

Structure-Forming Corals and Sponges and Their Use as Fish Habitat in Bering Sea Submarine Canyons

Robert J. Miller^{1*}, John Hocevar², Robert P. Stone³, Dmitry V. Fedorov⁴

1 Marine Science Institute, University of California Santa Barbara, Santa Barbara, California, United States of America, **2** Greenpeace USA, Washington D.C., United States of America, **3** Auke Bay Laboratories, Alaska Fisheries Science Center, National Marine Fisheries Service, Juneau, Alaska, United States of America, **4** Center for Bio-Image Informatics, Vision Research Lab, Electrical and Computer Engineering, University of California Santa Barbara, Santa Barbara, California, United States of America

Abstract

Continental margins are dynamic, heterogeneous settings that can include canyons, seamounts, and banks. Two of the largest canyons in the world, Zhemchug and Pribilof, cut into the edge of the continental shelf in the southeastern Bering Sea. Here currents and upwelling interact to produce a highly productive area, termed the Green Belt, that supports an abundance of fishes and squids as well as birds and marine mammals. We show that in some areas the floor of these canyons harbors high densities of gorgonian and pennatulacean corals and sponges, likely due to enhanced surface productivity, benthic currents and seafloor topography. Rockfishes, including the commercially important Pacific ocean perch, *Sebastes alutus*, were associated with corals and sponges as well as with isolated boulders. Sculpins, poachers and pleuronectid flounders were also associated with corals in Pribilof Canyon, where corals were most abundant. Fishes likely use corals and sponges as sources of vertical relief, which may harbor prey as well as provide shelter from predators. Boulders may be equivalent habitat in this regard, but are sparse in the canyons, strongly suggesting that biogenic structure is important fish habitat. Evidence of disturbance to the benthos from fishing activities was observed in these remote canyons. Bottom trawling and other benthic fishing gear has been shown to damage corals and sponges that may be very slow to recover from such disturbance. Regulation of these destructive practices is key to conservation of benthic habitats in these canyons and the ecosystem services they provide.

Citation: Miller RJ, Hocevar J, Stone RP, Fedorov DV (2012) Structure-Forming Corals and Sponges and Their Use as Fish Habitat in Bering Sea Submarine Canyons. PLoS ONE 7(3): e33885. doi:10.1371/journal.pone.0033885

Editor: John Murray Roberts, Heriot-Watt University, United Kingdom

Received: December 12, 2011; **Accepted:** February 21, 2012; **Published:** March 21, 2012

This is an open-access article, free of all copyright, and may be freely reproduced, distributed, transmitted, modified, built upon, or otherwise used by anyone for any lawful purpose. The work is made available under the Creative Commons CC0 public domain dedication.

Funding: This research was supported by the Aspenwood and Firedoll Foundations, John and Ginger Sall, the United States National Science Foundation awards III-0808772, #0941717 and iPlant Collaborative #DBI-0735191. The funders had no role in study design, data collection and analysis, decision to publish, or preparation of the manuscript.

Competing Interests: The authors have declared that no competing interests exist.

* E-mail: miller@msi.ucsb.edu

Introduction

Autogenic ecosystem engineers, such as trees or corals, modify habitats through their physical presence [1]. Ecosystem engineers can provide living space [2,3], alter and ameliorate physical conditions [4,5] and affect biological interactions [6], potentially enhancing diversity and changing patterns of species composition and dominance on local or landscape scales [5]. In the oceans, hermatypic corals are archetypical examples of autogenic engineers, forming massive reefs in shallow tropical waters that support >30% of described marine species [7].

In deeper water, the role of corals and sponges as autogenic engineers is not well understood; nevertheless, many fishes and macroinvertebrates inhabit deep-water coral [8,9,10,11] and sponge [12,13] habitats. Unlike shallow-water systems, where the processes connecting habitat with populations and communities of dependant organisms are relatively well understood, the role of habitat structure, including that of autogenic ecosystem engineers, in deep-water communities is still unclear due to lack of small-scale observational and experimental studies [14]. Biogenic structure can affect populations of associated animals through habitat selection at settlement, differential survival, and post-settlement migration [15,16,17]. The result of these processes is elevated abundances of benefited organisms associated with the habitat

feature in question. This conceptual framework is formalized in frequency-dependent habitat selection models [18]; e.g. the ideal free distribution model predicts positive correlation between abundance and habitat fitness value [19,20]. Comparison of species distribution patterns with respect to potential functionally equivalent habitats, e.g. corals versus rock outcrops, can provide a better indication of the importance of autogenic engineers to associated species compared with simple observations of high densities around corals [20]. Comparative approaches, no matter how well designed, will not shed much light on mechanisms of habitat effects on associated organisms; nevertheless such approaches are crucial for informing managers and designing future experimental work.

Slow growing fragile corals are highly vulnerable to damage by physical contact with fishing gear [11,21,22,23] leading the North Pacific Fishery Management Council (NPFMC) to identify gorgonian corals as essential fish habitat of particular concern [24]. Two general concepts motivating conservation of deep-water corals have been put forth: (1) corals are used as habitat by, and presumably provide some important benefit to economically important fishes and crustaceans [11,25,26] and (2) corals have intrinsic value, are slow growing and extremely sensitive to disturbance, and consequently have questionable potential for recovery [20]. Nevertheless, information is lacking on distribution

of corals and their use as fish habitat off Alaska (but see [11,27]), and the NPFMC has identified research on this topic as a critical need for fisheries management [28]. Here we evaluate density of structure-forming corals and sponges in Zhemchug and Pribilof Canyons, Bering Sea. We also measured densities of eight common taxa of demersal fishes, and evaluated their use of corals, sponges, and boulders as habitat in the canyons. We document and describe fishing damage to benthic habitats observed during our surveys.

Methods

Study sites

Zhemchug and Pribilof Canyons are enormous submarine canyons cutting into the continental slope under the northeastern boundary of the Aleutian Basin, southeastern Bering Sea. Volumes of Zhemchug and Pribilof canyons are 8500 and 1300 km³, respectively, and Zhemchug is likely the world's largest submarine canyon (for comparison, Monterey Canyon off California, often described as large, has a volume of only 450 km³) [29]. These canyons were probably excavated in the Pleistocene by mass wasting, slumping and creeping of sediment that accumulated at the heads of the Yukon and Kuskokwim rivers during periods of glacially lowered sea level [29,30,31]. Pribilof Canyon is ~150 km long and ~1500 m deep where it cuts the shelf, descending to the continental rise at ~3000 m depth. Zhemchug Canyon is ~160 km long, up to 2600 m deep, and intersects the continental Rise at 3400 m depth. The slopes of both canyons are largely composed of clay and marine-derived sediments [29,32]. Detailed geological descriptions of the canyons may be found in Scholl et al. [29]. Currents in the canyons are generally moderate, ~2–18 cm s⁻¹, and follow canyon topography [33]; however, these were measured at 50 m depth, and near bottom currents may be considerably stronger at times [34].

