NOAA Professional Paper NMFS 16

The ecology of deep-sea coral and sponge habitats of the central Aleutian Islands of Alaska

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April 2014

DEPARTMENT OF COMMERCE ★ UNITED STATES OF AMERICA

NOAA Professional Papers NMFS

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The Secretary of Commerce has determined that the publication of this series is necessary in the transaction of the public business required by law of this Department. Use of funds for printing of this series has been approved by the Director of the Office of Management and Budget.

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U.S. Department of Commerce
Seattle, Washington

Suggested reference

Stone, Robert P. 2014. The ecology of deep-sea coral and sponge habitats of the central Aleutian Islands of Alaska. NOAA Professional Paper NMFS 16, 52 p. doi:10.7755/PP.16

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Abstract—The first in situ exploration of deep-sea coral habitat in the central Aleutian Islands in 2002 confirmed expectations that had been based on fishery bycatch and research survey records which indicate corals are widespread, diverse, and abundant. This paper reports observations from analysis of video collected during 2003 and 2004 in a study area that expanded the range of earlier observations to depths beyond current fishing activities (~1000 m) and encompassed the entire central Aleutian Island region. Video of the seafloor was collected at 17 sites with a manned submersible to depths of 365 m and a remotely operated vehicle to 2947 m. Corals, sponges, and other emergent epifauna were widely distributed throughout the study area and present at all depths. Changes in density and species richness were observed at depths of 400–700 m, with abundance and diversity increasing as depth decreased. The distribution of individual fishes, crabs, and octopods was examined relative to emergent epifauna: 63% of the fishes, crabs, and octopods were found in the same sampled video frames as were corals, 69% of them were found in the same frames with sponges, and 55% of them were found in the same frames with "other" emergent epifauna. Most species at depths <1000 m were observed near emergent epifauna, and evidence indicates that epifauna may be essential to some taxa. The extensive closures implemented in 2006 as part of the Aleutian Islands Habitat Conservation Area provide important protection to much coral and sponge habitat that may serve as a source of recruits to nearby disturbed habitats, but observations made during this study indicate that the majority of garden habitat in the study area may currently remain open to bottom trawling.

The ecology of deep-sea coral and sponge habitats of the central Aleutian Islands of Alaska

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Introduction

Although the first biological expeditions to the Aleutian Islands (Fig. 1) more than a century ago returned with a diverse collection of corals (Nutting, 1912), benthic ecologists paid little attention to this region of Alaska until a little more than a decade ago, when an exploratory study was launched in 2002 with the submersible *Delta* (Stone, 2006). During that study, unique coral gardens were discovered to depths of 365 m in the central Aleutian Islands. Coral gardens are areas of exceptional coral diversity and abundance where coverage of emergent epifauna, primarily corals, approaches 100% (Stone, 2006). Examination of specimens collected during that study, from fishery surveys, and from fishery bycatch revealed that the Aleutian Islands harbored a diversity of coldwater corals that was extraordinary for a high-latitude ecosystem and that at least 51 species or subspecies of hydrocorals and gorgonians were endemic to the region (Stone and Shotwell, 2007). Corals are widespread on the continental shelf and slope throughout Alaska, but strong evidence indicates that a major shift in coral abundance and species diversity occurs west of the Alaska Peninsula (Heifetz et al., 2005).

Until 2002, scientists based their limited knowledge about deep-sea corals in the Aleutian Islands almost entirely on fishery bycatch specimens and fisheries survey data. These data provide useful information at the large scale of existing fisheries, but provide little detail about how corals are integrated into seafloor communities or how they are distributed relative to depth and seafloor habitat. Are there reserves of deep-sea corals in areas and at depths where fisheries and surveys do not presently occur? What are the most appropriate tools for protecting deep-sea corals from human activities and where, specifically, do they need protection? Answers to these basic questions will help managers develop effective measures for mitigation of adverse effects of fishing activities on these sensitive habitats—actions that are required under the Magnuson-Stevens Fishery Conservation and Management Reauthorization Act of 2006. Additionally, answers to these questions are necessary under reporting requirements of the Deep-sea Coral Research and Technology Program established by NOAA under this legislation.

The 2002 study also documented fine-scale associations between commercially targeted fish and crab species and corals (Stone, 2006). Such observations are important, given

Figure 1

Map of the study area in the North Pacific Ocean and the Aleutian Island Archipelago for this in situ exploration of deep-sea coral and sponge habitats in 2003 and 2004 through the collection of video along transects with a submersible and remotely operated vehicle. The red box indicates the location of the study area in the central Aleutian Islands.

the presence of major fisheries in the Aleutian Islands and their potential effects on deep-sea coral habitat. In situ observations elsewhere have documented the use of deep-sea coral habitat by fishes and invertebrates, including the provision of important refuge habitat for juvenile fishes and invertebrates (Fosså et al., 2002; Krieger and Wing, 2002; Stone, 2006; Ross and Quattrini, 2007). Some coral species are slow-growing, long-lived (Stone and Wing, 2001; Andrews et al., 2002; Andrews et al., 2009), and sensitive to perturbations, such as the ones caused by bottom-contact fishing gear (Krieger, 2001; Reed, 2002; Stone, 2006). Coral habitat is more at risk to damage from fishing gear if targeted species are associated with it.

This article presents data from a study conducted in 2003 and 2004 that expands on the 2002 study. I examined fine-scale associations between important fish, crab, and octopod species, including many species managed under a fishery management plan (fishes and crabs) and structure-providing invertebrates, such as corals, sponges, anemones, bryozoans, and hydroids. In this study, observations of fishes and crabs covered the depths commercially fished (down to about 1000 m) and depths well beyond that range (to 2947 m). I also included in the analyses species that are currently of little or no economic importance (e.g., grenadiers) because fisheries may develop for these species in the future and there is little information at this time regarding their distribution and habitat in the central Aleutian Islands. Other abundant species of noncommercial importance were included in the analyses because they also may play important ecological roles in deepwater ecosystems.

Since the initiation of this study, the North Pacific Fisheries Management Council has protected vast areas of seafloor habitat in the Aleutian Islands through the creation of the Aleutian Islands Habitat Conservation Area (AIHCA). Regulations for the closures were implemented in June 2006 and include an area (957,361 km^2) of seafloor west of the Islands of Four Mountains (170° W) that encompasses the entire EEZ in the region

(Fig. 2). At its implementation, the AIHCA was the largest bottom-trawl closure in the United States and the first in Alaska directed at protection of sensitive deep-sea coral habitat. The creation of the AIHCA (Fig. 2) closed approximately 100,000 km^2 of seafloor habitat within the depth zone of current fishing activities. About 40% of historically targeted fishing grounds (defined as habitat within the current depth range of trawl activities—a depth of about 1000 m) and largely unfished areas, including Bowers Ridge in the Bering Sea, were closed, while historically trawled areas that supported high catches of groundfishes and accounted for a combined total of approximately 42,611 km^2 of seafloor habitat remained open. Additionally, 6 coral gardens (for a total seafloor habitat of 377 km^2) that were discovered during the 2002 expedition (Stone, 2006) were closed to all bottom-contact fishing gear specifically as Coral Habitat Protection Areas or equivalently as Habitat Areas of Particular Concern (HAPCs) (Fig. 2).

This study, which used both the submersible *Delta* (in 2003 and 2004) and the remotely operated vehicle (ROV) *Jason II* (in 2004), provided an unparalleled opportunity to extend in situ observations for the region down to depths of almost 3000 m. This article presents in situ observations of coral and sponge habitat and of fishes, crabs, and octopods to depths throughout the range of current fishing activities and well beyond those depths anticipated to be affected by fishing activities in the near future in the central Aleutian Islands.

