Global Ecology and Conservation 4 (2015) 85–94

Contents lists available at ScienceDirect

Global Ecology and Conservation

journal homepage: www.elsevier.com/locate/gecco

Original research article

Submarine canyons as coral and sponge habitat on the eastern Bering Sea slope

Robert J. Miller [a,*], Claudette Juska [b], John Hocevar [b]

[a] *Marine Science Institute, University of California, Santa Barbara, CA, USA*
[b] *Greenpeace USA, Washington DC, USA*

ARTICLE INFO

Article history:
Received 23 May 2015
Received in revised form 28 May 2015
Accepted 28 May 2015

Keywords:
Marine benthos
Foundation species
Sessile invertebrates
Bottom trawling
Maxent

ABSTRACT

Submarine canyons have been shown to positively influence pelagic and benthic biodiversity and ecosystem function. In the eastern Bering Sea, several immense canyons lie under the highly productive "green belt" along the continental slope. Two of these, Pribilof and Zhemchug canyons, are the focus of current conservation interest. We used a maximum entropy modeling approach to evaluate the importance of these two canyons, as well as canyons in general, as habitat for gorgonian (alcyonacean) corals, pennatulacean corals, and sponges, in an area comprising most of the eastern Bering Sea slope and outer shelf. These invertebrates create physical structure that is a preferred habitat for many mobile species, including commercially important fish and invertebrates. We show that Pribilof canyon is a hotspot of structure-forming invertebrate habitat, containing over 50% of estimated high-quality gorgonian habitat and 45% of sponge habitat, despite making up only 1.7% of the total study area. The amount of quality habitat for gorgonians and sponges varied in other canyons, but canyons overall contained more high-quality habitat for structure-forming invertebrates compared to other slope areas. Bottom trawling effort was not well correlated with habitat quality for structure-forming invertebrates, and bottom-contact fishing effort in general, including longlining and trawling, was not particularly concentrated in the canyons examined. These results suggest that if conserving gorgonian coral habitat is a management goal, canyons, particularly Pribilof Canyon, may be a prime location to do this without excessive impact on fisheries.

1. Introduction

Foundation species define an ecosystem or community by modifying and providing physical habitat and food resources (Dayton, 1972; Ellison et al., 2005). Losses or reductions in abundance of foundation species (or autogenic engineers, Jones et al., 2010) may profoundly affect the ecosystems in which they occur, disrupting basic ecosystem processes including nutrient flux, decomposition, energy flow, and food web diversity (Bruno and Bertness, 2001; Ellison et al., 2005). In the oceans, corals are archetypical examples of foundation species, forming massive reefs in shallow tropical waters that support

---

[*] Corresponding author. Tel.: +1 805 708 4181.
E-mail address: miller@msi.ucsb.edu (R.J. Miller).

http://dx.doi.org/10.1016/j.gecco.2015.05.009

>30% of described marine species (Reaka-Kudla, 1997). In the deep sea and on continental shelves, sessile invertebrates also provide habitat for other organisms, and many fishes and invertebrates are positively associated with deep-water corals (Rogers, 1999; Husebøo et al., 2002; Mortensen and Buhl-Mortensen, 2005; Stone, 2006; Heifetz et al., 2007; Miller et al., 2012) and sponges (Beaulieu, 2001; Freese and Wing, 2003; Marliave et al., 2009; Miller et al., 2012). The mechanistic role of this biogenic habitat is still unclear due to lack of small-scale observational and experimental studies (Auster, 2005, 2007; Miller et al., 2012), but may affect populations of associated animals through processes including habitat selection at settlement, differential survival, and post-settlement migration (Auster et al., 1996; Lindholm et al., 2001; Hartney and Grorud, 2002).

Fisheries managers consider such habitat elements when defining essential fish habitat (EFH, where fish includes invertebrates) for exploited species (Rosenberg et al., 2000). The US Congress defined EFH as "those waters and substrate necessary to fish for spawning, breeding, feeding or growth to maturity" during any part of the species' life cycle. The EFH regulation (Magnuson-Stevens Act Provisions, 1997) clarified that "substrate" includes the associated biological communities that make these areas suitable fish habitats. Corals and sponges are prominent elements of these communities in deep temperate waters, and have often been viewed as EFH by fisheries managers (Witherell and Coon, 2000; Freese and Wing, 2003). Corals and sponges are also often fragile and slow growing, making them highly vulnerable to damage by physical contact with fishing gear (Auster et al., 1996; Koslow et al., 2001; Hall-Spencer et al., 2002; Stone, 2006; Waller et al., 2007; Bo et al., 2014). This vulnerability combined with their value as EFH led the North Pacific Fishery Management Council (NPFMC) to identify gorgonian corals as EFH of particular concern (Witherell and Coon, 2000). In addition to their potential value as habitat, it has also been argued that corals have intrinsic value, and that this alone combined with their questionable potential for recovery makes them important conservation targets (Auster, 2005).

Submarine canyons are steep-sided valleys that incise continental shelves across the globe, especially along active continental margins (Harris and Whiteway, 2011). Canyons and associated eddies can increase water column mixing rates (Mizobata and Saitoh, 2004), increasing primary productivity (Freeland and Denman, 1982) and efficiency of benthic–pelagic coupling (Carter and Gregg, 2002; Ryan et al., 2005). Canyons also act as traps and conduits of sediment and organic matter (Puig et al., 2014). Due to these processes, benthos in canyons can be more diverse and productive than other deep-water habitats (Tyler et al., 2009; De Leo et al., 2010; Vetter et al., 2010), and have been characterized worldwide as biological hotspots and targets for conservation (Vetter et al., 2010; Harris and Whiteway, 2011), particularly for cetaceans and seabirds (Hooker et al., 1999; Yen et al., 2004; Moors-Murphy, 2014).

In the eastern Bering Sea, two large canyons, Zhemchug and Pribilof, support relatively high densities of corals and sponges (Miller et al., 2012). Commercially important fish species, including the Pacific ocean perch (POP), have been found to be positively associated with corals and sponges in these canyons (Brodeur, 2001; Miller et al., 2012). Intense fishing pressure in the region, including bottom trawling for POP, as well as the perceived need for increased ecosystem-based management, has led environmental groups and Native communities in the nearby Pribilof Islands to call for protecting these two canyons from bottom contact fishing (Dischner, 2013). NPFMC is currently considering management actions to do so, but lacks information about the degree to which coral and sponge habitat is concentrated in the canyons relative to the rest of the outer shelf and slope, and has identified this information as a critical need for progress on this issue (NPFMC, 2010, 2013).