Video transects from submersible dives

Video transects were conducted in Zhemchug and Pribilof Canyons, Bering Sea (see map Figure 1), in Jul-Aug 2007 using Deep-Worker submersibles at depths of 168–533 m (n = 7 transects for Pribilof, n = 9 for Zhemchug). Deep-Workers are small, single-person piloted submersibles with maximum operating depth of 600 m. Transects were located to cover the geographical extent of the canyons and were located approximately equidistantly apart. Pilots flew upslope on a constant heading, with video camera (Sony HDR FX1) on the widest lens setting (58° horizontal and 32° vertical angle of view) and positioned at 30° downward from horizontal. Paired lasers 10 cm apart were projected onto the seafloor approximately in the center of the image and were used as a scale reference. Time and depth were recorded and cross-referenced to the video frames. Additional dives were done with the Deep-Worker submersibles specifically to collect specimens, and a remotely operated vehicle (ROV) was deployed to explore deeper habitats. Video footage from neither of these sources was used to quantify organism densities for this manuscript. Evidence of fishing impacts was recorded on these additional dives.

Data analysis

Non-overlapping frames were extracted from each video transect at a constant frequency of 1 frame per 30 s using open source utility software (Bio-Image Converter [35]). An image-processing algorithm developed in Matlab, using adaptive thresholding, connected component analysis, and the CIELAB color space was used to locate the laser dots. Each frame was then manually annotated using open-source software (Scientist's Digital

Notebook [36]). To ensure the quality of each frame, we checked overall scene quality, presence of overlap with adjacent images, and accuracy of automated laser dot detection. Final annotations comprise locations of laser dots and all objects of interest in the frame, and are stored in a hierarchical XML format within the Bisque system [37]. Each object was described by a location centroid and a type, which was a taxon or other identifier. We annotated a total of 54 object types, including taxa and bottom features, using an annotation template for Digital Notebook (see Text S1, Figure S1). These count data were compiled into comma-separated values files for analysis.

The area of each frame was estimated using a geometrical approach. Physical pixel resolution was computed based on the laser dots, and the area was projected from the image plane to the seabed, assuming that the seabed underneath the camera was planar [38]. Corals, sponges, and fishes were enumerated in each frame. Corals and sponges larger than ~5 cm height with their base in the frame were counted. Dominant (>50% cover) substrate type was scored in each frame following a generalized version of the Wentworth scale [39] with fine sediment categories grouped as soft sediment, and pebble categories grouped as pebbles. Obvious fishing damage, which comprised trawl scars and/or broken corals and sponges, were scored present/absent in each frame following methodology used previously in the region [11].

Image and meta data collected and annotated for this study are publicly available on the Bisque database (http://bisque.ece.ucsb.edu/client_service/view?resource=http://bisque.ece.ucsb.edu/data_service/dataset/1580770) maintained by the Center for Bio-Image Informatics at UC Santa Barbara for researchers, educators and students and providing advanced data query, visualization and summarization tools. All developed software is publicly available as Matlab and Python scripts distributed on the Center for Bio-Image Informatics web site (<http://www.bioimage.ucsb.edu/>).

Coral taxa were classified into two groups for data analysis: (1) gorgonians (Subclass Octocorallia, Order Gorgonacea), and (2) sea whips and sea pens (Subclass Octocorallia, Order Pennatulacea). True soft corals (Subclass Octocorallia, Order Alcyonacea) and stoloniferous corals (Subclass Octocorallia, Order Stolonifera) also occurred on some transects but were rare and not included in analyses. Sponge taxa were classified as hexactinellid sponges (Class Hexactinellida) or calcareous sponges (Class Calcarea) and demosponges (Class Demospongiae) combined into “other sponges.”

Associations of fishes with structure-forming biota (corals and sponges) and non-biogenic structure (boulders) were evaluated using logistic regression [Generalized linear model (GLM), binomial distribution with logit link] on presence/absence frame-specific data. The response variable (fish presence) was coded 0–1 (presence-absence) as were the covariates corals and sponges, to avoid giving too much weight to frames containing numerous fishes and corals. The null hypothesis for these analyses was of the form: fish sp. A was no more likely to occur in frames containing coral than in frames not containing coral. The generalized linear model was fit to the data by Firth-adjusted maximum likelihood estimation of the parameter vector. We used Firth-penalized maximum likelihood adjustment to minimize any possible effect of collinearity and small sample sizes on the results; non-Firth-adjusted values were very similar, suggesting that these issues were not a problem in the data. Model parameters were estimated numerically through an iterative fitting process. Statistical analyses were performed in JMP (SAS Institute, version 8.0.1).