Materials and methods

Study area

The Aleutian Archipelago spans more than 1900 km and extends from the Alaska Peninsula to the Kamchatka Peninsula in Russia (Fig. 1). This archipelago is supported by the Aleutian Ridge that forms the boundary between the deep North Pacific Ocean and the shallower Bering Sea. Strong tidal currents between island passes exchange water and nutrients between the 2 water bodies. The Aleutian Ridge is a volcanic arc that was formed along zones of convergence between the North American Plate and other tectonic plates and is the site of more than 20 active volcanoes and frequent earthquake activity. This combination of unique geological and oceanographic features provides 3 ingredients essential for most deep-sea corals and sponges: exposed rock substrate, plankton- and nutrient-rich waters, and water currents strong enough to provide nutrients and carry away metabolic wastes.

The study area consisted of 17 sites (Fig. 3) between Amlia Island (174° W) and Petrel Bank (180° W). Within the 17 sites, several shallow-water transects and one deepwater transect were selected for in situ observations of the seafloor through collection of video. Transect locations were selected to collectively cover a wide range of depths and habitats mapped from interpretation of data from surveys conducted with multibeam sonar systems (Heifetz et al.[1]). Study sites were further prioritized for exploration to provide a design that was balanced geographically and with respect to the spatial distribution of geological factors within the study site (e.g., active and inactive volcanism).

Experimental design

Three separate cruises were made to the study area to collect video of the seafloor and biological and geological specimens for examination (Appendix I). The first cruise, between 27 June and 11 July 2003, used the submersible *Delta* to collect video along 22 transects on the seafloor (Fig. 3). Four additional dives were made specifically to collect biological specimens. The second cruise, between 25 June and 10 July 2004, used the submersible *Delta* to collect video along 23 transects (Fig. 3). Eight additional dives were made specifically to collect biological specimens. The third cruise, between 24 July and 8 August 2004, used the ROV *Jason II* to collect video and specimens along 14 transects (Fig. 3).

The *Delta* (Fig. 4A) carried a pilot and a scientist and was equipped with external halogen lights, internal and external video cameras, gyro and magnetic compasses, sonar altimeter, sub-to-tender vessel communications, and a SBE 19*plus* SeaCAT Profiler CTD (Sea-Bird Electronics, Inc., Bellevue, WA) used to collect depth, temperature, salinity, and density data. The submersible also was equipped with an acoustic transponder that allowed for tracking of the submersible from the tender vessel with differential global positioning and an ultra-short baseline system for acoustic tracking.

The submersible followed a predetermined bearing generally oriented perpendicular to shore or from deep to shallow water along each transect, and its course was modified when necessary through communication with personnel on the tender vessel. Submersible speed varied approximately from 0.25 to 0.80 m s^{-1}, depending on the physical features of the seafloor and near-bottom currents. Video of the seafloor was collected with 2 externally mounted cameras. The primary camera was mounted with the imaging plane directed perpendicular to the seafloor and the camera lens at a near-constant altitude of 80 cm above the seafloor when the submersible was in contact with the seafloor. The width of the image area was not fixed, varying between 80 and 400 cm, and depended on the submersible's distance above the

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[1] Heifetz, J., D. Woodby, J. Reynolds, and R. P. Stone. 2007. Deep sea coral distribution and habitat in the Aleutian Archipelago. North Pacific Research Board Final Report. NPRB Project 304 Final Report, 303 p. [Available from the North Pacific Research Board, 1007 W 3rd Ave., Suite 100, Anchorage, AK 99501 or from http://doc.nprb.org/web/03_prjs/r0304_final.pdf.]

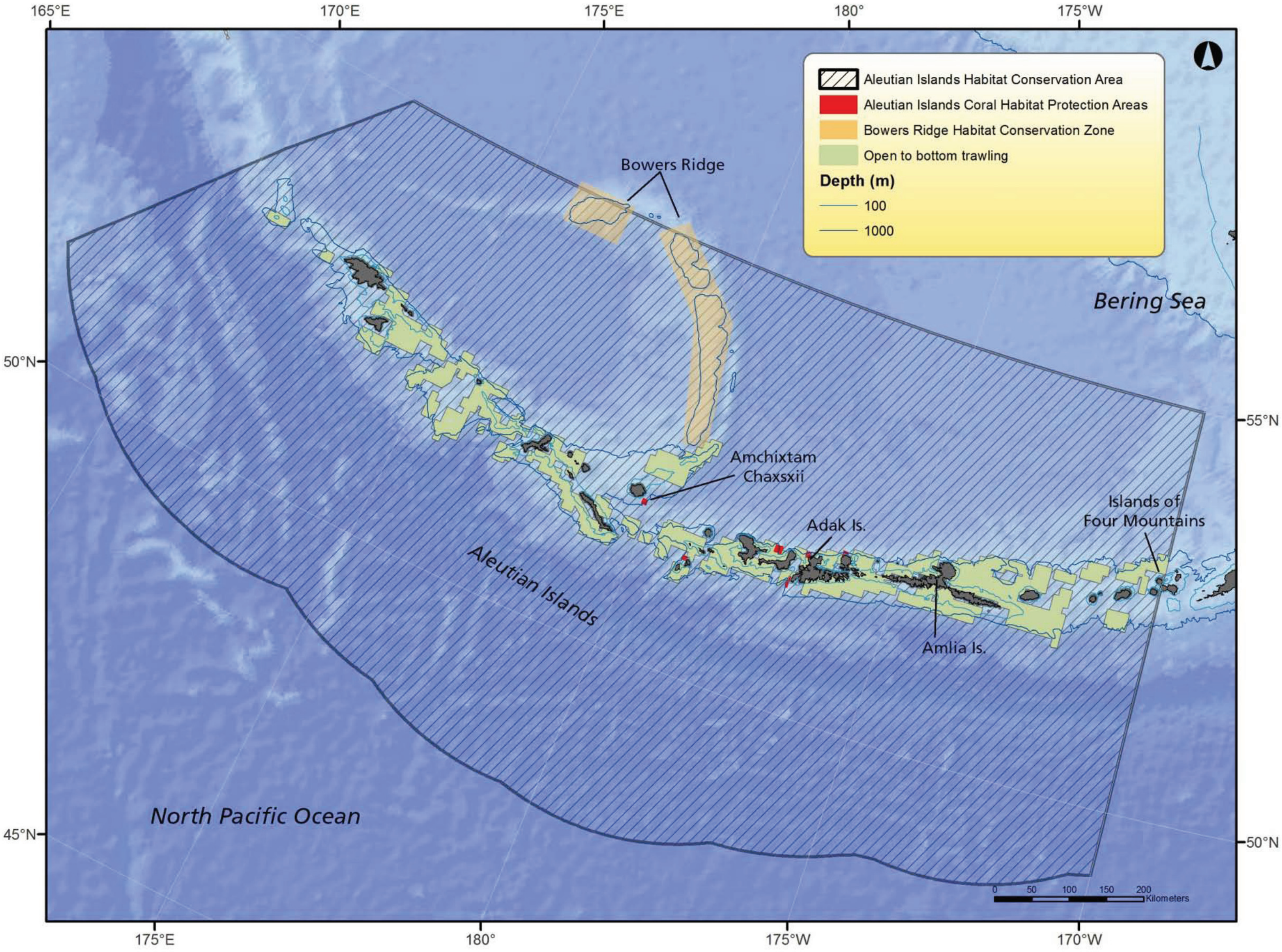

Figure 2

Map of the fishing closures in the Aleutian Islands, Alaska, that were implemented by the North Pacific Fisheries Management Council and National Marine Fisheries Service in June 2006.