Here we use a habitat suitability modeling approach, maximum entropy modeling, to predict suitable coral and sponge habitat on the outer shelf and slope of the eastern Bering Sea to help inform this important conservation issue. To do this we use presence-only coral and sponge data from multiple sources: long-term fishery-independent bottom trawl surveys done by NOAA in the region, NOAA fisheries observer records of coral and sponge bycatch, and visual surveys that used submersibles and remotely operated vehicles. Using several environmental variables as model predictors, we estimate how much suitable coral and sponge habitat is concentrated in Zhemchug and Pribilof canyons relative to the rest of the slope and shelf. We also ask whether canyons in general are hotspots of coral and sponge habitat along the eastern Bering Sea shelf. Finally, we examine historical fishing effort data to evaluate the degree to which bottom trawling has impacted sessile invertebrate habitat, and the potential impact on the fishing industry of restricting trawling and other bottom contact fishing in the canyons.

2. Materials and methods

2.1. Study area

The study region encompassed much of the continental slope of the eastern Bering Sea, which extends over 1000 km (Fig. 1). Our effort owes much to a study by Sigler et al. (2013); the authors provided us with environmental datasets compiled for the region. Similar to Sigler et al., we divided the region into three areas: outer shelf, canyon and non-canyon slope; we did not include the middle and inner shelf areas since our primary interest was the slope. The outer slope was defined as the area between the 100 m depth contour (Coachman, 1986) and the shelf break at ∼200 m depth (Sigler et al., 2013). The upper boundaries of each canyon were defined as the intersection of the canyon mouth with the continental slope; the canyon lateral boundaries were defined as the closest ridge crest on either side of the canyon axis. The outermost boundary of canyons and non-canyon slope was taken as the 1200 m depth contour.

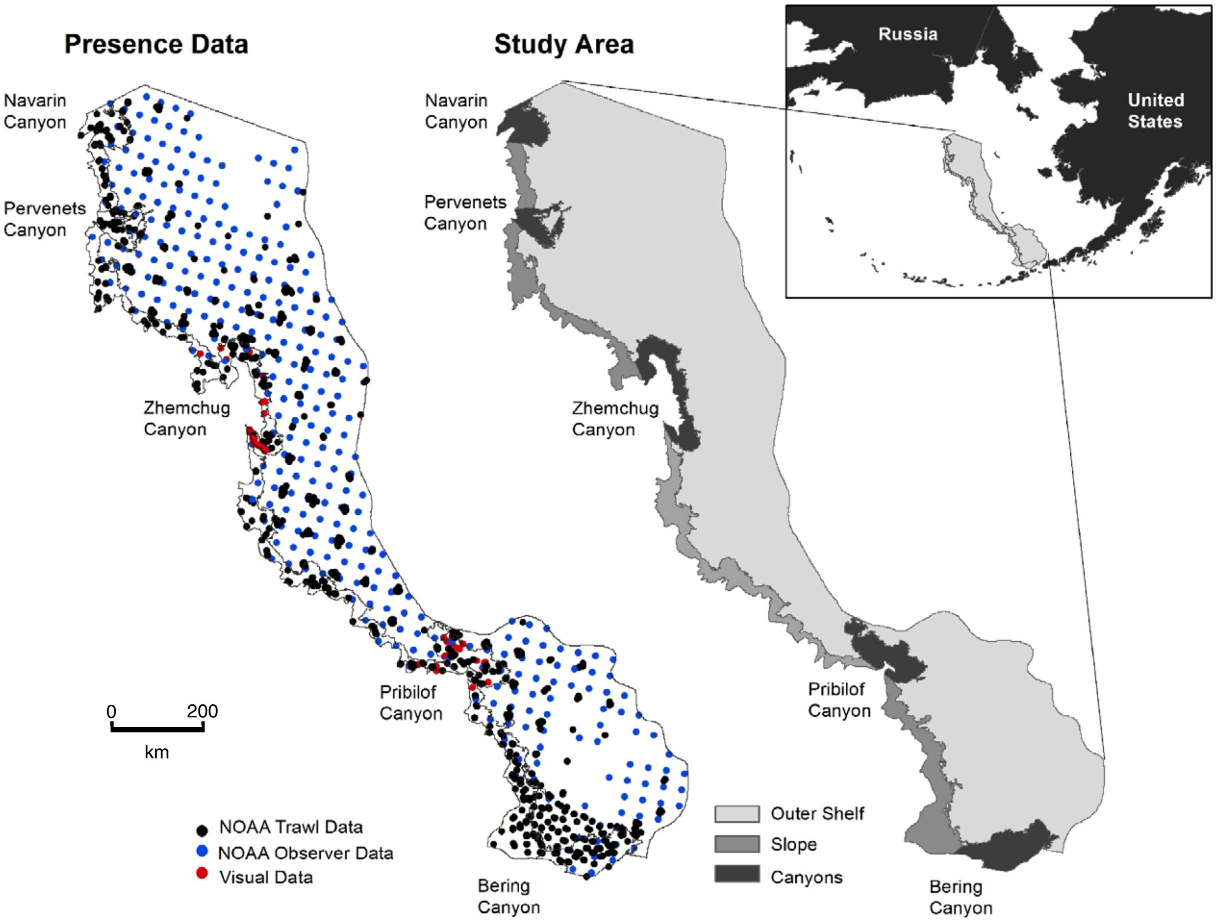

Fig. 1. Map of study area.

2.2. Coral and sponge data

Coral and sponge occurrence data were used from three sources: bottom trawl surveys conducted by NOAA across the Bering Sea shelf and slope, NOAA fisheries observer records of invertebrate bycatch, and visual surveys using video or drop cameras.

NOAA conducts annual bottom trawl surveys to monitor commercially and ecologically important groundfish and crab species. In our study area, bottom trawls are conducted at fixed sampling stations at the center of each cell of a regular 37.04 × 37.04 km (20 × 20 nautical mile) grid. Stauffer (2004) described survey methods in detail. Briefly, 83-112 eastern otter trawls are towed in trawlable areas behind 816 kg, 1.8 × 2.7 m, steel V-doors and paired 54.9 m dandylines at a speed of 1.29–1.54 m/s depending on depth, for a target fishing time of 30 min. Trawlable areas are characterized by relatively low relief substrate with at least 1.5 nautical miles of trawlable bottom within the target area. For small catches, all invertebrates captured are sorted to the lowest taxonomic level practical, and larger catches are subsampled. Survey data were available and used from 2002, 2004, 2008, 2010 and 2012.

NOAA's Observer Program collects data aboard fishing vessels in the Gulf of Alaska and the Eastern Bering Sea/Aleutian Islands. Observer coverage depends on the type of fishing gear used and vessel size. Non-crab invertebrate bycatch, though recorded, is not a high priority of the program, and an independent survey of observers confirmed that collecting data on bycatch was relatively low priority (MRAG, 2000). Data under three species codes in the observer database were used: red tree coral (*Primnoa willeyi*), unidentified sea whips, and unidentified sponges. Unfortunately, unidentified corals include bryozoans, making that category useless for our study. Data were available and used from 1993–2012.

