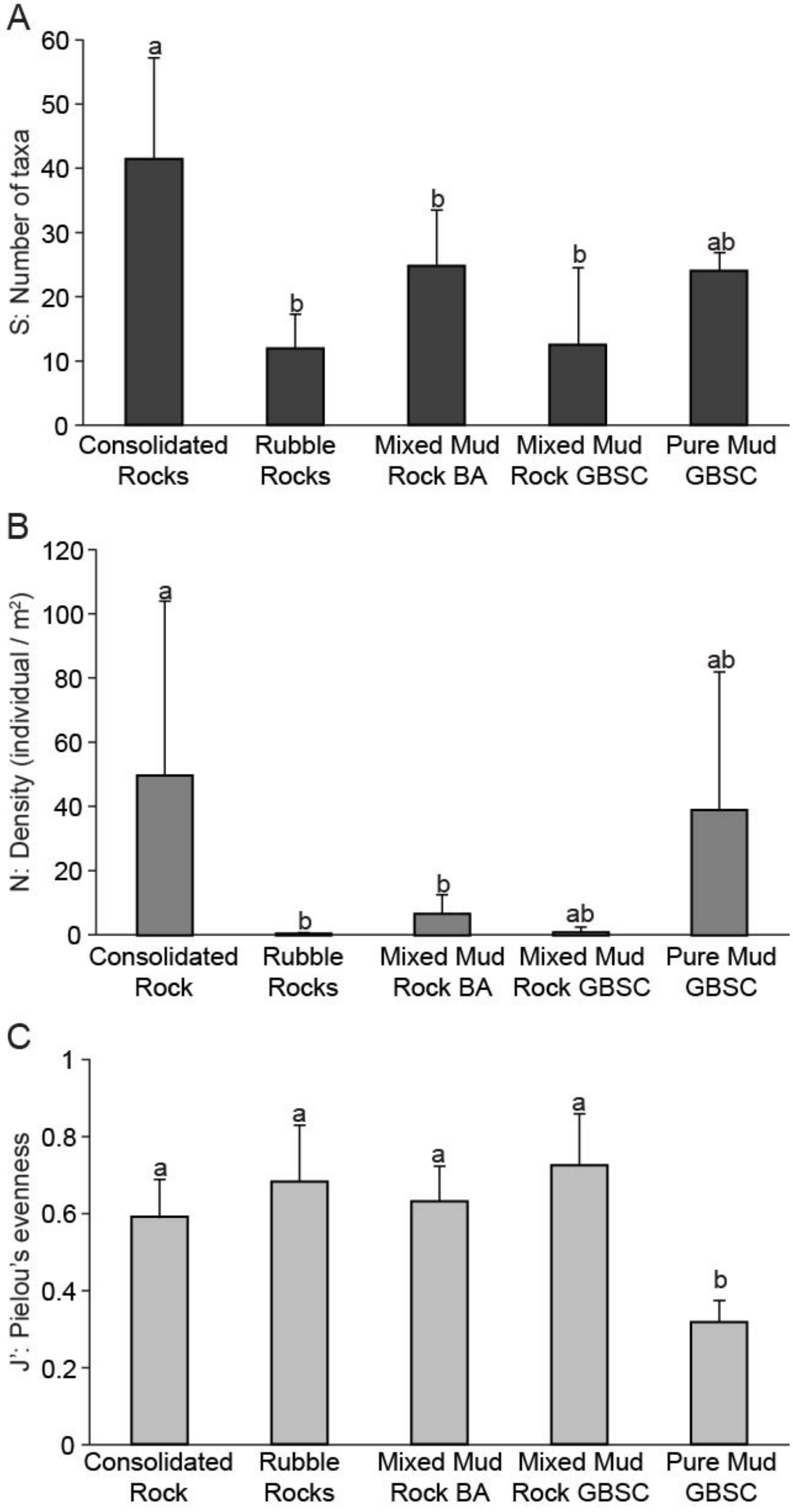