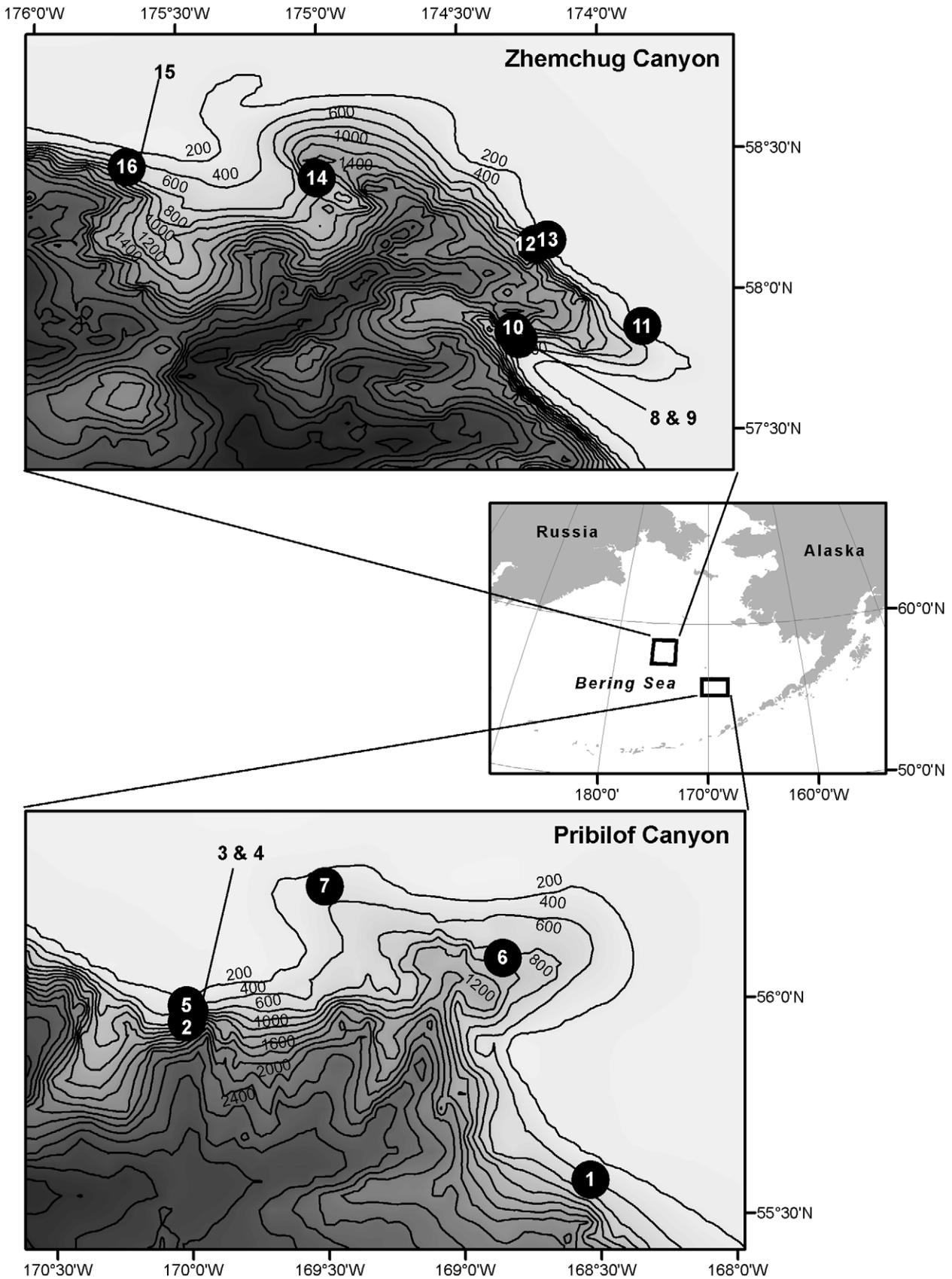


Figure 1. Map of study area showing locations of canyons and submersible transects.
 doi:10.1371/journal.pone.0033885.g001

Results

A total of 2,753 frames from 16 dives were analyzed, representing a total of 23.3 hours (884GB) of high definition video. The total area sampled was ~4202 m² (1528 m² in Pribilof, 2674 m² in Zhemchug). Area of frames averaged 1.5 m² (± 0.02 S.E.). Transects in both canyons were dominated by soft sediment substrate (mean 65.6% cover ± 15 S.E. for Pribilof Canyon, 85.4% ± 9 for Zhemchug Canyon), with lesser coverage of pebbles (32.3% cover ± 15 S.E. for Pribilof Canyon, 4.1% ± 4 for Zhemchug Canyon), and cobble/boulder field (6.3% cover ± 3 S.E. for Pribilof Canyon, 11.4% ± 7.5 for Zhemchug Canyon). Depth of transects ranged from 168 to 533 m; average depth of Pribilof transects was 306 m (± 2 S.E., range 168–417 m), while Zhemchug transects were deeper on average, 455 m (± 1 S.E., range 351–533 m); this difference was significant ($t = 4.9$, $df = 14$, $P < 0.001$). Gorgonacean corals (*Plumarella superba*, *P. echinata*, and *Swiftia pacifica*) were associated with pebble and cobble bottoms and were ~6 \times more abundant on the Pribilof Canyon transects (Table 1, transect means 0–2.41 gorgonians m⁻², compared to 0–0.96 gorgonians m⁻² in Zhemchug Canyon transects). Sponges were also associated with hard substrate and were ~20 \times more abundant in Pribilof Canyon compared with Zhemchug (Table 1). Hexactinellid sponges were more abundant than other sponge taxa at both canyons. Pennatulacean corals (*Halipterus willemoesi* and *Protophilum* sp.), however, were associated with fine sediment, and were still ~5 \times more abundant on Pribilof transects (Table 1). Overall, corals were ~5 \times more abundant on Pribilof Canyon transects. Gorgonian corals and sponges were most abundant between 200–300 m depth, whereas pennatulacean corals were most abundant between 200–400 m depth (Figure 2).

Commercially important Pacific ocean perch, *Sebastes alutus*, were more abundant by two orders of magnitude on Pribilof Canyon transects compared to Zhemchug Canyon (Table 2), and total rockfish abundance was likewise much higher in Pribilof Canyon (Table 2). Rajids (skates), cottids (sculpins), and zoarcids (eelpouts) were also more abundant on Pribilof Canyon transects (Table 2). Abundance of agonids (poachers), and the giant

grenadier, *Albatrossia pectoralis*, was higher in Zhemchug Canyon (Table 2). Densities of pleuronectid flounders were similar in transects at both canyons. Less common fishes counted included *Gadus macrocephalus* (Pacific cod), *Anoplopoma fimbria* (sablefish), *Zaprora silenus* (prowfish), and liparids (snailfishes).

Because the depth of transects was significantly different between canyons, we analyzed the associations of fishes with structure separately for each canyon. In both canyons, rockfish (combined) were significantly more likely to be encountered near boulders and gorgonian corals (Table 3). In Zhemchug Canyon, rockfish were also more likely to be encountered near pennatulacean corals. Pacific ocean perch were significantly associated with boulders, sponges, and gorgonian corals in Pribilof Canyon, where this species was most abundant (Figure 3). In Zhemchug canyon, Pacific ocean perch were significantly associated with pennatulacean corals, but not with boulders and gorgonians, which were less abundant there (Table 3). *Sebastes* spp. (*S. borealis*, the shortraker rockfish, and *S. aleutianus*, the roughey rockfish) were associated with boulders and gorgonians in Zhemchug Canyon; none were observed on Pribilof transects. *Sebastolobus alascanus*, the shortspine thornyhead, was significantly associated with gorgonian and pennatulacean corals in Zhemchug canyon, but showed no associations in Pribilof transects (Table 3). Poachers and sculpins were significantly associated with gorgonians in Pribilof Canyon. Pleuronectid flounders were not associated with corals or boulders in either canyon (Table 3).

Evidence of fishing disturbance was observed on a total of 13 occasions, (9 in Pribilof Canyon, 4 in Zhemchug Canyon) at depths of 154–966 meters (Table 4). Three of the 16 Deep-Worker transects had obvious evidence of fishing damage, which was recorded present in 0.26% of frames, covering 28.8 m². Additional observations of damage were made on collecting dives and ROV transects (Table 4). Most observations were trawl scars evident due to gouging of soft sediments (Figure 4A). In some cases, damage to corals was evident, e.g. in Pribilof Canyon, at 280 m depth, in the form of trawl scars on the seafloor and numerous gorgonians and the pennatulacean *Halipterus willemoesi* toppled and all lying in the same direction on the seafloor. Other evidence of fishing damage

Table 1. Mean density estimates (numbers m⁻² \pm S.E.) and depth range of common corals and sponges in Pribilof and Zhemchug Canyons, Bering Sea.

Taxon	Pribilof Canyon	Zhemchug Canyon	Depth range (m)
Gorgonacea			
<i>Plumarella</i> spp.	0.72 (± 0.4)	0	237–356
<i>Swiftia pacifica</i>	0	0.08 (± 0.1)	351–530
<i>Keratoisis</i> sp.	0.01 (± 0.01)	0.05 (± 0.1)	466–533
Total gorgonians	0.73 (± 0.4)	0.13 (± 0.1)	237–533
Pennatulacea			
<i>Protophilum</i> sp.	0.17 (± 0.1)	0.04 (± 0.02)	185–529
<i>Halipterus willemoisi</i>	0.07 (± 0.1)	0.001 (± 0.001)	254–488
Total pennatulaceans	0.24 (± 0.2)	0.05 (± 0.02)	185–529
Total corals	0.97 (± 0.4)	0.18 (± 0.1)	
Porifera			
Hexactinellidae	0.40 (± 0.3)	0.02 (± 0.01)	241–466
Other sponges	0.24 (± 0.2)	0.001 (± 0.002)	201–306
Total sponges	0.41 (± 0.4)	0.02 (± 0.01)	201–466