Visual corals and sponge occurrence data from three sources were used: (1) an ROV survey of benthic fishes and invertebrates in Pribilof Canyon ($n = 3$ transects, Brodeur, 2001), (2) a camera sled video survey of rockfish on Zhemchug Ridge ($n = 14$ transects, Rooper et al., 2010), and (3) two submersible surveys of Zhemchug and Pribilof canyons undertaken by Greenpeace. The authors of the first two studies provided us with presence/absence data on corals and sponges for each transect. The first Greenpeace survey was done in 2007, comprised 23 video transects taken using DeepWorker submersibles, and is described in Miller et al. (2012). An additional 14 transects were completed in the canyons in 2012 using similar methods. Corals and sponges larger than ∼5 cm height with their base in video frames were counted; data were reduced to presence only at the transect level for habitat modeling. For all trawl, observer, and visual data, sponge taxa were aggregated and corals were analyzed as two groups: gorgonians (now Order Alcyonacea) and pennatulaceans.

2.3. Environmental predictors

We used several environmental variables to predict habitat quality across the study region at a resolution of 1 × 1 km: bathymetry (depth and maximum gradient), sediment grain size and degree of sorting, bottom temperature, current speed, and surface chlorophyll concentrations, a proxy for phytoplankton productivity. Bathymetry was derived from National Ocean Service smooth sheets based on digitized soundings collected from hydrographic surveys. Depth data were transformed to continuous coverage on a 100 × 100 m grid using inverse distance weighting in ArcGIS. At each grid point, the maximum seafloor gradient, or slope, was defined as the maximum percent gradient among the eight grid cells adjacent to that point, and was calculated as rise divided by run multiplied by 100 using the Spatial Analyst package in ArcGIS (Rooper et al., 2014). Unfortunately no data on substrate type, other than sediment grain size, are available for the study region; gradient or slope is a measure of bottom topography that has been used as a proxy for substrate type, since areas of pronounced topographic relief are typically areas of low sediment accumulation with more hard substrate (Bryan and Metaxas, 2007). The depth and seafloor gradient data were aggregated into a regular 1 × 1 km grid for habitat modeling.

Mean grain size (in base two logarithmic phi units) and sorting (standard deviation of mean grain size) data for the top 10 cm of sediment were obtained from the Eastern Bering Sea Sediment Database (McConnaughey et al., 2000) and supplemented with data from the National Geophysical Data Center Seafloor Sediment Grain Size Database. These data were interpolated into a continuous coverage on a 1 × 1 km grid of the study area using ordinary kriging with an exponential model (Venables and Ripley, 2002; Rooper et al., 2014).

Bottom temperature data was collected at each bottom trawl survey station using a Sea-Bird SBE-39 temperature recorder attached to the headrope of the trawl. Temperature data from all survey years were kriged using a spherical semi-variance model (Sigler et al., 2013).

Ocean current data of two types were used. Regional Ocean Modeling System (ROMS) solutions for 1975–2010 for the eastern Bering Sea were used as estimates of average current speed near the bottom (Danielson et al., 2011). The ROMS resolution was 10 × 10 km with 60 evenly distributed depth layers. For this study we used average current speed and direction for the deepest depth bin for each grid cell; these data were transformed to a 1 × 1 km grid using inverse distance weighting (Rooper et al., 2014). Tidal current speeds were also estimated for 368 consecutive days (1 January 2009 to 3 January 2010) using a tidal inversion program (Egbert and Erofeeva, 2002). This tidal prediction model was used to produce a time series of 1 yr of tidal currents for spring and neap cycles at each bottom trawl survey location. The maxima of the time series of predicted tidal current for each site were interpolated across the study area using ordinary kriging (Sigler et al., 2013).

Net primary production data were obtained from the Oregon State University Ocean Productivity website (http://www.science.oregonstate.edu/ocean.productivity/) as monthly composites on a regular grid (11.9 × 18.5 km), based on the Vertically Generalized Production Model (Behrenfeld and Falkowski, 1997). Mean annual rates of primary production (gC m^{-2} d^{-1}) were calculated based on an average of monthly estimates for May through September for each grid cell for 2003–2011. Annual mean productivity was taken as the mean of the 9 years and interpolated using inverse distance weighting into a continuous coverage on a 1 × 1 km grid.

2.4. Habitat quality modeling

To evaluate coral and sponge habitat quality based on distribution data, we used maximum entropy modeling (MaxEnt version 3.3.3 k, http://www.cs.princeton.edu/schapire/MaxEnt/), which employs presence-only data (Phillips et al., 2006; Elith et al., 2011). Using presence-only data allowed us to take advantage of disparate data sources, including the trawl survey data and observer data, which are not reliable for estimation of absence. The trawl surveys are not designed to sample benthic invertebrates, and catchability of these species is unknown. NOAA designates corals and sponges as Habitat Area of Particular Concern (HAPC) fauna; the trawl survey metadata states: "The NMFS bottom trawl survey does not sample any of the HAPC fauna well. The survey gear does not perform well in many of the areas where these organisms are prevalent and survey effort is quite limited in these areas as a result. Even in areas where these habitats are sampled, the gear used in the survey is ill-suited for efficient capture of these organisms". Fisheries observer data includes multiple types of gear, training to identify corals and other invertebrate bycatch is variable (Sigler et al., 2013), and collecting data on corals and other sessile invertebrates is lower in priority than for fisheries species.

MaxEnt estimates the distribution of maximum entropy constrained in such a way that expected values for predictor variables match their empirical average. Its logistic output can be interpreted as the relative environmental suitability of each pixel in relation to the background of the study area (Phillips et al., 2006; Phillips and Dudík, 2008). Models were run using the default set of parameters of the software, using the whole set of environmental predictors (Table 2) and used 10-fold cross-validation to train and test the model. In all cases, 25% of the presence data was withheld from model fitting for testing the models (Table 1).

Table 1
Sample sizes and performance, as estimated by area under the receiver operating characteristic curve (AUC), of MaxEnt models.

Taxonomic group	# Training samples	# Test samples	Training AUC	Test AUC	AUC Std. Dev.
Gorgonians	82	27	0.9578	0.8723	0.0286
Pennatulaceans	461	153	0.7393	0.6734	0.0245
Sponges	849	282	0.7329	0.6934	0.0146

Table 2
Percent of study area comprising high-quality habitat for structure-forming invertebrates in canyons, on non-canyon slope, and on the outer shelf, at different modeled probability thresholds. Bottom row shows total area in each topographic category in km^2 for reference. The percentage in parentheses is the percent area represented in the study region (entire outer shelf and slope).