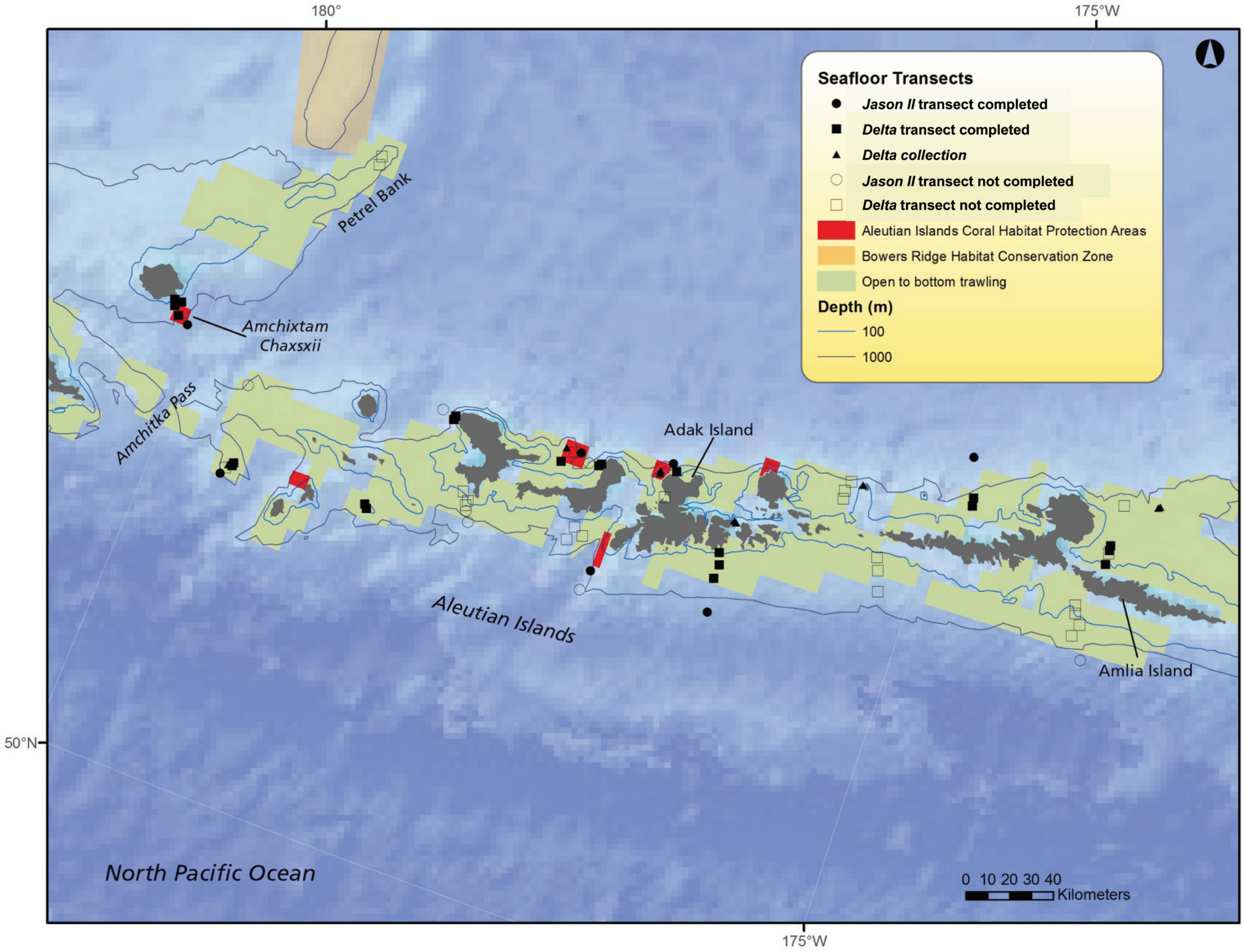

Figure 3

Map of the study area in the central Aleutian Islands showing the sites where dives were made along 29 transects with the submersible *Delta* and remotely operated vehicle *Jason II* to collect specimens and video of the seafloor in 2003 and 2004. This figure also illustrates the various fishing closures in the area to provide for a spatial relation of the closures to the survey transects.

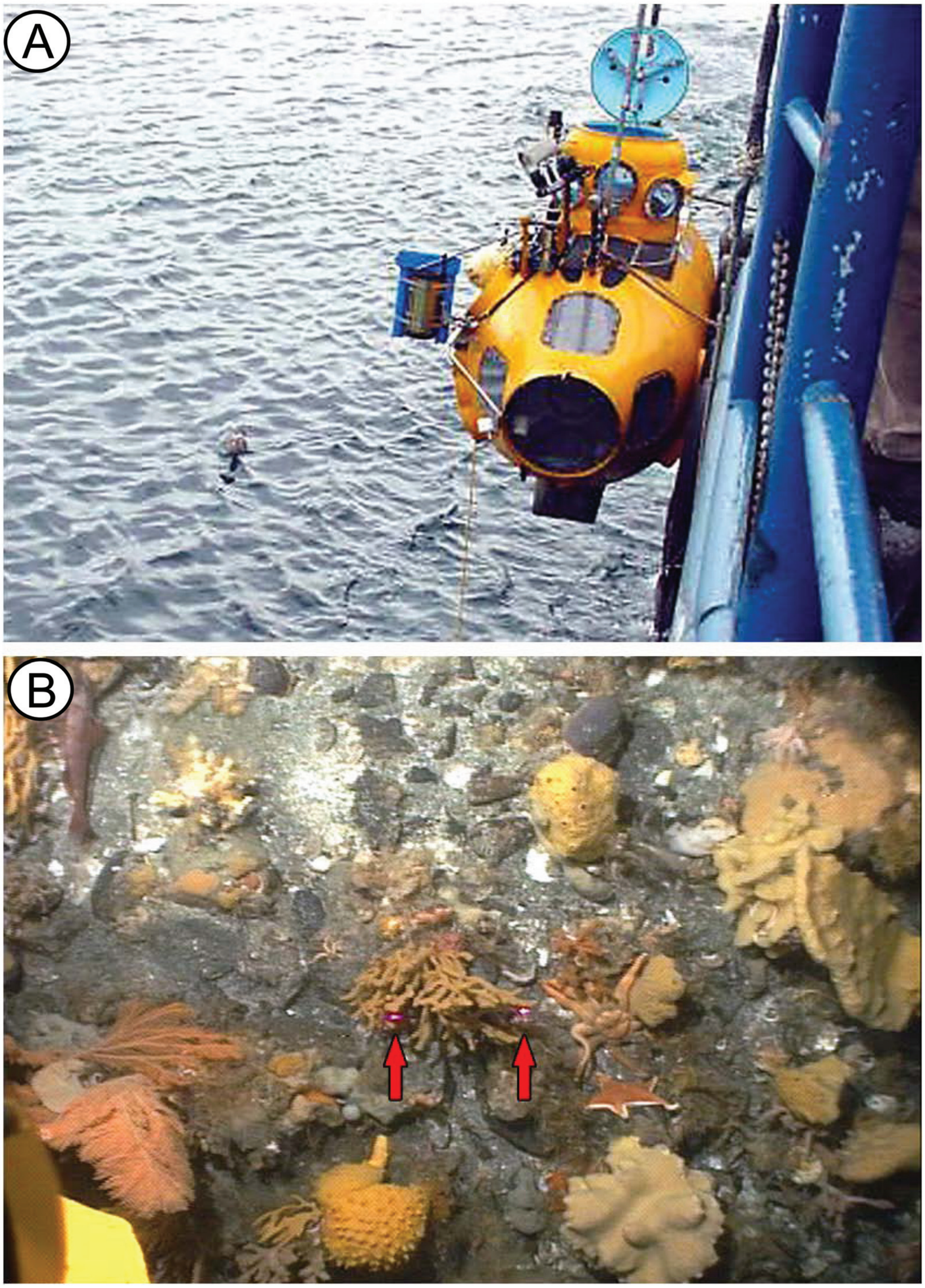

Figure 4

(**A**) The submersible *Delta* was used to examine coral habitat at depths <365 m in 2003 and 2004. (NOAA photo by Patrick Malecha). (**B**) A frame sampled from video footage collected with the submersible *Delta*. The 2 red laser marks (round marks above red arrows), which were recorded by the video cameras at the time of video collection, provide a 20-cm scaling tool for the measurement of the width and length of the frame, measurements that varied with the altitude of the submersible. This video frame, collected at a depth of 119 m, contains 3 gorgonians (*Plumarella* spp.), 18 demosponges, and 1 Northern Rockfish.

seafloor (Fig. 4B). The average width for all transects was 155 cm. A second camera was mounted laterally with the imaging plane directed at a 45° angle to the seafloor. This view was used to enumerate biota in areas where the seafloor was more vertical (>45°). Width of this image area was assumed to be a flat plane and calculated as symmetrical. Images were continuously recorded on digital video tape.