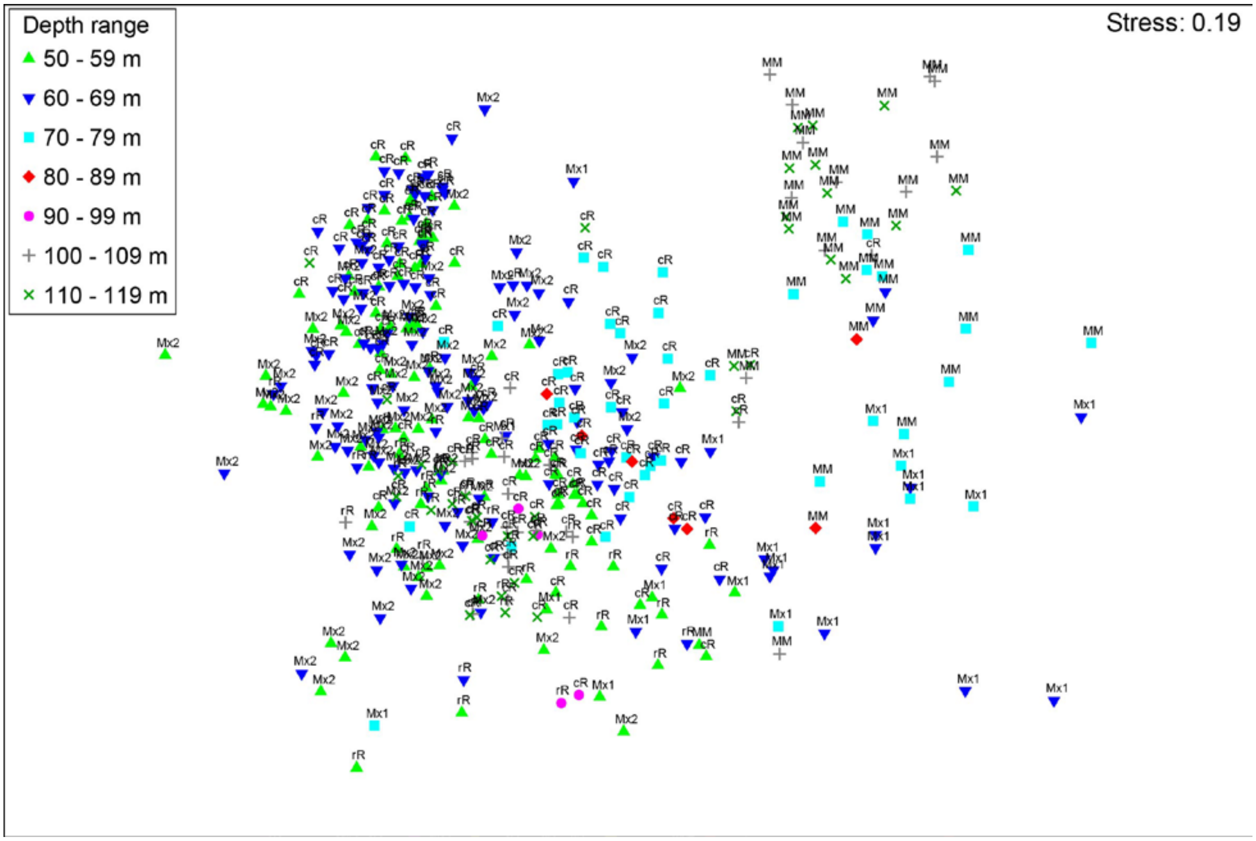