Taxon	Probability threshold	Pribilof canyon	Zhemchug canyon	All canyons	Non-canyon slope	Outer shelf
Gorgonians	>70%	57.6%	3.0%	80.4%	19.6%	0
	>90%	87.3%	0%	87.3%	12.7%	0
Pennatulaceans	>70%	0%	0%	8.5%	17.0%	74.5.0%
	>90%	0.7%	1.3%	0%	0%	0%
Sponges	>70%	45.1%	16.5%	69.9%	16.6%	13.1%
	>90%	0%	0%	0%	0%	0%
	Total area	2870 (1.7%)	3080 (1.9%)	12,700 (7.7%)	16,900 (10.2%)	135,380 (82.1%)

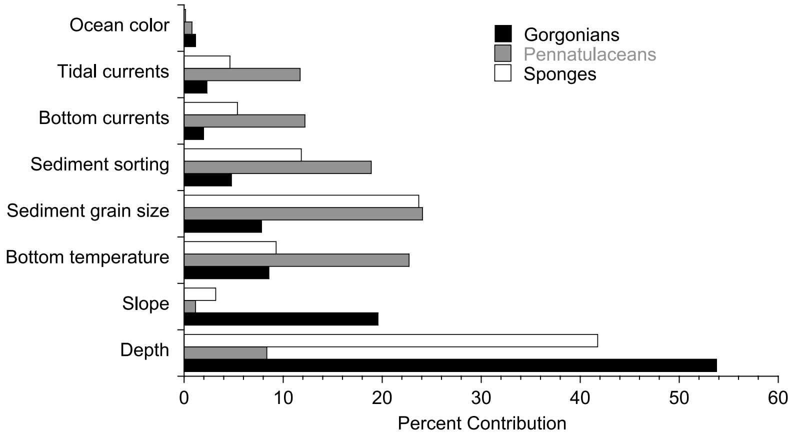

Fig. 2. Percent contributions of habitat variables to MaxEnt model results for each taxonomic group.

2.5. *Bottom trawling effort distribution*

We examined the distribution of bottom trawling effort across the study area using NOAA observer data available for the years 1993–2012. The spatial resolution of the data is 20 × 20 km. These cells overlap the boundaries of canyons and our other areas of comparison. Therefore, to estimate effort within canyons and our other areas of interest, we assigned cells to the area of interest that they most overlapped. We used number of total hauls (sampled and unsampled) as our measure of effort. To evaluate possible relationships between coral and sponge habitat quality and bottom trawl effort, we averaged habitat quality probability values produced with MaxEnt across each 20 × 20 km grid cell. Relationships were evaluated using least-squares regression.

3. Results

3.1. *MaxEnt model performance and predictors*

MaxEnt model performance was best for the gorgonians, with a training Area Under the Curve (AUC) of 0.96 and test AUC of 0.87 (Table 1). Model performance was similar for pennatulaceans and sponges, with AUCs of ~0.7 (Table 1). For gorgonians, depth contributed 54% of model predictive power, and slope was the second most important variable, contributing 20% (Fig. 2). For pennatulaceans, sediment grain size (24%), sorting (19%) and bottom temperature (23%) contributed similarly to the modeled predictions. For sponges, depth was the most important contributor to the model at 42%, followed by sediment grain size (24%).

3.2. *Habitat quality and distribution*

The output of MaxEnt can be described as percent habitat suitability, given the environmental conditions at a site. We focus here on areas that were predicted to be high-quality habitat for corals and sponges, and chose thresholds of 70% and 90% suitability to define high-quality habitat.

Gorgonian coral habitat was strongly aggregated along the slope, and the outer shelf was predicted to be poor habitat for gorgonians (Fig. 3, Table 2). All five canyons on the slope contained 80.4% of high-quality gorgonian habitat that was >70% suitability, and 87.3% of the >90% suitability area. These areas, however, were predominantly in one canyon, Pribilof, which contained all of the >90% suitability habitat that was located in canyons, and 71.6% of the >70% suitability habitat located in canyons. Navarin Canyon was also predicted to contain significant high-quality gorgonian habitat (Fig. 3). Zhemchug Canyon was predicted to contain 3% of the >70% suitability habitat for gorgonians. Non-canyon slope areas were predicted to contain 19.6% of high-quality habitat that was >70% suitability, and 12.7% of the >90% suitability area.

Results for pennatulacean corals were quite different than those for gorgonians, which was expected due to their different habitat requirements. Pennatulacean habitat was more uniformly distributed across the shelf and slope compared to gorgonian habitat, although most high-quality habitat was found along the slope and outer portion of the outer shelf (Fig. 3). On the whole, 74.5% of high-quality pennatulacean habitat was predicted to occur on the outer shelf (Table 2).

Sponge habitat was concentrated along the slope, though not as starkly as gorgonian habitat (Fig. 3). 45.1% of high-quality sponge habitat occurred in Pribilof Canyon, 16.5% in Zhemchug Canyon (Table 2). All five canyons combined contained 69.9% of high-quality sponge habitat. Non-canyon slope area contained 16.6% of high-quality sponge habitat and the outer shelf contained only 13.1% despite making up >80% of the study area (Table 2).

3.3. *Fishing effort*

Observers recorded a total of 41 261 non-pelagic trawls in our study area in 1993–2012. On average 2063 trawls were observed per year, and 70% were on the outer shelf (Fig. 4(A)). A relatively small amount of average annual bottom trawl effort was located in Pribilof (1.6%) and Zhemchug (1.4%) canyons, approximately proportional to their area (Table 2).

Habitat quality for all three taxonomic groups was significantly correlated with bottom trawl effort across 1993–2012, but the relationships had little explanatory power. Gorgonian habitat quality was negatively related to total bottom trawling effort but the relationship was weak (Average gorgonian habitat $= 0.07 + 0.00002 * \log$ total observed hauls (TOH), $P < 0.0001$, $r^2 = 0.01$). Habitat quality for both pennatulaceans and sponges was positively related to bottom trawling effort (average sea pen habitat $= 0.33 + 0.03 * \log \text{TOH}$, $P < 0.0001$, $r^2 = 0.17$; average sponge habitat $= 0.30 + 0.03 * \log \text{TOH}$, $P < 0.0001$, $r^2 = 0.19$).

A much larger number of pelagic trawls, 192 924, were recorded in our study area in 1993–2012. On average 9187 trawls were observed per year, and the majority, 84.5%, were on the outer shelf (Fig. 4(B)). A relatively small amount of average annual pelagic trawl effort was located in Zhemchug canyon (0.7%), and a larger amount in Pribilof (4.1%). A total of 137 188 bottom longline sets were observed in our study area in 1993–2012. On average 6533 trawls were recorded per year, and 77.5% were on the outer shelf (Fig. 4(C)). Compared to bottom trawling, a larger amount of average annual longline effort was located in both Pribilof (2.3%) and Zhemchug (5%) canyons.