The scientist aboard the submersible viewed the image area laterally and recorded voice observations. Data continuously displayed on the video images included real time and height of the camera lens above the seafloor. In addition, the video cameras recorded 2 parallel laser marks 20 cm apart projected onto the seafloor to provide calibration for measurements of the width of the image area (i.e., transect width), transect length, and size of fauna. The mechanical arm of the submersible was used to collect voucher specimens for taxonomic identification and specimens for ecological studies.

An unoccupied ROV, the *Jason II,* was tethered to the tender vessel with 10 km of fiber-optic cable (Fig. 5A). The cable delivered electrical power and commands to the ROV and live video imagery back to the command center aboard the tender vessel. The ROV was equipped with external incandescent lamps, multiple video cameras, a flux-gate compass, a Simrad SM 2000 multibeam sonar (Kongsberg AS, Horten, Norway), and a SBE 19*plus* SeaCAT Profiler CTD. The position of the ROV was tracked by personnel on the tender vessel with differential global positioning and a long baseline system for acoustic tracking. Three video cameras were available to the science team for real-time observation, and they all were capable of recording video continually for later laboratory processing.

The primary video camera (1-chip) was mounted on the “light-bar” approximately 2.4 m above the seafloor. This camera was mounted with the imaging plane directed nearly perpendicular to the seafloor, and it recorded 2 sets of parallel laser marks (144 cm and 10 cm apart) projected onto the seafloor to provide calibration for measurements of transect length and size of fauna (Fig. 5B). The perspective provided by this camera was used to make counts and measurements along the transect within sampled frames, and the projected laser marks provided a fixed-width transect of 144 cm (Fig. 5B). A 3-chip camera (called the “science camera”) had pan and tilt functions and was operated by the science team to provide close-up views of transects and surrounding areas of the seafloor, biota, and geological features. The third camera, operated by the ROV pilot, was a 1-chip camera with pan and tilt functions and provided an additional perspective of transects and surrounding seafloor areas. Images from all cameras were continuously recorded on DVDs, and data displayed on the video images included real time, directional bearing, and depth. Two hydraulic manipulator arms were used to collect voucher specimens for taxonomic identification and specimens for ecological studies.

Video processing

Analog video was collected with a Hi8 color camera and recorded on a Sony MiniDV cassette recorder (Sony Corp., Tokyo) during the *Delta* cruises in 2003 and 2004. In the laboratory, video was encoded to MPEG-2 format at 30 frames per second and copied onto DVDs for long-term storage. The video collected with all cameras during the *Jason II* cruise in 2004 was recorded on DVDs. Files were read directly from DVDs (*Jason II*) or copied onto a PC hard drive (*Delta*) for post-processing. Event logging software (VideoRuler, vers. 7, C-map Systems, Inc., Red Lodge, MT) was used in post-processing of all video (Stone and Brown, 2005). The software plays back the video with keyboard controls that allow normal playback speed, fast forward, and frame-by-frame advancement. Custom lists of taxa and habitat features were created, and each taxon or feature was assigned a keystroke.

A video image library was constructed to assist in identification of fauna. The library consisted of video images of collected voucher specimens and other fauna that were identified by taxonomists familiar with that group of organisms. Regional field guides for corals (Wing and Barnard, 2004), sponges (Stone et al., 2011), rockfishes (Love et al., 2002), and octopods (Jorgensen, 2009) also were used to make identifications. Still frames were captured at prescribed sampling intervals (detailed later), and data were entered with a keyboard. The survey area on the seafloor was automatically calculated through calibration of the 2 laser marks spaced 20 cm apart (*Delta* transects) and 144 cm or 10 cm apart (*Jason II* transects). The size of organisms or habitat features also was measured through the use of the laser marks as a scaling tool. Each frame was associated with a time code and data file. This information was displayed on the primary computer monitor, while video from all cameras was viewed full screen on additional monitors (Stone and Brown, 2005).

Initially, all frames were sampled for observations within the transects on the seafloor; however, they were ultimately subsampled at a rate of 50% or 10% in an effort to process more video footage (Table 1). Frames were systematically subsampled at a rate of 50% by sampling 5 consecutive frames and then skipping the next 5 frames, and so on. Frames were systematically subsampled at a rate of 10% by sampling 1 frame and then skipping the next 9 frames, and so on. The following data were collected from each sampled frame: 1) depth, 2) length, width, and area, 3) seafloor roughness, 4) slope, 5) vertical relief of emergent epifauna, 6) percent cover of emergent epifauna, and 7) surficial substrate texture.