Means are based on estimated transect densities, n = 7 transects for Pribilof, n = 9 for Zhemchug.

doi:10.1371/journal.pone.0033885.t001

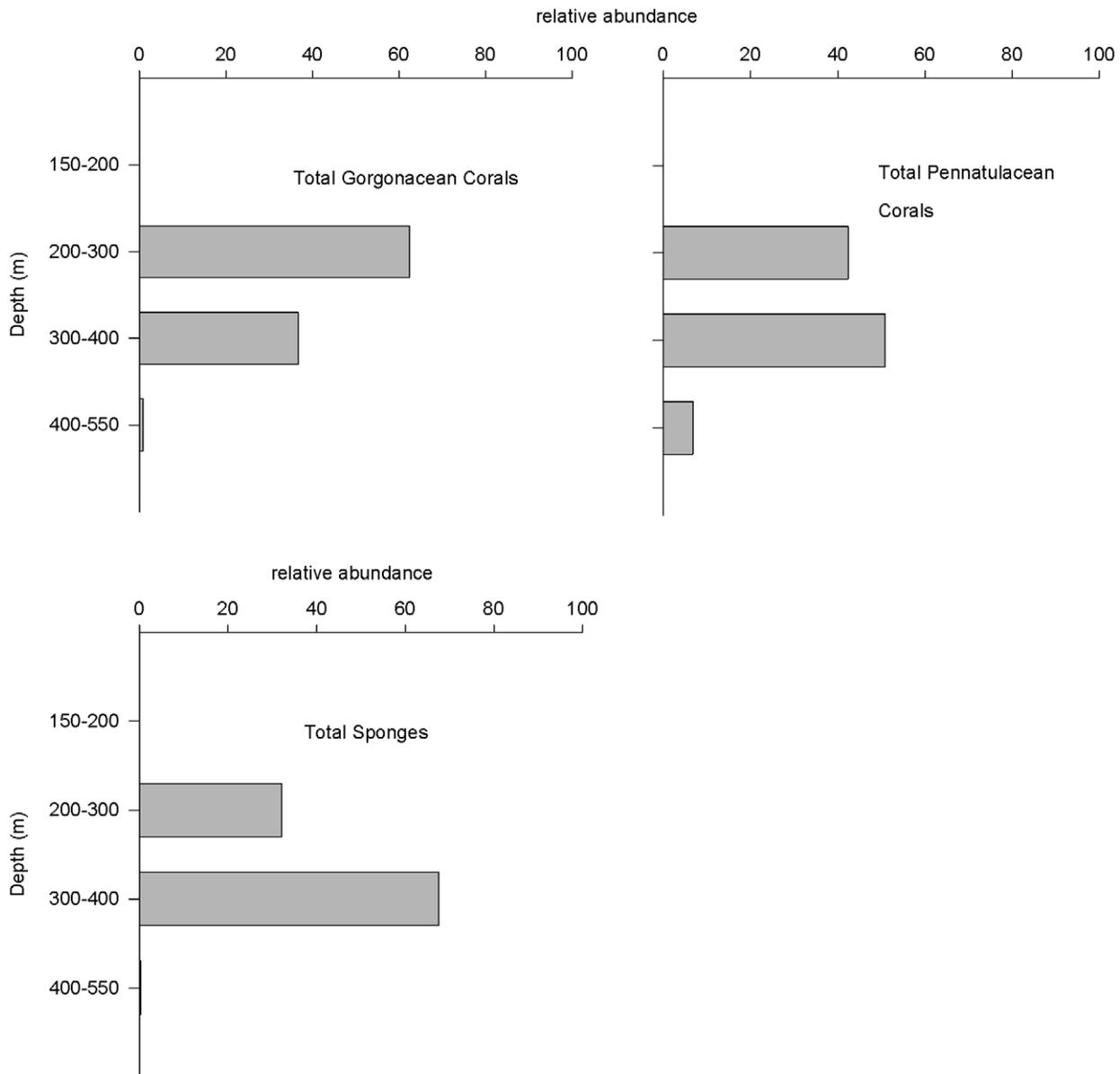


Figure 2. Relative abundance by depth of corals (total gorgonians $n=1301$, total pennatulaceans $n=552$) and total sponges ($n=1039$) in Pribilof and Zhemchug Canyons, Bering Sea. Sample sizes (# images analyzed) for each depth strata were: 150–200: $n=77$, 200–300: $n=483$, 300–400: $n=396$, 400–550: $n=1872$.
doi:10.1371/journal.pone.0033885.g002

included debris such as large tangles of line and netting (e.g. Figure 4B).

Discussion

Submarine canyons have been identified as potential hotspots of deep-water biomass and productivity due to enhanced substrate and topographic complexity compared to slope habitats, as well as topographic enhancement of flux and deposition of organic matter [40]. In one of the few biological studies comparing shelf areas to a deep-sea canyon, De Leo et al [40] measured infaunal biomass in Kaikoura Canyon off New Zealand that was 100-fold higher than ever measured for a non-chemosynthetic deep-sea benthic habitat, and 10 times higher than nearby shelf benthos. Zhemchug and Pribilof Canyons lie in the highly productive “green belt” along

the Bering Sea shelf edge [41], and primary production over the canyons is stimulated by stationary mesoscale eddies that enhance upwelling and can temporally extend spring phytoplankton blooms [42]. Surface-derived particulate organic carbon (POC) comprised the main source of carbon for deep-water corals, as revealed by stable isotope analyses [43,44]. Thus, upwelling along the shelf edge and resultant high flux of phytodetritus to the seafloor, combined with the availability of hard substrate (albeit limited) on canyon slopes, likely sustains the high densities of corals and sponges measured in this study.

Abundance data for deep-water corals are scarce and are most often only reported as present or absent. Highest densities of corals within the depth range investigated were found at depths between 200–400 m, similar with other studies of corals in that depth range [11,26,45]. Overall mean coral density estimated in both canyons

Table 2. Mean density estimates (numbers $m^{-2} \pm$ S.E.) of common fishes in Pribilof and Zhemchug Canyons, Bering Sea.

Taxon	Pribilof Canyon	Zhemchug Canyon
Scorpaenidae		
<i>Sebastes alutus</i>	0.11 (\pm 0.03)	0.002 (\pm 0.001)
<i>Sebastes</i> spp.	0	0.02 (\pm 0.02)
<i>Sebastolobus alascanus</i>	0.07 (\pm 0.1)	0.02 (\pm 0.01)
Total rockfish	0.18 (\pm 0.1)	0.04 (\pm 0.02)
Agonidae (poachers)	0.01 (\pm 0.003)	0.05 (\pm 0.02)
Cottidae (sculpins)	0.01 (\pm 0.004)	0.002 (\pm 0.001)
Macrouridae (grenadiers)		
<i>Albatrossia pectoralis</i>	0	0.004 (\pm 0.002)
Pleuronectidae (right-eyed flounders)	0.02 (\pm 0.01)	0.02 (\pm 0.004)
Rajidae (skates)	0.01 (\pm 0.004)	0.004 (\pm 0.001)
Zoarcidae (eelpout)	0.01 (\pm 0.01)	0.002 (\pm 0.001)

Sebastes spp. includes *S. borealis*, the shortraker rockfish, and *S. aleutianus*, the roughey rockfish.