4. Discussion

Pribilof Canyon contained over half of the high-quality (>70% suitability) gorgonian habitat, and nearly half of the high-quality sponge habitat, in the entire study region, despite making up only 1.7% of the total area. This corresponds with results of Sigler et al. (2013) who estimated using GAM modeling that 33% of coral habitat on the Eastern Bering Sea shelf and slope was in Pribilof Canyon. These results suggest that Pribilof Canyon is a hotspot of gorgonian and sponge habitat on the eastern Bering Sea shelf. The five canyons in total contained a majority of high-quality coral and sponge habitat (Table 2). If Pribilof is subtracted, the remaining 4 canyons still contained 22.8% of coral habitat and 24.7% of sponge habitat at the 70% level. This is about three times greater than their relative area within the total study area (7.7%). Canyons were heterogeneous in their habitat quality; for both groups, Pribilof Canyon was a hotspot, and for gorgonians Navarin Canyon also had relatively extensive high-quality habitat (Fig. 3). Non-canyon slope had 19.6% of coral habitat and 16.6% of sponge habitat at the 70% level, and made up 10.2% or the total study area. Overall these results suggest that coral and sponge habitat in the eastern Bering Sea is most abundant on the slope and more likely to occur in canyons than in other slope areas.

Pacific ocean perch (POP) were positively associated with corals and sponges in Pribilof and Zhemchug Canyons (Brodeur, 2001; Miller et al., 2012). In 2012, 31.6% of the total trawl rockfish catch, which is primarily POP, came from Pribilof Canyon, and the average was 19.5% from 2004–2012 (NPFMC, 2013), despite the overall low bottom trawl effort in Pribilof. In contrast, only 1.7% of the rockfish catch came from Zhemchug Canyon, which contained only 3% of the high-quality gorgonian habitat in the study region (although it did contain a relatively large proportion of high-quality sponge habitat, 16.5%). This pattern could be explained by the abundance of gorgonians and corals in Pribilof, as indicated by the model results showing that Pribilof has most of the high-quality habitat for these species. Alternatively, corals and POP may have overlapping habitat requirements. In either case, these data collectively suggest that Pribilof Canyon is excellent POP habitat, and in part that may be due to abundant POP essential fish habitat, in this case structure-forming invertebrates.

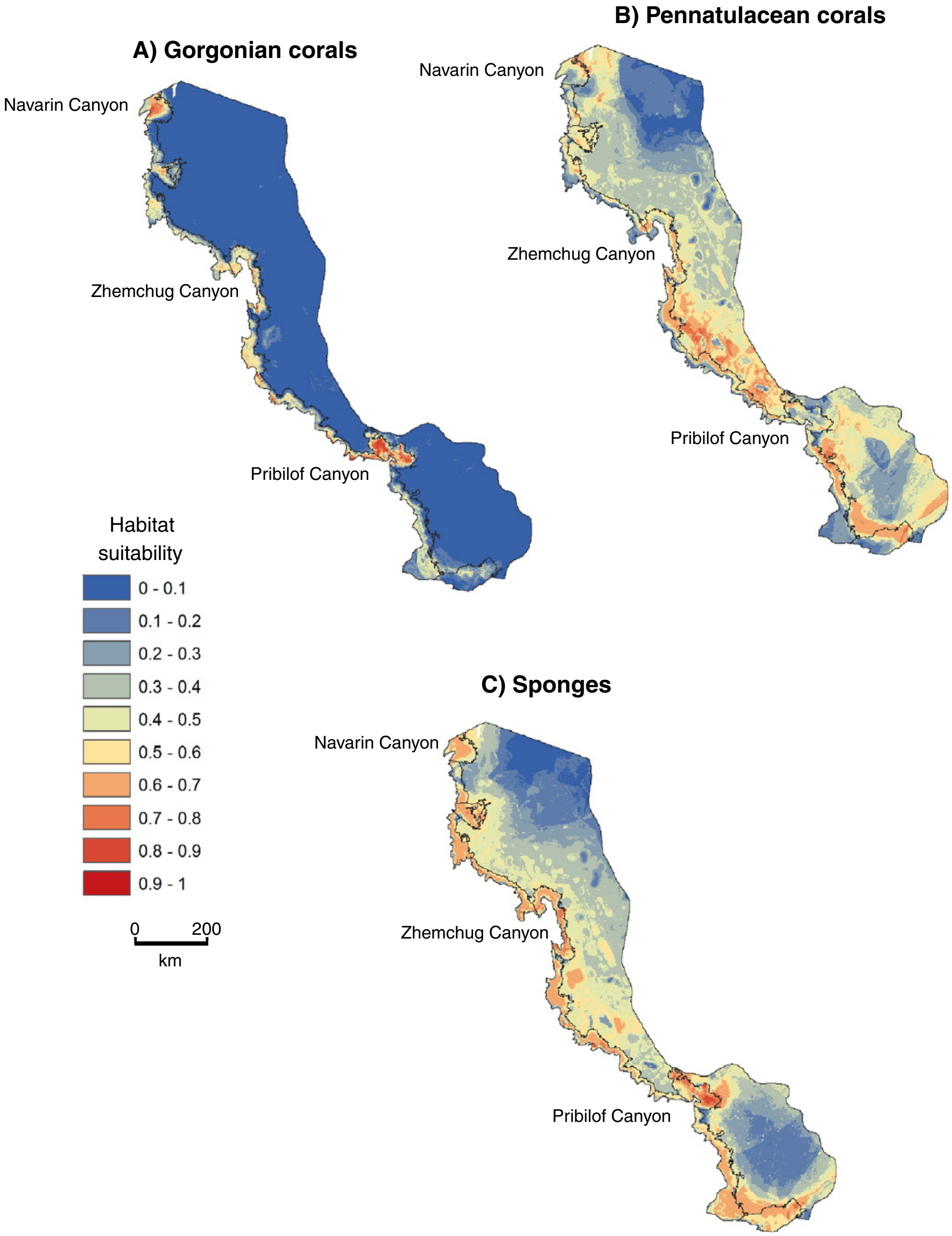

Fig. 3. Habitat suitability values for (A) gorgonian corals, (B) pennatulacean corals, and (C) sponges, across the study area. Resolution is 1 × 1 km.