A
S: Number of taxa
0
10
20
30
40
50
60
a
b
b
b
ab
Consolidated Rocks
Rubble Rocks
Mixed Mud Rock BA
Mixed Mud Rock GBSC
Pure Mud GBSC
B
N: Density (individual / m²)
0
20
40
60
80
100
120
a
b
b
ab
ab
Consolidated Rock
Rubble Rocks
Mixed Mud Rock BA
Mixed Mud Rock GBSC
Pure Mud GBSC
C
J': Pielou's evenness
0
0.2
0.4
0.6
0.8
1
a
a
a
a
b
Consolidated Rock
Rubble Rocks
Mixed Mud Rock BA
Mixed Mud Rock GBSC
Pure Mud GBSC

Figure 7


Depth range
▲ 50 - 59 m
▼ 60 - 69 m
■ 70 - 79 m
◆ 80 - 89 m
● 90 - 99 m
+ 100 - 109 m
× 110 - 119 m
Stress: 0.19
MM
Mx1
Mx2
cR
rR

TABLES

Table 1 Metadata associated to the ROV transects. GB = Grays Bank, SC = Siltcoos Reef, BA = Bandon-Arago

	Depth (m)	**Temp. (°C)**	**Salinity (PSU)**	**Av. Duration (min.)**	**Year**
GB	55 - 82	7.25 - 7.33	33.76 - 33.83	13:48 ± 02:46	2011
SC	97 - 119	7.75 - 7.92	33.84 - 33.88	17:49 ± 04:46	2011
BA	54 - 68	8.29 - 8.94	33.72 - 33.78	17:59 ± 03:11	2012

Table 2 Total number of mega-invertebrate taxa and individuals per phylum recorded at each site. Includes total counted (n = 138,416) and each phylum's percent contribution to the total count; details of taxa are given in Online Support 1

Taxon	GB	SC	BA	Total	%
ANNELIDA					
N taxa	0	0	2	2	
N individuals	0	0	83	83	0.06
ARTHROPODA					
N taxa	8	6	8	9	
N individuals	698	5388	102	6188	4.47
CHORDATA					
N taxa	1	1	1	1	
N individuals	212	48	1976	2236	1.62
CNIDARIA					
N taxa	13	10	11	14	
N individuals	12592	5133	6736	24461	17.7
ECHINODERMATA					
N taxa	22	26	24	30	
N individuals	8562	14043	31249	53854	38.9
MOLLUSCA					
N taxa	12	6	10	12	
N individuals	257	90	2543	2890	2.09
NEMERTEA					
N taxa	1	1	1	1	
N individuals	12	5	4	21	0.02
PORIFERA					
N taxa	11	7	13	16	
N individuals	5561	6692	36430	48683	35.2
Total N taxa				85	
Total N individuals				138416	

Table 3 Significance level of the pairwise comparisons of the ANOSIM performed on the groups resulting from the nMDS (Global R = 0.700). Upper matrix is the R values of the test; lower matrix is the associated p-value.

p \ R	cR	Mx-BA	rR	MM-GBSC	Mx-GBSC
cR		0.337	0.829	0.828	0.892
Mx-BA	0.005		0.548	1	0.921
rR	0.001	0.001		0.994	0.692
MM-GBSC	0.015	0.022	0.013		0.714
Mx-GBSC	0.001	0.002	0.003	0.067	

Table 4 Percent of dissimilarity between assemblages given by the SIMPER analyses

	cR	Mx-BA	rR	MM-GBSC	Mx-GBSC
Mx-BA	70.81				
rR	90.47	77.74			
MM-GBSC	91.91	93.54	95.64		
Mx-GBSC	95.24	93.18	86.17	93.33	
PG	99.47	98.37	96.38	99.19	93.90

Table 5 Assemblage characteristics given by the SIMPER analyses. % Sim = percent of similarity within the group, Av dst = average density of the taxon within the group (individuals / m^2), Cum % = cumulative percent of contribution of the taxon to similarity within the group

Group	% Sim	Taxa	Av dst	Cum %
Consolidated Rocks	37.13	Shelf sponge	1.60	19.34
		Branching sponge	1.56	31.93
		Branching red gorgonian	1.35	44.46
		Small orange brittle star	1.57	54.28
		Metridium farcimen	0.72	61.28
		Parastichopus californicus	0.57	66.58
		Munida quadrispina	0.50	71.81
		Mediaster aequalis	0.56	75.70
		Foliose sponge	0.62	78.59
		Henricia spp.	0.42	81.40
Mixed Mud-Rock-BA	46.03	Shelf sponge	1.00	35.91
		Branching sponge	0.52	49.01
		Small orange brittle star	0.51	58.79
		Mediaster aequalis	0.24	65.91
		Branching red gorgonian	0.26	72.63
		Parastichopus californicus	0.23	78.95
		Cucumaria spp.	0.14	82.73
Rubble Rocks	35.83	Shelf sponge	0.22	56.68
		Parastichopus californicus	0.05	71.67
		Branching sponge	0.04	82.04
Mud -GBSC	32.88	Burrowing brittle star	2.57	63.59
		Subselliflorae	1.13	85.48
Mixed Mud-Rock-GBSC	16.03	*Stomphia coccinea*	0.28	30.86
		Metridium farcimen	0.09	49.84
		Urticina spp.	0.11	68.74
		Shelf sponge	0.02	81.94