Means are based on estimated transect densities, $n=7$ transects for Pribilof Canyon, $n=9$ for Zhemchug Canyon.

doi:10.1371/journal.pone.0033885.t002

**Figure 3.** Pacific ocean perch (*Sebastes alutus*) with the gorgonian coral *Plumarella* sp. at a depth of 230 m in Pribilof Canyon, Bering Sea.

doi:10.1371/journal.pone.0033885.g003

were much lower ($0.18 \text{ colonies } m^{-2}$), but similar or higher than those observed in other coral-rich areas of the world (e.g. the Weddell Sea, Antarctica ($0.12 \text{ colonies } m^{-2}$ [46]), Atlantic Canada ($0.005\text{--}0.048 \text{ colonies } m^{-2}$ [45]), and Norway ($0.043\text{--}0.069 \text{ colonies } m^{-2}$ [25]), indicating that both canyons support significant deep-water coral habitats. The somewhat deeper average depth of the Zhemchug Canyon transects may have influenced the lower coral density found there.

The overall density of corals estimated for the Bering Sea canyons are low compared to those measured via a census in the central Aleutian Islands [11] and the habitats formed by the corals

was $0.43 \text{ colonies } m^{-2}$, approximately one third the density measured in the central Aleutian Islands via a census [11]. Density in the two canyons, however, differed considerably; Pribilof Canyon had coral densities estimated at $0.97 \text{ colonies } m^{-2}$ only somewhat lower than that measured in the Aleutian Islands ($1.23 \text{ colonies } m^{-2}$). Coral densities estimated at Zhemchug Canyon

Table 3. Significance values (p levels) for all GLM covariates.

Pribilof Canyon								
covariate	Fish taxa							
	<i>Sebastes alutus</i>	<i>Sebastes</i> spp.	<i>Sebastolobus alascanus</i>	Total rockfish	Agonidae	Cottidae	Pleuronectidae	
depth	-0.01 (0.003) <0.0001	-	0.02 (0.006) <0.0001	-0.004 (0.002) <0.0001	0.0007 (0.004) 0.001	0.18	0.01 (0.003) <0.0001	
boulders	2.96 (0.9) 0.0007	-	1.00	2.72 (0.9) 0.001	1.00	0.67	1.00	
gorgonian corals	1.12 (0.3) 0.0003	-	1.00	0.88 (0.3) 0.001	-3.00 (1.5) 0.04	1.63 (0.8) 0.04	0.42	
pennatulacean corals	0.65	-	0.67	0.14	0.75	0.17	0.16	
sponges	0.74 (0.3) 0.01	-	1.00	0.45 (0.3) 0.04	0.27	0.71	0.48	
Zhemchug Canyon								
covariate	Fish taxa							
	<i>Sebastes alutus</i>	<i>Sebastes</i> spp.	<i>Sebastolobus alascanus</i>	Total rockfish	Agonidae	Cottidae	Pleuronectidae	
depth	0.01 (0.01) <0.002	-0.001 (0.01) 0.001	0.01 (0.006) 0.0002	0.007 (0.004) 0.0002	0.003 (0.003) 0.001	0.33	0.001 (0.003) 0.001	
boulders	1.00	7.71 (1.6) <0.0001	1.00	6.54 (1.6) <0.0001	1.00	0.85	1.00	
gorgonian corals	1.00	2.27 (0.8) 0.03	2.48 (0.5) <0.0001	2.26 (0.5) <0.0001	0.11	0.22	0.20	
pennatulacean corals	3.61 (0.9) 0.003	0.32	2.00 (0.7) 0.04	2.07 (0.5) 0.0007	0.37	0.11	0.37	
sponges	1.00	1.00	0.44	0.22	0.91	0.53	1.00	

Parameter values (standard error) are given above bolded p values for significant covariates. *Sebastes* spp. includes *S. borealis*, the shortraker rockfish, and *S. aleutianus*, the roughey rockfish.

Fish, coral, sponge and boulder data were analyzed as presence-absence. Transect data were pooled. Each fish taxa or category was analyzed separately. Significance was evaluated at $\alpha=0.05$. Fish taxa from Table 2 not presented here exhibited no significant relationships with any covariate.

doi:10.1371/journal.pone.0033885.t003

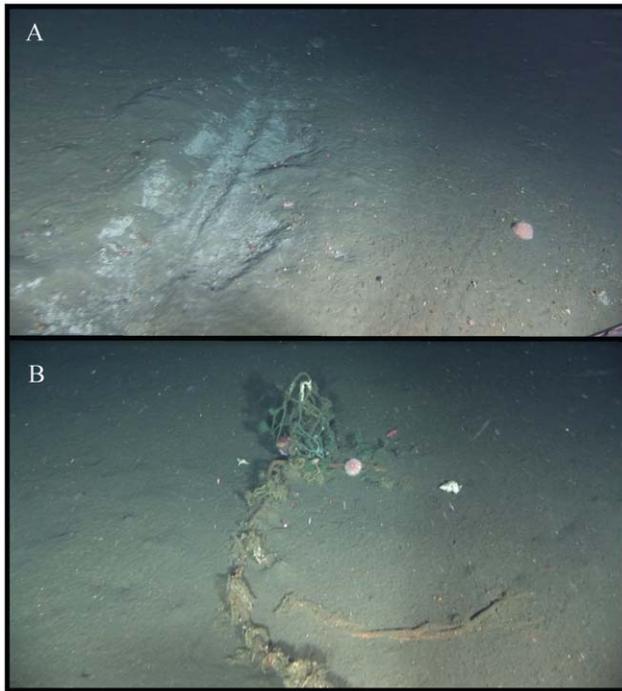


Figure 4. Examples of fishing damage to benthos in Pribilof Canyon, Bering Sea. A) trawl scar, 264 m depth, B) derelict fishing gear entangled on corals, 405 m depth.
doi:10.1371/journal.pone.0033885.g004

are very different in the two regions (i.e. dense coral and sponge gardens were not observed in the canyons). The fields of gorgonians and pennatulaceans observed in the canyons are quite patchy in distribution and separated by large areas of open silt/sand habitat (85% of the total frames contained no corals). Nonetheless, however, the habitats formed by the corals and sponges appear to be utilized by many of the fish species present in the Canyons. Aleutian Island coral gardens (sensu [11]) have extremely high local densities of corals [11], more than three times the overall density of Pribilof Canyon, and are also particularly

species rich (more than 40 species total). By contrast, we observed 15 total coral species in the Bering Sea Canyons. However, our collections (and photo identifications) included many northern range extensions and new records for the region, indicating that the canyons are more species rich than previously known [47]. Our collections included one scleractinian (*Caryophyllia alaskensis* – a northern range extension), one antipatharian (*Bathypathes* sp. – northernmost record in the Pacific Ocean), one alcyonacean (*Anthomastus* sp. – likely representing a northern range extension), one stoloniferan (*Clavularia* sp. – a new record for the region), seven gorgonians (*Plumarella superba*, *P. echinata*, *Primnoa pacifica*, *P. wingi*., *Keratoisis* sp., *Swiftia pacifica*, and *Paragorgia arborea* – several of which represent new records for the region and northern range extensions), and three pennatulaceans (*Halipteris willemoesi*, *Protoptilum* sp., and cf. *Pennatula* sp. – the latter two taxa representing probable range extensions).