Gorgonian habitat quality was negatively related, and pennatulacean and sponge habitat positively related, to bottom trawl effort. These relationships, however, were weak. The negative relationship with gorgonian habitat reflects the fact that the majority of bottom trawling in our study area took place on the outer shelf, which had no predicted high-quality gorgonian habitat. The positive relationships with sponges and pennatulaceans may reflect positive associations between these taxa and quality fishing grounds, though this is speculative. Finer-grained data on trawl effort could be used to better address these relationships. Chronically trawled areas in the eastern Bering Sea had lower abundances of sessile macrofauna, including anemones, soft corals, sponges, bryozoans, and ascidians, when compared to protected areas (McConnaughey et al., 2000). Our study area did not include any areas where trawling is restricted. At this point, after intense fishing since the 1950's (McConnaughey et al., 2000), any detectable differences due to trawling may have long vanished. Gorgonian corals in Pribilof and Zhemchug Canyons were mostly relatively small (Miller et al., 2012). Stands of large gorgonians and

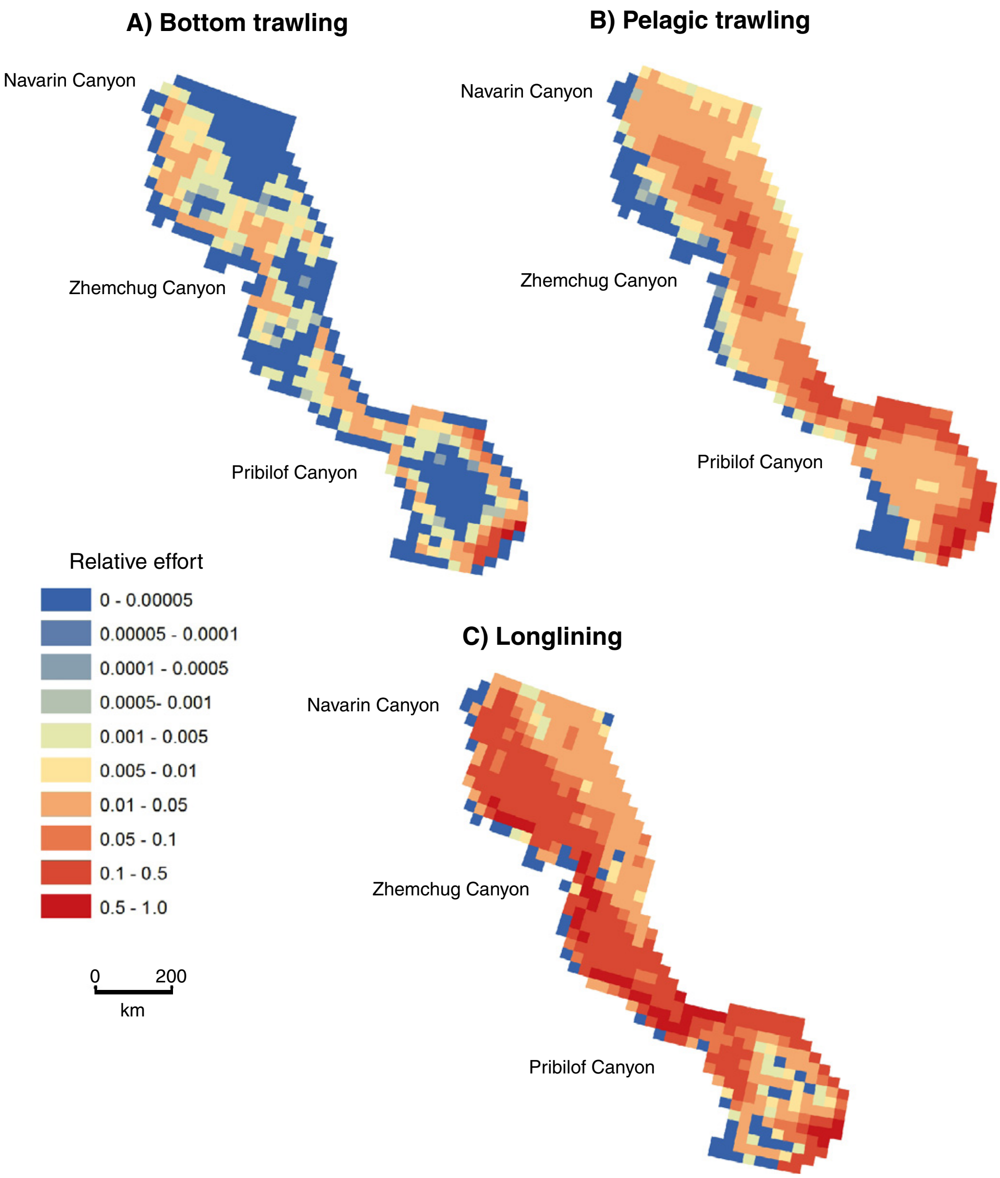

Fig. 4. Relative distribution of fishing effort in the study area for (A) bottom trawling, (B) pelagic trawling, and (C) longlining. Resolution is 20 × 20 km.

sponges would be particularly vulnerable to impacts of bottom trawling and would take decades to recover (Rooper et al., 2011).

Our study region has been subjected to a large amount of fishing by pelagic trawls and bottom longlines as well as bottom trawling. Benthic longlines, like bottom trawls, can impact invertebrates like corals and sponges (Stone, 2006), and this impact may currently be underestimated (Stone and Shotwell, 2007). Pelagic trawls are modified bottom trawls used to harvest groundfish, but, at least in theory, not on the seafloor. The National Marine Fisheries Service prohibits the use of protective gear on the footrope to discourage direct bottom contact. However, bycatch by pelagic trawls does include sessile benthos, and NOAA has estimated that 44% of "pelagic" trawl effort is spent on the seafloor (NMFS, 2005).

Bottom trawling and other bottom contact gear clearly negatively impact structure-forming sessile invertebrates (e.g. Koslow et al., 2001; NRC, 2002; Heifetz et al., 2009), and these species are often positively associated with fishes, including fishery species (e.g. Heifetz, 2002; Krieger and Wing, 2002; Rooper and Boldt, 2005; Rooper et al., 2007; Miller et al., 2012). The fishing effort in the canyons was for the most part approximately proportional to their area, suggesting that restricting bottom-contact fishing in the canyons would not have a disproportionately negative effect on fisheries overall. If a management goal is to preserve gorgonian coral and sponge habitat, either due to intrinsic value of these species or their role as structure-forming invertebrates and essential fish habitat, then our results suggest that canyons, and Pribilof Canyon in particular, are hotspots of such habitat that could be targeted for protection.

References

Auster, P.J., 2005. Are deep-water corals important habitats for fishes? In: Cold-Water Corals and Ecosystems. Springer, Berlin, Heidelberg, pp. 747–760.

Auster, P.J., 2007. Linking deep-water corals and fish populations. In: Conservation and Adaptive Management of Seamount and Deep-Sea Coral Ecosystems. Rosenstiel School Marine and Atmospheric Science, Miami, Florida, pp. 93–99.

Auster, P.J., Malatesta, R.J., Langton, R.W., Watling, L., 1996. The impacts of mobile fishing gear on seafloor habitats in the Gulf of Maine: Implications for conservation of fish populations. Bull. Ecol. Soc. Am. 77, 349.

Beaulieu, S.E., 2001. Life on glass houses: Sponge stalk communities in the deep sea. Mar. Biol. 138, 803–817.

Behrenfeld, M.J., Falkowski, P.G., 1997. Photosynthetic rates derived from satellite-based chlorophyll concentration. Limnol. Oceanogr. 42, 1–20.

Bo, M., Bava, S., Canese, S., Angiolillo, M., Cattaneo-Vietti, R., Bavestrello, G., 2014. Fishing impact on deep Mediterranean rocky habitats as revealed by ROV investigation. Biol. Conserv. 171, 167–176.