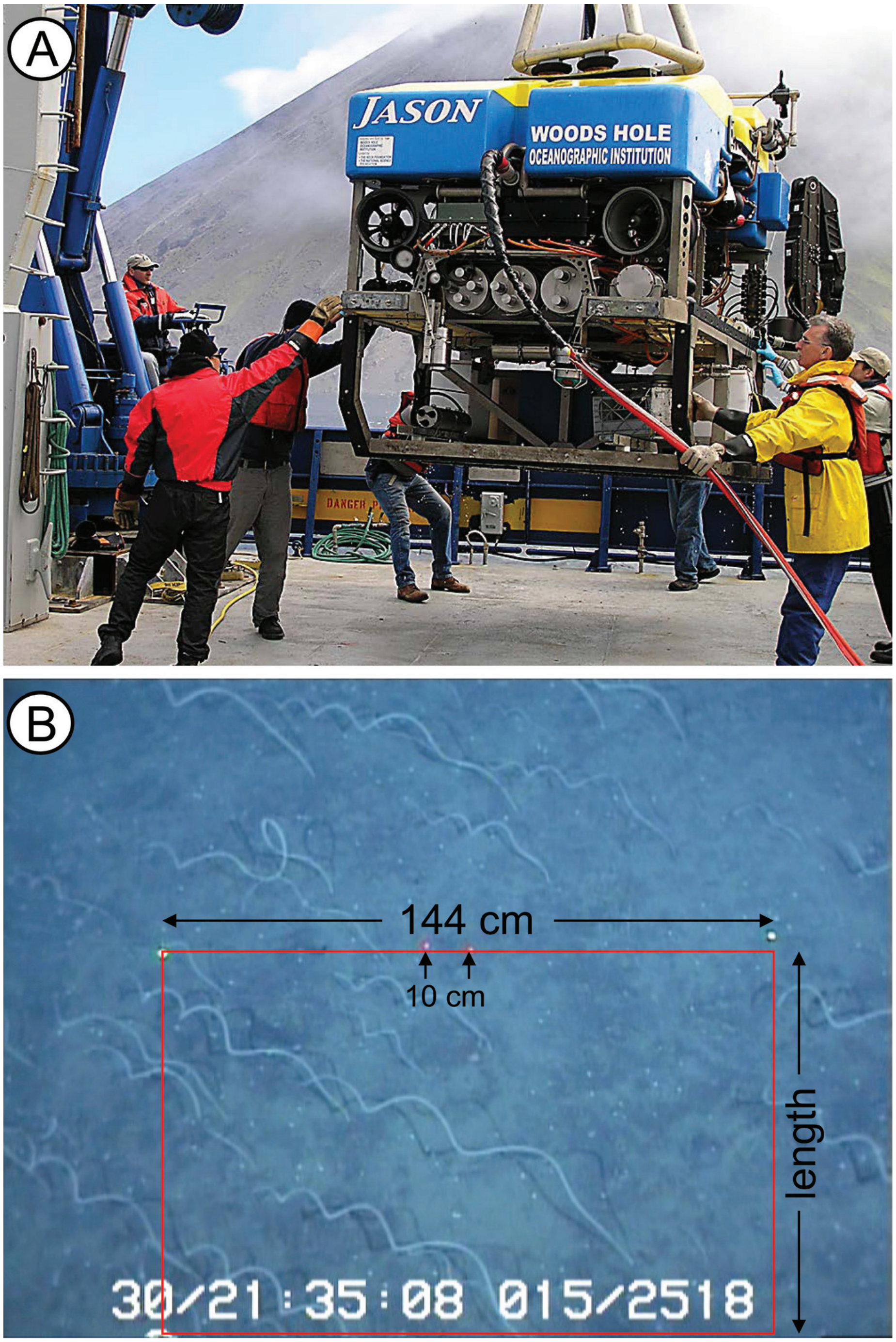

Figure 5

(**A**) The remotely operated vehicle (ROV) *Jason II* was used to examine coral habitat at depths between 170 m and 2947 m in 2004 (NOAA photo by Sean Rooney). (**B**) A frame sampled from video footage collected with the *Jason II*. The 2 green laser marks (round marks near ends of horizontal black arrows) provide a fixed-width transect of 144 cm and the 2 red laser marks (round marks at end of short, vertical black arrows) provide a 10-cm scaling tool for the measurement of small fauna. The lengths of sampled video frames were variable and dependent on the altitude of the ROV. This video frame, collected at a depth of 2518 m, contains 13 *Radicipes verrilli*, a chrysogorgiid gorgonian.

Table 1

Sampling effort for surveys conducted on 29 transects with the submersible *Delta* in 2003 and 2004 and the remotely operated vehicle *Jason II* in 2004 in the central Aleutian Islands of Alaska. Transects were sampled at rates between 10% and 100%. Total area is the extrapolated area of each transect on the seafloor on the basis of the sampling rate.

Transect	Depth range (m)	Transect length (m)	Sampling rate (%)	Area sampled (m^2)	Total area (m^2)
Delta 5985	103–122	564	100	605	605
Delta 5986	102–104	557	100	510	510
Delta 5987	113–113	549	100	572	572
Delta 5988	70–351	635	100	1072	1072
Delta 5991	63–359	770	100	1429	1429
Delta 5993*	99–295	2075	100/50	2753	3917
Delta 5994	101–130	440 (×2)	50	685	1371
Delta 5996	110–341	128 (×10)	10	220	2204
Delta 5997	95–354	930 (×2)	50	1262	2523
Delta 6000	117–361	43 (×10)	10	97	968
Delta 6001	199–300	101 (×10)	10	162	1625
Delta 6002	235–318	95 (×10)	10	134	1345
Delta 6003	85–106	70 (×10)	10	79	787
Delta 6006	91–358	54 (×10)	10	91	911
Delta 6010	122–131	440 (×2)	50	436	871
Delta 6011	175–345	964 (×2)	50	1489	2978
Delta 6207	300–316	598 (×2)	50	857	1715
Delta 6208	152–162	798 (×2)	50	1096	2193
Delta 6209	52–108	201 (×10)	10	435	4350
Delta 6213	116–273	28 (×10)	10	61	606
Delta 6216	115–272	112 (×10)	10	179	1794
Delta 6217	100–330	68 (×10)	10	112	1124
Jason II 096	2153–2947	10,500	100	15,161	15,161
Jason II 097	1225–1734	1498 (×2)	50	2149	4298
Jason II 099	1270–2528	2245 (×2)	50	3241	6482
Jason II 102	170–1843	3409 (×2)	50	4899	9799
Jason II 103	399–1349	958 (×2)	50	1357	2713
Jason II 106A	361–1346	2359 (×2)	50	3384	6768
Jason II 107	697–1570	3118	100	4457	4457
Totals	52–2947	57,041	10–100	48,985	85,148

*Sampled at 100% and then 50%; length = 813.4 + (630.6×2) = 2074.6; area = 1590 + (1163.4×2) = 3917.

Seafloor roughness was visually estimated and was recorded on a 5-point scale as follows: 1) very low (e.g., smooth), 2) low (e.g., sand with a few small cobbles), 3) moderate (e.g., approximately one-third of the seafloor not smooth), 4) high (e.g., approximately two-thirds of the seafloor not smooth), and 5) very high (e.g., highly jagged substrate with no smooth areas). Slope was visually estimated and was recorded on a 4-point scale as follows: 1) no slope or slope of <1°, 2) low or <10°, 3) medium or 10–30°, and 4) high or >30°. Slope was measured at the scale of the surrounding area (i.e., hundreds of square meters), whereas roughness was measured at the scale of the frame (i.e., less than about 10 square meters). Roughness accounted for the abiotic component of vertical structure on the seafloor, and vertical relief accounted for the biotic component of vertical structure on the seafloor. Vertical relief was visually estimated and was recorded on a 3-point scale as follows: 1) low or <15 cm, 2) medium or 15–29 cm, and 3) high or >30 cm.

Percent cover of biota was recorded as zero and then in 10% increments thereafter. Vertical relief and percent cover were measured separately for corals, sponges, and "other" emergent epifauna. Other emergent epifauna included sedentary, structure-providing invertebrates, namely hydroids, actiniarians, bryozoans, tunicates, and corallimorpharians. Crinoids and nonerrant holothurians (e.g., *Psolus* spp.), although not truly sedentary, were also included in this group. Substratum texture was determined on the basis of the Wentworth grade classification (Holme and McIntyre, 1971) and was recorded on a hierarchal 4-point scale. Siltstone and hexactinellid sponge skeletons also were included in the classification of substratum texture. In addition, in situ observations recorded by the observer (*Delta* only) were used when classifying seafloor roughness, slope, vertical relief and percent cover of emergent epifauna, and surficial substrate texture.

Corals and sponges were enumerated individually within sampled video frames (sponges were not enumerated on *Delta* dives) if their bases (e.g., physa, mat, stalk, or stolon) were within the boundaries of the video frame. Numbers of corals and sponges were standardized by area for comparability and reported as densities. Specifically, densities were computed as the total number of animals divided by the total area sampled. Densities stratified by depth were computed the same way: the sum of the numbers of animals observed in all frames recorded at a particular depth range was divided by the total area sampled at that depth range (sum of the frame areas).

Corals were identified to the lowest possible taxon (see Appendix II). Morphologically similar corals that could not be definitively identified were grouped at higher taxonomic levels. *Arthrogorgia* spp. included *A. utinomii*, *A. kinoshitai*, and *A. otsukai*. *Fanellia* spp. included *F. fraseri* and *F. compressa*. *Plumarella* spp. included *P. profunda*, *P. hapala*, *P. aleutiana*, *P. superba*, *P. nuttingi*, *P. echinata*, *P. robusta*, and *P. spicata*. *Thouarella* spp. included *T. cristata* and *T. trilineata*. Sponges were identified to class and recorded as either a hexactinellid or as a member of a single group, referred to hereafter as demosponges, that combined demosponges and calcareous sponges (see Stone et al. [2011] for a pictorial guide of the sponges enumerated in this study). Damaged corals and sponges also were noted, except in 2 taxa. The ultra-fine structure of *Radicipes verrilli* and the unknown structure of Gorgonacea (unidentified) precluded reliable determination of the incidence of damage to those taxa. Fishes, crabs, and octopods were counted if their presence on the transect did not appear to be in response to the submersible or ROV (Buckland et al., 1993), and they were counted in the first frame in which any portion of their body was present. Video was frequently viewed from all available cameras to track an individual's movement and prevent duplicate counting in subsequent frames.