Abundance of hexactinellid sponges in Pribilof Canyon was similar to that of the corals at 0.40 m^{-2} ; unfortunately few sponge abundance data from other areas are available for comparison. In the Eastern Gulf of Alaska, large sponges were found at mean densities of $0\text{--}0.12\text{ m}^{-2}$ in untrawled areas; experimental trawling significantly reduced sponge densities [48]. Deep-water bioherms off the Pacific Coast of Canada harbored abundant (11.6–26%) cover of hexactinellid sponges [49]. Density of the hexactinellid sponge *Phoronema carpenteri* in the Porcupine Seabight (Northeast Atlantic), averaged 0.34 m^{-2} at 1000–1300 m depth, with local aggregations attaining higher densities [50]. Density of *Hyalonema* sp. averaged 0.01 m^{-2} at 4100 m depth off California, but densities of dead hexactinellid stalks were much higher and harbored a high-diversity epifaunal community [12]. Overall, the hexactinellid sponge densities observed in this study were comparable to those reported as high density in areas elsewhere.

Fishes, particularly rockfishes, were associated with corals significantly more often than would be expected given the abundance of corals, a result consistent with other studies of Alaskan corals [11,27,51]. Rockfishes were also, significantly associated with boulders, and it is unclear at present whether corals generally serve as hard structure interchangeably with rocks and other forms of structure, or provide added fitness benefits to fishes such as food sources [20]. Both corals and sponges harbor diverse and abundant assemblages of macroinvertebrates that may be prey for fishes [8,12,52]. Pacific ocean perch

Table 4. Locations and depths of benthic fishing damage observed at Pribilof and Zhemchug Canyons.

Date	Damage type	Canyon	Depth (m)	vehicle	position
7/29/2007	debris (line)	Pribilof	410	DW	N 55°52.5718 W 168°56.4128
7/30/2007	trawl scar	Pribilof	275	DW	N 56°09.5988 W 168°48.6511
8/2/2007	trawl scar	Pribilof	336	DW	N 55°59.9834 W 169°40.6453
8/2/2007	trawl scar	Pribilof	264	DW	N 55°59.9834 W 169°40.6453
8/2/2007	trawl scar	Pribilof	284	DW	N 55°59.9834 W 169°40.6453
8/2/2007	trawl scar	Pribilof	860	ROV	N 55°57.716 W 169°39.965
8/2/2007	trawl scar	Pribilof	852	ROV	N 55°57.716 W 169°39.965
8/2/2007	debris (chain, line)	Pribilof	821	ROV	N 55°57.716 W 169°39.965
8/4/2007	debris (net)	Zhemchug	966	ROV	N 57°50.47 W 174°17.64
8/6/2007	trawl scar	Zhemchug	154	ROV	N 57°50.6 W 174°17.7
8/8/2007	debris (cable)	Zhemchug	161	ROV	N 57°51.67 W 173°50.14
8/8/2007	debris (line)	Zhemchug	317	ROV	N 58°10.08 W 174°10.51

Coordinates represent the initial starting position of each dive. DW = Deep Worker.
doi:10.1371/journal.pone.0033885.t004

was found preferentially inhabiting flat pebble bottoms in the eastern Gulf of Alaska [53]. In that study, presence of corals was not evaluated as a factor influencing fish distribution, although we note that the photo of *S. alutus* in the paper shows the fish among a dense grove of the pennatulacean *Halimopterus willemoesi* [53]. Later, Brodeur [54] observed aggregations of Pacific ocean perch associated with *H. willemoesi*, and suggested that the sea pens filled the need for vertical structure for this fish species. Our results support this observation, but do not provide evidence for the relative importance of corals, sponges, and other biogenic structure versus nonbiogenic structure, e.g. boulders, to these fishes. Nevertheless, boulders, seamounts, and other sources of high-profile vertical relief are relatively rare in the deep sea [55] and abundant corals likely provide important fish habitat in low-relief areas even if their habitat quality does not differ from that of abiotic structure.

Pacific ocean perch is a late-maturing, slow-growing viviparous species and were historically the target of an important trawl fishery in the eastern Bering Sea until stocks were severely depleted about a decade ago [56]. Stocks have since increased and recently a small directed fishery has been reopened, and Pacific ocean perch continue to be taken as bycatch by other trawl fisheries. Dispersal of Pacific ocean perch is apparently quite limited, with genetic structure evident at geographic scales of 70–400 km, indicating that management of this species should be on a finer geographic scale than the current assessment areas [57]. Pacific ocean perch populations in areas such as the Canyons studied here, therefore, may be rendered less resilient if local habitats are degraded by benthic fishing impacts.

An ecosystem approach to management [58,59], which recognizes that the value of intact ecosystems is greater than the sum of their parts [60], is now the general, though sometimes necessarily imprecise, goal of fisheries management [61]. Witherell et al [62] summarized progress towards, and future implementation of, an ecosystem approach to management of Alaskan groundfish fisheries by the North Pacific Fishery Management Council. This included, as required under the 1996 Magnuson–Stevens Act amendments, identification and conservation of essential fish habitat (EFH), as well as habitat areas of particular concern (HAPC), which are specific EFH's distinguished by their particularly important ecological function and vulnerability to anthropogenic impacts [63]. Corals were used as the *prima facie* example of a HAPC in Alaskan waters [28,62]. Our results support this notion, indicating that commercially important fishes preferentially utilize corals for habitat. Although some of these fishes also use boulders, boulders and corals are typically associated [64], and together they comprise inseparable elements of the habitat. Although it is of ecological and evolutionary interest to separate the relative fitness values of these different forms of habitat, from a resource management standpoint, a conservative approach suggests that they be considered at least equivalent. Like most deep ocean habitats, these canyons are dominated by low-

relief soft substrate, making corals important habitat elements providing vertical relief. Thus, based on the survey data reported here, Pribilof and Zhemchug Canyons can be regarded as harboring areas of high densities of slow-growing corals that form the foundation of complex communities as well as habitat areas of particular concern due to their vulnerability and use by commercially important fishes.

Deep-water gorgonian corals grow slowly and can live for hundreds of years [65,66,67], making likely recovery times after disturbance very long [68]. Anthropogenic disturbance by bottom trawling has been shown to devastate corals, not surprisingly, since bottom trawls typically incorporate heavy chains and doors that are dragged along the seafloor [69]. Heavily trawled areas in the Aleutian Islands were devoid of hydrocorals, and levels of damage to corals were positively correlated with trawling effort [70]. Bottom longline and pot gear can also damage corals, although this damage is likely less intense than that from trawling [11]. In this study, fishing damage was observed on several dives (Figure 4, Table 4); suggesting that bottom-contact fishing is clearly a source of disturbance to corals in Pribilof and Zhemchug Canyons. The high densities of corals in these shelf-edge canyons, and their use as fish habitat, suggests that conservation of these unique areas be given priority status in fisheries management decisions. Canyons and other topographic features on the edges of continental shelves likely represent high productivity areas throughout the deep sea [40], and the ecology and conservation of these habitats and the ecosystem services they provide deserve more attention.