Brodeur, R.D., 2001. Habitat-specific distribution of Pacific ocean perch *Sebastes alutus* in Pribilof Canyon, Bering Sea. Cont. Shelf Res. 21, 207–224.

Bruno, J.F., Bertness, M.D., 2001. Habitat modification and facilitation in benthic marine communities. In: Bertness, M.D., Hay, M.E., Gaines, S.D. (Eds.), Marine Community Ecology. Sinauer, Sunderland, Massachusetts, pp. 201–218.

Bryan, T.L., Metaxas, A., 2007. Predicting suitable habitat for deep-water gorgonian corals on the Atlantic and Pacific Continental Margins of North America. Mar. Ecol. Prog. Ser. 330, 113–126.

Carter, G.S., Gregg, M.C., 2002. Intense, variable mixing near the head of Monterey Submarine Canyon. J. Phys. Oceanogr. 32, 3145–3165.

Coachman, L.K., 1986. Circulation, water masses and fluxes on the southeastern Bering Sea shelf. Cont. Shelf Res. 5, 23–108.

Danielson, S., Curchitser, E., Hedstrom, K., Weingartner, T., Stabeno, P., 2011. On ocean and sea ice modes of variability in the Bering Sea. J. Geophys. Res. 116, C12034. http://dx.doi.org/10.1029/2011JC007389.

Dayton, P.K., 1972. Toward an understanding of community resilience and the potential effects of enrichments to the benthos at McMurdo Sound, Antarctica. In: Parker, B.C. (Ed.), Proceedings of the Colloquium on Conservation Problems in Antarctica. Allen Press, Lawrence, Kansas, pp. 81–96.

De Leo, F., Smith, C., Rowden, A., Bowden, D., Clark, M., 2010. Submarine canyons: hotspots of benthic biomass and productivity in the deep sea. Proc. R. Soc. B—Biol. Sci. 277, 2783–2792.

Dischner, M., 2013. Bering Sea canyons research approved with wide support. Alaska J. Commer. June issue.
Available from: http://www.alaskajournal.com/Alaska-Journal-of-Commerce/June-Issue-3-2013/Bering-Sea-canyons-research-approved-with-wide-support/ (accessed February 2015).

Egbert, G.D., Erofeeva, S.Y., 2002. Efficient inverse modeling of barotropic ocean tides. J. Atmos. Ocean. Technol. 19, 183–204.

Elith, J., Phillips, S.J., Hastie, T., Dudík, M., Chee, Y.E., Yates, C.J., 2011. A statistical explanation of MaxEnt for ecologists. Divers. Distrib. 17, 43–57.

Ellison, A.M., Bank, M.S., Clinton, B.D., Colburn, E.A., Elliott, K., Ford, C.R., Foster, D.R., Stone, J.K., Swan, C.M., Thompson, J., Von Holle, B., Webster, J.R., 2005. Loss of foundation species: consequences for the structure and dynamics of forested ecosystems. Front. Ecol. Environ. 3, 479–486.

Freeland, H.J., Denman, K.L., 1982. A topographically controlled upwelling center off southern Vancouver Island. J. Mar. Res. 40, 1069–1093.

Freese, J.L., Wing, B.L., 2003. Juvenile red rockfish, *Sebastes* sp., associations with sponges in the Gulf of Alaska. Mar. Fish. Rev. 65, 38–42.

Hall-Spencer, J., Allain, V., Fosså, J.H., 2002. Trawling damage to Northeast Atlantic ancient coral reefs. Proc. R. Soc. Lond. Ser. B-Biol. Sci. 269, 507–511.

Harris, P.T., Whiteway, T., 2011. Global distribution of large submarine canyons: Geomorphic differences between active and passive continental margins. Mar. Geol. 285, 69–86.

Hartney, K.B., Grorud, K.A., 2002. The effect of sea urchins as biogenic structures on the local abundance of a temperate reef fish. Oecologia 131, 506–513.

Heifetz, J., 2002. Coral in Alaska: Distribution, abundance, and species associations. Hydrobiologia 471, 19–28.

Heifetz, J., Stone, R.P., Shotwell, S.K., 2009. Damage and disturbance to coral and sponge habitat of the Aleutian Archipelago. Mar. Ecol. Prog. Ser. 397, 295–303.

Heifetz, J., Woodby, D., Reynolds, J., Stone, R.P., 2007. Deep-sea coral distribution and habitat in the Aleutian Archipelago. North Pacific Research Board final report 304.

Hooker, S.K., Whitehead, H., Gowans, S., 1999. Marine protected area design and the spatial and temporal distribution of cetaceans in a submarine canyon. Conserv. Biol. 13, 592–602.

Husebøo, A., Nøttestad, L., Fosså, J., Furevik, D., Jørgensen, S., 2002. Distribution and abundance of fish in deep-sea coral habitats. Hydrobiologia 471, 91–99.

Jones, C.G., Gutiérrez, J.L., Byers, J.E., Crooks, J.A., Lambrinos, J.G., Talley, T.S., 2010. A framework for understanding physical ecosystem engineering by organisms. Oikos 119, 1862–1869.

Koslow, J.A., Gowlett-Holmes, K., Lowry, J.K., O'Hara, T., Poore, G.C.B., et al., 2001. Seamount benthic macrofauna off southern Tasmania: community structure and impacts of trawling. Mar. Ecol. Prog. Ser. 213, 111–125.

Krieger, K., Wing, B., 2002. Megafauna associations with deepwater corals (*Primnoa* spp.) in the Gulf of Alaska. Hydrobiologia 571, 83–90.

Lindholm, J.B., Auster, P.J., Ruth, M., Kaufman, L., 2001. Modeling the effects of fishing and implications for the design of marine protected areas: Juvenile fish responses to variations in seafloor habitat. Conserv. Biol. 15, 424–437.

Marliave, J.B., Conway, K.W., Gibbs, D.M., Lamb, A., Gibbs, C., 2009. Biodiversity and rockfish recruitment in sponge gardens and bioherms of southern British Columbia, Canada. Mar. Biol. 156, 2247–2254.

McConnaughey, R.A., Mier, K.L., Dew, C.B., 2000. An examination of chronic trawling effects on soft-bottom benthos of the eastern Bering Sea. ICES J. Mar. Sci. 57, 1377–1388. Journal du Conseil.

Miller, R.J., Hocevar, J., Stone, R.P., Fedorov, D.V., 2012. Structure-forming corals and sponges and their use as fish habitat in Bering Sea submarine canyons. PLoS One 7, e33885.

Mizobata, K., Saitoh, S., 2004. Variability of Bering Sea eddies and primary productivity along the shelf edge during 1998–2000 using satellite multisensor remote sensing. J. Mar. Syst. 50, 101–111.

Moors-Murphy, H.B., 2014. Submarine canyons as important habitat for cetaceans, with special reference to the Gully: A review. Deep Sea Res. Part II 104, 6–19.