Fish species enumerated on transects (see Appendix III) included Pacific Cod (*Gadus macrocephalus*), Sablefish (*Anoplopoma fimbria*), righteye flounders (Pleuronectidae), skates (Rajidae), sculpins (Cottidae and Psychrolutidae), Shortspine Thornyhead (*Sebastolobus alascanus*), Atka Mackerel (*Pleurogrammus monopterygius*), Pacific Ocean Perch (*Sebastes alutus*), Blackspotted Rockfish (*S. melanostictus*), Shortraker Rockfish (*S. borealis*), Sharpchin Rockfish (*S. zacentrus*), Northern Rockfish (*S. polyspinis*), Light Dusky Rockfish (*S. variabilis*), Prowfish (*Zaprora silenus*), eelpouts (Zoarcidae), lanternfishes (Myctophidae), snailfishes (Liparidae), pricklebacks (Stichaeidae), poachers (Agonidae), and ronquils (Bathymasteridae).

Righteye flounders included Pacific Halibut (*Hippoglossus stenolepis*), Greenland Halibut (*Reinhardtius hippoglossoides*), Flathead Sole (*Hippoglossoides elassodon*), Arrowtooth Flounder (*Atheresthes stomias*), Dover Sole (*Microstomus pacificus*), Rex Sole (*Glyptocephalus zachirus*), and Deepsea Sole (*Embassichthys bathybius*). Sculpins included numerous species, most notably the Yellow Irish Lord (*Hemilepidotus jordani*), and Darkfin Sculpin (*Malacocottus zonurus*). Righteye flounders and rockfishes were further classified as juveniles if a fish's total length was <20 cm. Most rockfish species attain sexual maturity at a size >20 cm (Love et al., 2002). Hereafter, as a matter of notational convenience, "taxon" and "taxa" include the juvenile life-history classes of pleuronectids and rockfishes as categories separate from adults of the same groups.

Crab species enumerated on transects (see Appendix III) included golden king crab (*Lithodes aequispinus*), southern Tanner crab (*Chionoecetes bairdi*), and hair crab (*Erimacrus isenbeckii*). Octopod species enumerated on transects (see Appendix III) included the North Pacific giant octopus (*Enteroctopus dofleini*) and several rare deepwater species, most notably *Graneledone boreopacifica*, *Cirrothauma* cf. *murrayi*, *Opisthoteuthis* sp., and *Grimpoteuthis* sp.

Several deepwater species that currently are not of local commercial importance or not listed in a fishery management plan also were enumerated on transects because they may be commercially targeted in the future. These species included grenadiers (Macrouridae), the Pacific Flatnose (*Antimora microlepis*), the Longnose Tapirfish (*Polyacanthonotus challengeri*), deep-sea lithodid crabs, a spiny *Paralomis* crab (*Paralomis multispina*), Verrill's *Paralomis* crab (*P. verrilli*), and deep-sea Tanner crabs. Grenadiers included at least 3 species: Giant Grenadier (*Coryphaenoides pectoralis*), Popeye Grenadier (*C. cinereus*), and Pacific Grenadier (*C. acrolepis*). Deep-sea lithodid crabs included the scarlet king crab (*Lithodes couesi*) and one unknown species. Deep-sea Tanner crabs included both the triangle (*Chionoecetes angulatus)* and grooved (*C. tanneri*) Tanner crabs.

Species richness (number of unique taxa) was calculated for corals and sponges for each 100-m depth strata surveyed in this study. The depth range for each taxon in the study area was determined on the basis of published records, archived museum specimens, specimens collected during this study, and confirmed identifications made during detailed examination of video collected during this study. Note that corals and sponges routinely enumerated from video footage were typically identified to higher taxonomic groupings that precluded calculation of species diversity indices and associated community analyses.

To determine fine-scale (i.e., within a sampled video frame) associations of fishes, crabs, and octopods with emergent epifauna, the frequency at which a particular species was found in the same sampled frame (mean frame size equaled 1.5 m^2) with each epifauna group was calculated. This measure of association, however, did not necessarily take into account the abundance or availability of a particular habitat type (i.e., emergent epifauna). Auster (2005) proposed that examination of fish distribution in relation to all available habitats is one method for assessment of the essential role of emergent epifauna. Accordingly, a second method (odds ratios) was used to assess the role of emergent epifauna through examination of whether a species used a particular habitat type more frequently than would be expected on the basis of that habitat's overall availability (Rice, 1995; Valencia et al., 2005). An individual was considered to be actively associating with corals, for example, if it was found more frequently in video frames with corals than would be expected given the number of frames with corals present. Because corals, sponges, and other emergent epifauna are not uniformly distributed with depth, only those video frames collected within the observed depth range of each fish, crab, or octopod taxa were considered for this second method.

The odds of event *A* occurring was defined with this equation:

$$\mathrm{odds}(A) = \frac{P(A)}{1 - P(A)}, \qquad 1)$$

where *P(A)* is the probability of the event occurring. The odds ratio is then defined with this equation:

$$\Delta = \frac{\mathrm{odds}(S \mid E)}{\mathrm{odds}(S \mid \bar{E})}, \qquad 2)$$

where *E*, in this study, represents the event that an emergent epifauna group is present in the frame, $\bar{E}$ is the complementary event, and *S* represents the event that a particular species is present in the frame. Odds ratios were calculated with the software program S-Plus, vers. 7 (Insightful Corp., now TIBCO Spotfire, Somerville, MA) for pairwise species and emergent epifauna groups. Frames were classified to a 2-way contingency table with rows (or columns) representing the presence or absence of an emergent epifauna group and the columns (or rows) representing the presence or absence of a particular species. To measure the uncertainty of the estimated odds ratios, 10,000 boot strappings were calculated, assuming table cell numbers were multinomially distributed with probabilities calculated from the observed numbers of frames classified to the 4 table cells (Rice, 1995).

Results

In 2003 and 2004, 57 dives were completed with the submersible *Delta*. Those dives, ranging in depth from 52 to 369 m, included 45 dives on transects and 12 dives made specifically to collect biological specimens (Appendix I). Video data were processed for 22 of the 45 transect dives (Table 1). Ranging in depth from 129 to 2947 m, 14 dives were completed with the ROV *Jason II* in 2004. Video data were processed for 7 of those dives (Table 1). In total, 33,719 frames of video collected on 29 transects were processed. The area sampled within frames totaled 48,985 m^2 and was distributed along 57,041 m of seafloor (Table 1). The remaining dives were not quantitatively analyzed because of funding limitations, but the dives that were processed were carefully selected to cover the entire study area both geographically and bathymetrically and to provide a balanced design with respect to the spatial distribution of geological factors within the overall study site.

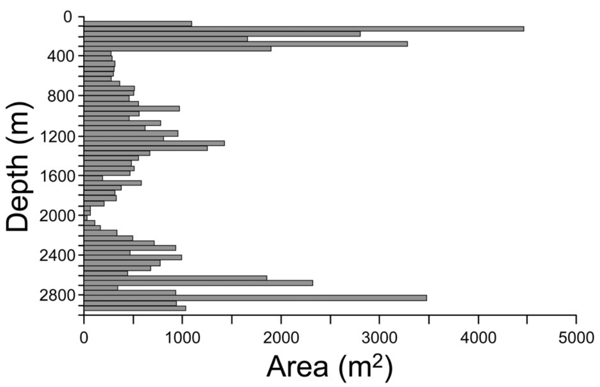

Figure 6

Area of seafloor per depth strata (50-m) within frames sampled (*n*=33,719) from video collected along 29 transects with the submersible *Delta* and remotely operated vehicle *Jason II* in 2003 and 2004 in the central Aleutian Islands.