Supporting Information

Figure S1 Screenshot of Digital notebook while in graphical annotation mode.

(TIF)

Text S1 Supplementary material describing access to annotated data, extraction and annotation process.

(DOCX)

Acknowledgments

We thank D. Guggenheim, K. Lowyck, T. Marshall, and M. Ridgway for field assistance. C. Juska made the map for Figure 1. F. Archibald assisted with video analysis. Nuytco Research, Vancouver, B.C., supported submersible dives. The findings and conclusions in the paper are those of the authors and do not necessarily represent the views of the National Marine Fisheries Service, NOAA.

Author Contributions

Conceived and designed the experiments: JH RPS. Performed the experiments: JH RPS. Analyzed the data: RJM DVF. Contributed reagents/materials/analysis tools: DVF. Wrote the paper: RJM JH RPS DVF.

References

- Jones CG, Lawton JH, Shachak M (1994) Organisms as ecosystem engineers. *Oikos* 69: 373–386.
- Hacker SD, Gaines SD (1997) Some implications of direct positive interactions for community species diversity. *Ecology* 78: 1990–2003.
- Jones CG, Lawton JH, Shachak M (1997) Positive and negative effects of organisms as physical ecosystem engineers. *Ecology* 78: 1946–1957.
- Anderson R (1992) Diversity of eukaryotic algae. *Biodiversity Conservation* 1: 267–292.
- Badano EI, Cavieres LA (2006) Impacts of ecosystem engineers on community attributes: effects of cushion plants at different elevations of the Chilean Andes. *Diversity and Distributions* 12: 388–396.
- Crain CM, Bertness MD (2006) Ecosystem engineering across environmental gradients: Implications for conservation and management. *Bioscience* 56: 211–218.
- Reaka-Kudla ML (1997) The global diversity of coral reefs: a comparison with rain forests. In: Reaka-Kudla ML, Wilson DE, Wilson EO, eds. *Biodiversity II: understanding and protecting our biological resources*. Washington, DC: Joseph Henry Press. 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. *International Review of Hydrobiology*. pp 315–406.
- Huseboo A, Nøttestad L, Fosså J, Furevik D, Jørgensen S (2002) Distribution and abundance of fish in deep-sea coral habitats. *Hydrobiologia* 471: 91–99.