ONLINE RESOURCES

Online Resource 1 Totals for each mega-invertebrate taxon threat each site. Includes total counted (n = 138,416) and each taxon's percent contribution to the total count

Taxon	**GB**	**SC**	**BA**	**Total indiv**	**% of total**
ANNELIDA					
Feather-duster worm	-	-	74	74	0.05
Bamboo worm	-	-	9	9	0.01
			Total of individuals	**83**	**0.06**
			Total of taxa	**2**	
ARTHROPODA					
Pandalus sp.	1	4617	3	4621	3.34
Munida quadrispina	541	759	74	1374	0.99
Hermit crab	110	-	6	116	0.08
Cancer spp.	15	9	1	25	0.02
Lithod crab	18	1	5	24	0.02
Unidentified shrimp	8	1	10	19	0.01
Decorator crab	4	1	-	5	0.00
Loxorhynchus crispatus	1	-	2	3	0.00
Long-legged crab	-	-	1	1	0.00
			Total of individuals	**6188**	**4.47**
			Total of taxa	**9**	
CHORDATA					
Transparent tunicate	212	48	1976	2236	1.62
			Total of individuals	**2236**	**1.62**
			Total of taxa	**1**	
CNIDARIA					
Branching red gorgonian	6173	3153	5622	14948	10.80
Metridium farcimen	1407	1256	695	3358	2.43
Subselliflorae	2178	117	-	2295	1.66
Single stalk red gorgonian	1410	110	79	1599	1.16
Stomphia coccinea	682	82	142	906	0.65
Urticina spp.	671	11	166	848	0.61
Burrowing anemone (white)	11	270	2	283	0.20
Burrowing anemone (brown)	8	116	22	146	0.11
Cribrinopsis fernaldi	20	11	1	32	0.02
Metridium senile	13	7	3	23	0.02
Ptilosarcus gurneyi	15	-	3	18	0.01

White sea-pen	3	-	-	3	0.00
Clavactinia milleri	-	-	1	1	0.00
Anthomastus ritteri	1	-	-	1	0.00
	Total of individuals			**24461**	**17.67**
		Total of taxa		**14**	
ECHINODERMATA					
Small orange brittle star	3083	193	21532	24808	17.92
Burrowing brittle star	1583	10016	88	11687	8.44
Parastichopus californicus	796	1199	1664	3659	2.64
Cucumaria spp.	3	2	2760	2765	2.00
Mediaster aequalis	95	719	1783	2597	1.88
Henricia spp.	575	165	1157	1897	1.37
Pentamera sp.	1734	1	1	1736	1.25
Psolus chitonoides	61	29	1137	1227	0.89
Gorgonocephalus eucnemis	38	191	709	938	0.68
Large orange brittle star	19	445	4	468	0.34
Leptosynapta cf. *clarki*	-	418	-	418	0.30
Parastichopus leukothele	1	382	1	384	0.28
Stylasterias forreri	148	109	89	346	0.25
Pteraster tesselatus	133	13	54	200	0.14
Luidia foliolata	106	27	4	137	0.10
Orthasterias koehleri	7	15	76	98	0.07
Pisaster brevispinus	75	-	18	93	0.07
Florometra serratissima	-	12	78	90	0.07
Pycnopodia helianthoides	44	16	23	83	0.06
Crossaster papposus	11	56	4	71	0.05
Solaster spp.	29	9	26	64	0.05
Allocentrotus fragilis	17	2	29	48	0.03
Hippasteria spinosa	-	14	-	14	0.01
Dermasterias imbricata	2	2	10	14	0.01
Ceramaster patagonicus	-	4	-	4	0.00
Poraniopsis inflata	-	3	-	3	0.00
Strongylocentrotus sp.	2	-	-	2	0.00
Pteraster militaris	-	1	-	1	0.00
Gephyreaster swifti	-	-	1	1	0.00
Unidentified sea star	-	-	1	1	0.00
	Total of individuals			**53854**	**38.91**
		Total of taxa		**30**	
MOLLUSCA					
Chlamys sp.	22	-	2185	2207	1.59