Sampling effort (the number of video frames sampled) spanned the entire depth range of all transects surveyed, but most sampling effort was completed at depths of 100–350 m, where the majority of the *Delta* dives were conducted (Fig. 6). Other areas of high sampling effort were at depths of 2600 and 2850 m, where vast areas of relatively flat seafloor were traversed with the *Jason II* (Fig. 6). Sampling effort was not equally distributed with respect to substrate type (Appendix IV), with the majority of effort occurring in habitats dominated by sand (59.8%) and silt (27.6%). The seafloor within the sampled video frames was generally a heterogeneous mixture of substrate types and typically not a homogeneous mixture of a single sediment type (36.6% of total frames) with the exception of silt and sand. Bedrock and boulder were the sole sediment type within only 0.8% of the sampled frames combined.

Sampling effort also was not distributed uniformly with respect to seafloor roughness, with the majority of the total habitat sampled in areas of very low (38%) and low (51%) roughness and very little habitat categorized

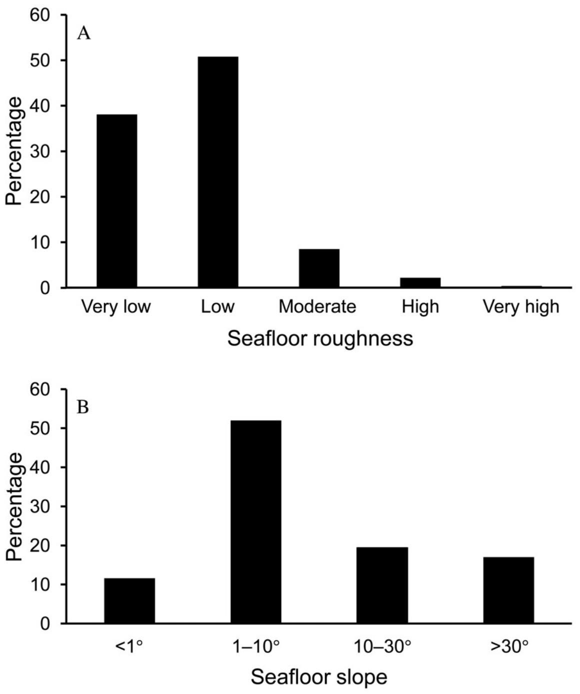

Figure 7

Seafloor (**A**) roughness and (**B**) slope observed in frames sampled (*n*=33,719) from video collected along 29 transects with the submersible *Delta* and remotely operated vehicle *Jason II* in 2003 and 2004 in the central Aleutian Islands. Data are presented as a percentage of the total area sampled.

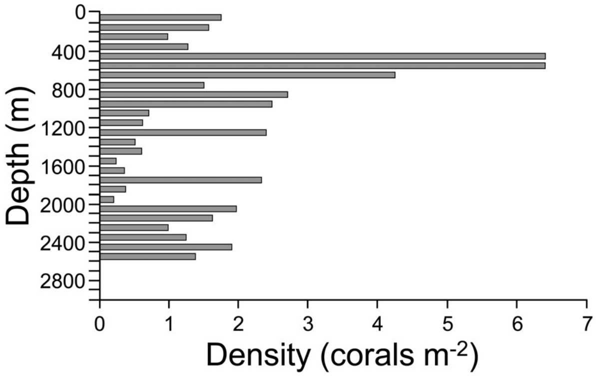

Figure 8

Absolute density of corals (corals m^{-2}) per depth strata (100-m) observed in analysis of video collected along transects with the submersible *Delta* and remotely operated vehicle *Jason II* in 2003 and 2004 in the central Aleutian Islands. Corals were observed at depths below 2600 m, but at densities (<0.03 m^2) that cannot be shown in the scale of this figure.

as moderate (8.5%), high (2.2%), and very high (0.4%) roughness (Fig. 7A). Sampling effort was distributed more uniformly, however, with respect to seafloor slope (Fig. 7B). Of the sampled habitat, 52% occurred in areas with low (<10°) slope and 12% in areas with no slope, but 20% were in habitats with medium (10–30°) slope and 17% in habitats of high (>30°) slope.

Corals

Within sampled video frames, 59,522 corals comprising 7 major taxonomic groups were observed at an overall (i.e., over the entire study area) density of 1.22 corals m^{-2} (59,522 corals / 48,985 m^2) (Table 2). Gorgonians were the most abundant of the corals (52.5% of the total number of corals observed), followed by scleractinians (17.2%), hydrocorals (16.0%), pennatulaceans (11.9%), alcyonaceans (2.0%), stoloniferans (0.2%), and antipatharians (0.1%). Corals were observed on all transects, spanning depths between 52 and 2930 m (Table 2). Corals were most dense at depths of 400–700 m, where they were found at densities of more than 4 corals m^{-2} and up to 6.4 corals m^{-2} (Fig. 8 and Table 3). Other high-density areas were located at depths of 1200–1300 m (dense patches of scleractinians), 1700–1800 m (almost exclusively groves of pennatulaceans), and 2000–2600 m (almost exclusively fields of the gorgonian *Radicipes verrilli*) (Fig. 8 and Table 3). Most major taxonomic groups with the exception of stoloniferans spanned a broad depth range, although distribution within groups differed for individual species.

Gorgonians were the most common (97% of transects) taxa and had the second broadest depth distribution (52–2599 m). Many gorgonian taxa were observed over a broad depth range (e.g., bubble gum coral [*Paragorgia arborea*]), but a few of them, such as *R. verrilli* and *Acanthogorgia* sp., were restricted to deeper water (Table 2). In contrast, several species, such as *Cryogorgea koolsae* and *Calcigorgia spiculifera*, were restricted to shallow water (Table 2). The broad depth distribution exhibited by *Arthrogorgia* spp., *Plumarella* spp., and *Thouarella* spp. likely indicates that the multiple species lumped within those taxonomic categories have disparate depth ranges. *Plumarella* spp. (*n*=10,173) and *Thouarella* spp. (*n*=5325) were the first and third most common taxa and contained at least 8 species and 2 species, respectively (Cairns, 2011), few of which could be distinguished from congeners in the video footage. The chrysogorgiid *R. verrilli* was the most abundant deepwater gorgonian, forming dense fields in areas of unconsolidated soft sediment (silt, sand, or pebbles) at depths >2083 m (this species was observed as shallow as 1612 m off transect). Bamboo corals (Family Isididae) were locally common at depths between 392 and1634 m (but observed as deep as 2826 m off transect) and included *Isidella tentaculum* and at

Table 2

Total number, frequency of occurrence (proportion of transects), and depth range of corals observed on 29 transects surveyed through collection of video with the submersible *Delta* in 2003 and 2004 and the remotely operated vehicle *Jason II* in 2004 in the central Aleutian Islands of Alaska. Number of corals is not standardized by sampling effort. Totals include damaged corals. Depth range observed on all video collected in this study (i.e., including footage not quantitatively analyzed) is noted in parentheses if it differs from range of transect observations.