Mortensen, P.B., Buhl-Mortensen, L., 2005. Morphology and growth of the deep-water gorgonians *Primnoa resedaeformis* and *Paragorgia arborea*. Mar. Biol. 147, 775–788.

MRAG Americas, 2000. Independent review of the North Pacific groundfish observer program. Report to National Marine Fisheries Service by MRAG Americas Inc. Tampa, Florida.

National Research Council (NRC), 2002. Effects of trawling and dredging on seafloor habitat. In: Committee on Ecosystem Effects of Fishing: Phase 1—Effects of Bottom Trawling on Seafloor Habitats. National Research Council, National Academy of Sciences, Washington, DC.

NOAA National Marine Fisheries Service (NMFS), 2005. Final environmental impact statement for essential fish habitat identification and conservation in Alaska, Appendix B: Evaluation of fishing activities that may adversely affect essential fish habitat. Available from: http://www.alaskafisheries.noaa.gov/habitat/seis/efheis (accessed February 2015).

North Pacific Fishery Management Council (NPFMC), 2010. Five-year research priorities, 2011–2015. Available at http://www.npfmc.org/wp-content/PDFdocuments/conservation_issues/Research_priorities10.pdf (Accessed February 2015).

North Pacific Fishery Management Council (NPFMC), 2013. Council's five-year research priorities: 2013 through 2017. Available from: https://npfmc.legistar.com/View.ashx?M=F&ID=3100882&GUID=DE720512-35BF-411D-B5E0-CBE998EA7363 (accessed February 2015).

Phillips, S.J., Anderson, R.P., Schapire, R.E., 2006. Maximum entropy modeling of species geographic distributions. Ecol. Modell. 190, 231–259.

Phillips, S.J., Dudík, M., 2008. Modeling of species distributions with MaxEnt: new extensions and a comprehensive evaluation. Ecography 31, 161–175.

Puig, P., Palanques, A., Martín, J., 2014. Contemporary sediment-transport processes in submarine canyons. Ann. Rev. Mar. Sci. 6, 53–77.

Reaka-Kudla, M.L., 1997. The global diversity of coral reefs: a comparison with rain forests. In: Reaka-Kudla, M.L., Wilson, D.E., Wilson, E.O. (Eds.), Biodiversity II: Understanding and Protecting our Biological Resources. Joseph Henry Press, Washington, DC, pp. 83–108.

Rogers, A., 1999. The biology of *Lophelia pertusa* (Linnaeus 1758) and other deep-water reef-forming corals and impacts from human activities. Int. Rev. Hydrobiol. 84, 315–406.

Rooper, C.N., Boldt, J.L., 2005. Distribution of juvenile Pacific ocean perch *Sebastes alutus* in the Aleutian Islands in relation to benthic habitat. Alaska Fish. Res. Bull. 11, 102–112.

Rooper, C.N., Boldt, J.L., Zimmermann, M., 2007. An assessment of juvenile Pacific ocean perch (*Sebastes alutus*) habitat use in a deepwater nursery. Estuar. Coast. Shelf Sci. 75, 371–380.

Rooper, C.N., Hoff, G., De Robertis, A., 2010. Assessing habitat utilization and rockfish (*Sebastes* spp.) biomass on an isolated rocky ridge using acoustics and stereo image analysis. Can. J. Fish. Aquat. Sci. 67, 1658–1670.

Rooper, C.N., Wilkins, M.E., Rose, C.S., Coon, C., 2011. Modeling the impacts of bottom trawling and the subsequent recovery rates of sponges and corals in the Aleutian Islands, Alaska. Cont. Shelf Res. 31, 1827–1834.

Rooper, C.N., Zimmermann, M., Prescott, M.M., Hermann, A.J., 2014. Predictive models of coral and sponge distribution, abundance and diversity in bottom trawl surveys of the Aleutian Islands, Alaska. Mar. Ecol. Prog. Ser. 503, 157–176.

Rosenberg, A., Bigford, T., Leathery, S., Hill, R., Bickers, K., 2000. Ecosystem approaches to fishery management through essential fish habitat. Bull. Mar. Sci. 66, 535–542.

Ryan, J.P., Chavez, F.P., Bellingham, J.G., 2005. Physical–biological coupling in Monterey Bay, California: topographic influences on phytoplankton ecology. Mar. Ecol. Prog. Ser. 287, 23–32.

Sigler, M.F., Rooper, C.N., Hoff, G.R., Stone, R.P., McConnaughey, R.A., Wilderbuer, T.K., 2013. Are Bering Sea canyons unique habitats within the eastern Bering Sea? Draft paper presented for Review by North Pacific Fishery Management Council. Available at: http://www.npfmc.org/wp-content/PDFdocuments/conservation_issues/BSHC/BeringSeaCanyons_a_513.pdf (accessed February 2015).

Stauffer, G., 2004. NOAA protocols for groundfish bottom trawl surveys of the nation's fishery resources. NOAA Technical Memo NMFS-F/SPO-65.

Stone, R.P., 2006. Coral habitat in the Aleutian Islands of Alaska: depth distribution, fine-scale species associations, and fisheries interactions. Coral Reefs 25, 229–238.

Stone, R.P., Shotwell, S.K., 2007. State of the deep coral ecosystems of the Alaska Region: Gulf of Alaska, Bering Sea, and the Aleutian Islands. In: Lumsden, S., Hourigan, T., Bruckner, A., Dorr, G. (Eds.), The State of Deep Coral Ecosystems of the United States. NOAA Technical Memorandum CRCP-3. Silver Spring, Maryland, pp. 65–108.

Tyler, P., et al., 2009. Europe's grand canyon: Nazaré submarine canyon. Oceanography 22, 46–57.

Venables, W.N., Ripley, B.D., 2002. Modern Applied Statistics with S. Springer Science and Business Media.

Vetter, E.W., Smith, C.R., De Leo, F.C., 2010. Hawaiian hotspots: enhanced megafaunal abundance and diversity in submarine canyons on the oceanic islands of Hawaii. Mar. Ecol. 31, 183–199.

Waller, R., Watling, L., Auster, P., Shank, T., 2007. Anthropogenic impacts on the corner rise seamounts, north-west Atlantic Ocean. J. Mar. Biol. Assoc. U. K. 87, 1075–1076.

Witherell, D., Coon, C., 2000. Protecting gorgonian corals off Alaska from fishing impacts. In: Willison, J., Hull, J., Gass, S., Kenchington, E., Butler, M., et al. (Eds.), Proceedings of the First International Symposium on Deep-Sea Corals. Ecology Action Centre and Nova Scotia Museum, Halifax, Nova Scotia, pp. 117–125.

Yen, P.P., Sydeman, W.J., Hyrenbach, K.D., 2004. Marine bird and cetacean associations with bathymetric habitats and shallow-water topographies: implications for trophic transfer and conservation. J. Mar. Syst. 50, 79–99.