10. Mortensen PB, Buhl-Mortensen L (2005) Morphology and growth of the deep-water gorgonians *Primnoa resedaeformis* and *Paragorgia arborea*. *Marine Biology* 147: 775–788.
11. Stone RP (2006) Coral habitat in the Aleutian Islands of Alaska: depth distribution, fine-scale species associations, and fisheries interactions. *Coral Reefs* 25: 229–238.
12. Beaulieu SE (2001) Life on glass houses: Sponge stalk communities in the deep sea. *Marine Biology* 138: 803–817.
13. Marliave JB, Conway KW, Gibbs DM, Lamb A, Gibbs C (2009) Biodiversity and rockfish recruitment in sponge gardens and bioherms of southern British Columbia, Canada. *Marine Biology* 156: 2247–2254.
14. Auster PJ (2007) Linking deep-water corals and fish populations. Conservation and Adaptive Management of Seamount and Deep-Sea Coral Ecosystems. Rosenstiel School Marine And Atmospheric Science, Miami, FL USA. pp 93–99.
15. Auster PJ, Malatesta RJ, Langton RW, Watling L (1996) The impacts of mobile fishing gear on seafloor habitats in the Gulf of Maine: Implications for conservation of fish populations. *Bulletin of the Ecological Society of America* 77: 349.
16. Lindholm JB, Auster PJ, 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. *Conservation Biology* 15: 424–437.
17. Hartney KB, Grorud KA (2002) The effect of sea urchins as biogenic structures on the local abundance of a temperate reef fish. *Oecologia* 131: 506–513.
18. Kramer DL, Rangeley RW, Chapman LJ (1997) Habitat selection: patterns of spatial distribution from behavioural decisions. In: Godin J, ed. *Behavioural Ecology of Teleost Fishes*. New York: Oxford University Press. pp 37–80.
19. Fretwell S, Lucas HJ (1969) On territorial behavior and other factors influencing habitat distribution in birds Part 1: theoretical development. *Acta Biotheoretica* 19: 16–36.
20. Auster PJ (2005) Are deep-water corals important habitats for fishes? In: Freiwald A, Roberts JM, eds. *Cold-water Corals and Ecosystems*. Berlin Heidelberg: Springer-Verlag. pp 747–760.
21. Waller R, Watling L, Auster P, Shank T (2007) Anthropogenic impacts on the corner rise seamounts, north-west Atlantic Ocean. *Journal of the Marine Biological Association of the United Kingdom* 87: 1075–1076.
22. Hall-Spencer J, Allain V, Fossà JH (2002) Trawling damage to Northeast Atlantic ancient coral reefs. *Proceedings of the Royal Society of London Series B-Biological Sciences* 269: 507–511.
23. Koslow JA, Gowlett-Holmes K, Lowry JK, O'Hara T, Poore GCB, et al. (2001) Seamount benthic macrofauna off southern Tasmania: community structure and impacts of trawling. *Marine Ecology-Progress Series* 213: 111–125.
24. 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., editor. *Proceedings of the First International Symposium on Deep-sea Corals*. Halifax, Nova Scotia: Ecology Action Centre and Nova Scotia Museum. pp 117–125.
25. Mortensen PB, Hovland M, Brattegard T, Farestveit R (1995) Deep water bioherms of the scleractinian coral *Lophelia pertusa* (L.) at 64 degrees on the Norwegian shelf: Structure and associated megafauna. *Sarsia* 80: 145–158.
26. Fossà JH, Mortensen PB, Furevik DM (2002) The deep-water coral *Lophelia pertusa* in Norwegian waters: Distribution and fishery impacts. *Hydrobiologia* 471: 1–12.
27. Heifetz J (2002) Coral in Alaska: Distribution, abundance, and species associations. *Hydrobiologia* 471: 19–28.
28. North Pacific Fishery Management Council (2010) Five-Year Research Priorities, 2011–2015.
29. Scholl D, Buffington E, Hopkins D, Alpha T (1970) Structure and origin of large submarine canyons of the Bering Sea. *Marine Geology* 8: 187–210.
30. Shepard FP, Dill RF (1966) Submarine canyons and other sea valleys. *Rand McNally geology series* xiii: 381.
31. Carlson P, Karl H (1988) Development of large submarine canyons in the Bering Sea, indicated by morphologic, seismic, and sedimentologic characteristics. *Geological Society of America Bulletin*. pp 1594–1615.
32. Gardner J, Dean W, Vallier T (1980) Sedimentology and geochemistry of surface sediments, outer continental-shelf, southern Bering Sea. *Marine Geology*. pp 299–329.
33. Schumaker J, Reed R (1992) Characteristics of currents over the continental slope of the eastern Bering Sea. *Journal of Geophysical Research Oceans*. pp 9423–9433.
34. Gross T, Williams A, Nowell A (1988) A deep-sea sediment transport storm. *Nature*. pp 518–521.
35. Center for BioImage Informatics (2011) Converter B-I. Center for BioImage Informatics. Santa Barbara, CA, USA: University of California.
36. Center for BioImage Informatics (2011) Notebook SsD. Center for BioImage Informatics. Santa Barbara, CA, USA: University of California.
37. Kvillekval K, Fedorov D, Obara B, Singh A, Manjunath BS (2010) Bisque: a platform for bioimage analysis and management. *Bioinformatics* 26: 544–552.
38. Wildish DJ, Akagi HM, McKeown DL, Pohle GW (2008) Pockmarks influence benthic communities in Passamaquoddy Bay, Bay of Fundy, Canada. *Marine Ecology Progress Series* 357: 51–65.
39. Holme NA, McIntyre AD (1971) Methods for the study of marine benthos. *IBP handbook no 16*: xii, 334.
40. De Leo F, Smith C, Rowden A, Bowden D, Clark M (2010) Submarine canyons: hotspots of benthic biomass and productivity in the deep sea. *Proceedings of the Royal Society B-Biological Sciences*. pp 2783–2792.
41. Springer A, McRoy C, Flint M (1996) The Bering Sea Green Belt: Shelf-edge processes and ecosystem production. *Fisheries Oceanography* 5: 205–223.
42. 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. *Journal of Marine Systems* 50: 101–111.
43. Griffin S, Druffel E (1989) Sources of carbon to deep-sea corals. *Radiocarbon* 31: 533–543.
44. Druffel E, Griffin S, Witter A, Nelson E, Southon J, et al. (1995) *Gerardia* - bristlecone-pine of the deep-sea. *Geochimica Et Cosmochimica Acta* 59: 5031–5036.
45. Mortensen P, Buhl-Mortensen L (2004) Distribution of deep-water gorgonian corals in relation to benthic habitat features in the Northeast Channel (Atlantic Canada). *Marine Biology*. pp 1223–1238.
46. Orejas C, Lopez-Gonzalez P, Gili J, Teixido N, Gutt J, et al. (2002) Distribution and reproductive ecology of the Antarctic octocoral *Ainigmaption antarcticum* in the Weddell Sea. *Marine Ecology Progress Series*. pp 101–114.
47. Stone R, Shotwell SK (2007) State of the deep coral ecosystems of the Alaska Region: Gulf of Alaska, Bering Sea, and the Aleutian Islands; Lumsden S, Hourigan T, Bruckner A, Dorr G, editors. Silver Spring, MD: Northwest and Alaska Fisheries Center, National Marine Fisheries Service, National Oceanic and Atmospheric Administration. 365 p.
48. Freese L, Auster PJ, Heifetz J, Wing BL (1999) Effects of trawling on seafloor habitat and associated invertebrate taxa in the Gulf of Alaska. *Marine Ecology Progress Series*. pp 119–126.
49. Chu JWF, Leys SP (2010) High resolution mapping of community structure in three glass sponge reefs (Porifera, Hexactinellida). *Marine Ecology Progress Series* 417: 97.
50. Rice A, Thurston M, New A (1990) Dense aggregations of a hexactinellid sponge *Pheronema carpenteri* in the Porcupine Seabight, northeast Atlantic Ocean, and possible causes. *Progress in Oceanography* 24: 179–196.
51. Du Preez C, Tunnicliffe V (2011) Shortspine thornyhead and rockfish (Scorpaenidae) distribution in response to substratum, biogenic structures and trawling. *Marine Ecology Progress Series* 425: 217–231.
52. Krieger K, Wing B (2002) Megafauna associations with deepwater corals (*Primnoa* spp.) in the Gulf of Alaska. *Hydrobiologia* 571: 83–90.
53. Krieger K (1993) Distribution and abundance of rockfish determined from a submersible and by bottom trawling. *Fishery Bulletin* 91: 87–96.
54. Brodeur R (2001) Habitat-specific distribution of Pacific ocean perch (*Sebastes alutus*) in Pribilof Canyon, Bering Sea. *Continental Shelf Research* 21: 207–224.
55. Gage JD, Tyler PA (1991) *Deep-sea biology: a natural history of organisms at the deep-sea floor* Cambridge University Press. 504 p.
56. Ito DH, Kimura DK, Wilkins ME (1987) Status and future prospects for the Pacific Ocean perch resource in waters off Washington and Oregon as assessed in 1986. National Oceanic and Atmospheric Administration Technical Memorandum NMFS F/NWC-113. 50 p.
57. Palof KJ, Heifetz J, Gharrett AJ (2011) Geographic structure in Alaskan Pacific ocean perch (*Sebastes alutus*) indicates limited lifetime dispersal. *Marine Biology* 158: 779–792.
58. Sissenwine MP, Mace PM (2003) Governance for responsible fisheries: An ecosystem approach. *Responsible fisheries in the marine ecosystem*. , 10 E. 40th Street, Suite 3203, New York, NY, 10016, USA: CABI Publishing. pp 363–391.
59. Sherman K, Sissenwine M, Christensen V, Duda A, Hempel G, et al. (2005) A global movement toward an ecosystem approach to management of marine resources. *Marine Ecology Progress Series* 300: 275–279.
60. Browman H, Stergiou K (2004) Perspectives on ecosystem-based approaches to the management of marine resources. *Marine Ecology-Progress Series*. pp 269–270.
61. Link J (2002) What does ecosystem-based fisheries management mean? *Fisheries*. pp 18–21.
62. Witherell D, Pautzke C, Fluharty D (2000) An ecosystem-based approach for Alaska groundfish fisheries. *Ices Journal of Marine Science*. pp 771–777.
63. Rosenberg A, Bigford T, Leathery S, Hill R, Bickers K (2000) Ecosystem approaches to fishery management through essential fish habitat. *Bulletin of Marine Science*. pp 535–542.
64. Etnoyer P, Morgan L (2005) Habitat-forming deep-sea corals in the Northeast Pacific Ocean. *Cold-Water Corals and Ecosystems*. pp 331–343.
65. Andrews F, Cordes E, Mahoney M, Munk K, Coale K, et al. (2002) Age, growth and radiometric age validation of a deep-sea, habitat-forming gorgonian (*Primnoa resedaeformis*) from the Gulf of Alaska. *Hydrobiologia* 471: 101–110.
66. Risk M, Heikoop J, Snow M, Beukens R (2002) Lifespans and growth patterns of two deep-sea corals: *Primnoa resedaeformis* and *Desmophyllum cristagalli*. *Hydrobiologia* 471: 125–131.
67. Williams B, Risk M, Stone R, Sinclair D, Ghaleb B (2007) Oceanographic changes in the North Pacific Ocean over the past century recorded in deep-water gorgonian corals. *Marine Ecology Progress Series* 335: 85–94.
68. Althaus F, Williams A, Schlacher TA, Kloser RJ, Green MA, et al. (2009) Impacts of bottom trawling on deep-sea coral ecosystems of seamounts are long-lasting. *Marine Ecology Progress Series* 397: 279–294.
69. Roberts CM (2002) Deep impact: The rising toll of fishing in the deep sea. *Trends in Ecology and Evolution* 17: 242–245.
70. Heifetz J, Stone RP, Shotwell SK (2009) Damage and disturbance to coral and sponge habitat of the Aleutian Archipelago. *Marine Ecology Progress Series* 397: 295–303.