Dorid nudibranch	145	67	273	485	0.35
Dendronotid nudibranch	11	10	36	57	0.04
Octopus rubescens	40	5	3	48	0.03
Unidentified nudibranch	14	-	14	28	0.02
Aeolid nudibranch	3	-	18	21	0.02
Unidentified snail	2	-	9	11	0.01
Moon snail	8	-	3	11	0.01
Dironid nudibranch	3	6	-	9	0.01
Mud scallop	4	1	1	6	0.00
Enteroctopus dofleini	4	-	1	5	0.00
Rossia pacifica	1	1	-	2	0.00
	Total of individuals			**2890**	**2.09**
	Total of taxa			**12**	
NEMERTEA					
Nemertean	12	5	4	21	0.02
	Total of individuals			**21**	**0.02**
	Total of taxa			**1**	
PORIFERA					
Branching sponge	2128	825	22722	25675	18.55
Shelf sponge	2021	5736	9961	17718	12.80
Foliose sponge	207	92	2563	2862	2.07
Yellow tall branching sponge	47	-	749	796	0.58
Yellow ball sponge	314	18	231	563	0.41
Tube sponge	485	-	3	488	0.35
Semisuberites cribrosa	301	-	-	301	0.22
Cliona sp.	5	-	90	95	0.07
Spheciospongia confoederata	-	8	-	8	0.01
Ball sponge	14	-	47	61	0.04
Polymastia sp.	-	-	58	58	0.04
Phakellia sp.	31	-	-	31	0.02
Upright flat sponge	8	12	3	23	0.02
Barrel sponge	-	1	1	2	0.00
Fan-like sponge	-	-	1	1	0.00
Leucandra sp.	-	-	1	1	0.00
	Total of individuals			**48683**	**35.17**
	Total of taxa			**16**	
	Grand Total of individuals			**138416**	**100**
	Grand Total of taxa			**85**	

Online Resource 2 Table of dissimilarities between mixed mud-rock at Bandon-Arago (Mx-BA) and mixed mud-rock at Grays and Siltcoos (Mx-GBSC), and between consolidated rocks (cR) and rubble rocks (rR). Av dst = average density of the taxon within the group (individuals.m^{-2}), Cum % = cumulative percent of contribution of the taxon to dissimilarity between groups

Percent dissimilarity = 93.18	Mx-BA	Mx-GBSC	
Taxa	Av dst	Av dst	Cum %
Shelf sponge	1.0	0.0	24.2
Branching sponge	0.5	0.0	34.7
Small orange brittle star	0.5	0.0	44.4
Stomphia coccinea	0.0	0.3	50.7
Branching red gorgonian	0.3	0.0	56.2
Mediaster aequalis	0.2	0.0	61.5
Parastichopus californicus	0.2	0.0	66.3
Metridium farcimen	0.1	0.1	70.1
Urticina spp.	0.1	0.1	73.4
Cucumaria spp.	0.1	0.0	76.4
Foliose sponge	0.2	0.0	79.4
Transparent tunicate	0.2	0.0	82.4

Percent dissimilarity = 90.47	cR	rR	
Taxa	Av dst	Av dst	Cum %
Shelf sponge	1.60	0.22	12.07
Small orange brittle star	1.57	0.01	22.88
Branching sponge	1.56	0.04	33.19
Branching red gorgonian	1.35	0.03	42.39
Munida quadrispina	0.50	0.03	48.06
Metridium farcimen	0.72	0.03	53.49
Parastichopus californicus	0.57	0.05	57.28
Foliose sponge	0.62	0.01	61.00
Mediaster aequalis	0.56	0.01	64.57
Single stalk red gorgonian	0.38	0.00	67.36
Henricia spp.	0.42	0.00	69.79
Pentamera sp.	0.27	0.00	72.10
Transparent tunicate	0.43	0.00	74.27
Burrowing brittle star	0.15	0.00	76.28
Urticina spp.	0.21	0.02	77.98
Leptosynapta cf. *clarki*	0.10	0.00	79.59
Cucumaria spp.	0.34	0.00	81.00