Taxon	Number	Frequency	Depth range
Class Anthozoa			
Order Scleractinia (stony corals)	10,235	22/29	56–1675 (2301)
Order Antipatharia (black corals)	87	6/29	(436) 464–1715 (2828)
Subclass Octocorallia, Order Alcyonacea (true soft corals)	1165	20/29	52–2564 (2828)
Anthomastus spp.	950	14/29	85–2040
Anthothela cf. *grandiflora*	204	13/29	52–352
Nephtheidae	11	3/29	(804) 1005–2564 (2829)
Suborder Stolonifera (stoloniferans)	114	5/29	116–591
Clavularia sp.	114	5/29	116–591
Order Gorgonacea (gorgonians)	31,304	28/29	52–2599 (2852)
Acanthogorgia sp.	40	5/29	(1092) 1130–2087
Alaskagorgia aleutiana	231	10/29	91–614
Arthrogorgia spp.	1983	11/29	99–1348
Calcigorgia beringi	63	4/29	(92) 898–1390 (1512)
Calcigorgia spiculifera	457	12/29	(50) 70–512
Cryogorgia koolsae	96	6/29	52–218
Fanellia spp.	1295	17/29	(74) 94–1174 (1341)
Gorgonacea (unidentified)	1513	13/29	102–2210
Isididae	2625	5/29	392–1634 (2826)
Muriceides nigra	795	13/29	99–930 (1195)
Paragorgia arborea	178	8/29	95–1326 (2022)
Plumarella spp.	10,173	23/29	52–2392 (2846)
Primnoa pacifica	23	1/29	(308) 493–899
Primnoa wingi	24	1/29	(354) 414–899 (1280)
Radicipes verrilli	6004	2/29	(1612) 2083–2599 (2852)
Swiftia sp.	148	1/29	274–342
Swiftia pacifica	331	5/29	513–1582
Thouarella spp.	5325	20/29	95–1249 (1267)
Order Pennatulacea (sea pens)	7083	16/29	63–2930 (2947)
Anthoptilum grandiflorum	866	1/29	2153–2397 (2511)
Halipteris willemoesi	1282	4/29	102–133
Halipteris sp. A	435	6/29	284–1381
Halipteris sp. B	3305	2/29	1667–2707
Pennatulidae (unidentified species)	122	1/29	2239–2930
Ptilosarcus gurneyi	996	7/29	63–162 (195)
Umbellula lindahli	77	1/29	2546–2909 (2947)
Class Hydrozoa			
Order Anthoathecatae (hydrocorals)	9534	19/29	94–2223
All corals	59,522	29/29	52–2930 (2947)

least one species of *Keratoisis*. *Isidella tentaculum*, with its characteristic "sweeper tentacles," was observed over a broader depth range (604–1468 m) than the range reported for this species on seamounts in the Gulf of Alaska (720–1050 m) by Etnoyer (2008). Gorgonians were most abundant at depths of 400–1000 m, 2000–2200 m, and 2400–2600 m (Table 3).

Scleractinians were the second most common (76% of transects) taxa and were observed at depths between 56 and 1675 m on transects (Table 2). Scleractinians formed dense patches (up to 278 corals m^{-2}) in some areas, particularly at depths of 400–600 m and 1200–1300 m (Table 3), but they generally provided little vertical structure to the seafloor because of their small size. Scleractinians included *Javania borealis*, *Balanophyllia elegans*, *Caryophyllia alaskensis*, and *C. arnoldi*, but all were indistinguishable on video footage and consequently were lumped into a single category.

Hydrocorals (Order Anthoathecatae) were observed on 66% of the transects at depths between 94 and 2223 m (Table 2) and were most abundant at depths between 400 and 1000 m (Table 3). Hydrocorals were

Table 3

Absolute density (corals m^{-2}) of 5 major groups of corals stratified by depth strata (100 m) along transects surveyed with the submersible *Delta* and remotely operated vehicle *Jason II* in 2003 and 2004. Values for all corals include antipatharians and stoloniferans.

Depth strata (m)	All corals	Scleractinians	Alcyonaceans	Gorgonians	Pennatulaceans	Hydrocorals
0–99	1.81	0.33	0.17	0.43	0.80	0.09
100–199	1.60	0.33	0.07	0.92	0.19	0.09
200–299	0.93	0.10	0.01	0.65	0	0.17
300–399	1.10	0.04	0.06	0.88	0.01	0.11
400–499	6.40	1.25	0.08	3.15	0.02	1.90
500–599	6.36	0.92	0.04	3.72	0.03	1.65
600–699	4.24	0.52	0.01	2.11	0.03	1.58
700–799	1.55	0.05	0	0.82	0.02	0.66
800–899	2.71	0.19	0.01	1.77	0.04	0.70
900–999	2.48	0.42	0.05	1.33	0.06	0.62
1000–1099	0.70	0.03	0	0.55	0.04	0.07
1100–1199	0.68	0.14	0	0.34	0.05	0.15
1200–1299	2.38	1.76	0.05	0.26	0.03	0.28
1300–1399	0.52	0.02	0.01	0.14	0.01	0.35
1400–1499	0.61	0.03	0.01	0.06	0	0.51
1500–1599	0.21	0.09	0	0.03	0	0.09
1600–1699	0.35	0.01	0	0.05	0.27	0.02
1700–1799	2.34	0	0	0.04	2.29	0.01
1800–1899	0.37	0	0	0.02	0.29	0.07
1900–1999	0.18	0	0	0.06	0	0.12
2000–2099	1.96	0	0.04	1.79	0	0.13
2100–2199	1.65	0	0	1.27	0.36	0.02
2200–2299	1.00	0	0	0.22	0.78	0
2300–2399	1.26	0	0	0.50	0.76	0
2400–2499	1.92	0	0	1.90	0.02	0
2500–2599	1.39	0	0	1.38	0.01	0
2600–2699	0.01	0	0	0	0.01	0
2700–2799	0.02	0	0	0	0.02	0
2800–2899	0.03	0	0	0	0.03	0
2900–2947	0	0	0	0	0	0
56–2947	1.22	0.20	0.02	0.63	0.14	0.19

lumped into a single category because most typically could not be identified to species from the video footage. Examination of close-up video footage collected occasionally with the *Jason II* science camera, however, did provide for definitive identifications and, when used in conjunction with examination of collected specimens, allowed for determination of the maximum depth for some taxa: *Distichopora borealis* (1361 m), *Cyclohelia lamellata* (691 m), *Errinopora nanneca* (190 m), *E. zarhyncha* (1520 m), *Crypthelia trophostega* (1503 m), *Stylaster campylecus* (1260 m), *S. alaskanus* (2124 m), and at least one other species of *Stylaster* (2223 m).

Pennatulaceans, although locally abundant, were found on only 55% of the transects (Table 2) and were most abundant at depths of 56–100 m, 1700–1800 m, and 2200–2400 m (Table 3). Pennatulaceans are the only corals that do not attach to hard substrate; instead, they anchor into soft sediments. Consequently, they are generally limited to habitats with unconsolidated, soft sediment. They were distributed over the broadest depth range of all coral groups (Table 2), however, and were represented by 2 strictly shallow-water species (*Halipteris willemoesi* and *Ptilosarcus gurneyi*) and several strictly bathyal species (*Anthoptilum grandiflorum*, *Umbellula lindahli*, *Halipteris* sp. B, and an unidentified small, white sea pen). In contrast, an unidentified species (*Halipteris* sp. A), possibly *H. californica*, had one of the broadest depth ranges of any single coral observed in this study (284–1381 m).

Alcyonaceans, or true soft corals, were observed on 69% of the transects at depths between 52 and 2564 m (Table 2) and were not found at high densities at any depth over that range (Table 3). This group was represented by a shallow-water species (*Anthothela* cf. *grandiflora*), a deepwater species (a large unidentified nephtheid), and several species of *Anthomastus* that occurred over a broad depth range (Table 2). A single species of stoloniferan coral (*Clavularia* sp.) was observed on 5 transects at depths between 116 and 591 m (Table

Table 4

Density and species richness (number of taxa) of corals per primary substrate type within frames sampled (*n*=33,719) from video collected along transects with the submersible *Delta* and the remotely operated vehicle *Jason II* in 2003 and 2004. Density is calculated as the number of corals for all frames sampled per substrate type. Substrate types were reduced to the primary sediment type for this calculation.

Substrate	Area (m^2)	Corals (number)	Density	Taxa (number)
Bedrock	3107	18,262	5.88	25
Siltstone	357	35	0.10	6
Hexactinellid	211	674	3.19	14
Boulder	779	2217	2.85	21
Cobble	695	2567	3.69	17
Pebble	1000	2196	2.20	17
Sand	29,302	30,268	1.03	29
Silt	13,510	3680	0.27	22
Shell	24	4	0.17	3

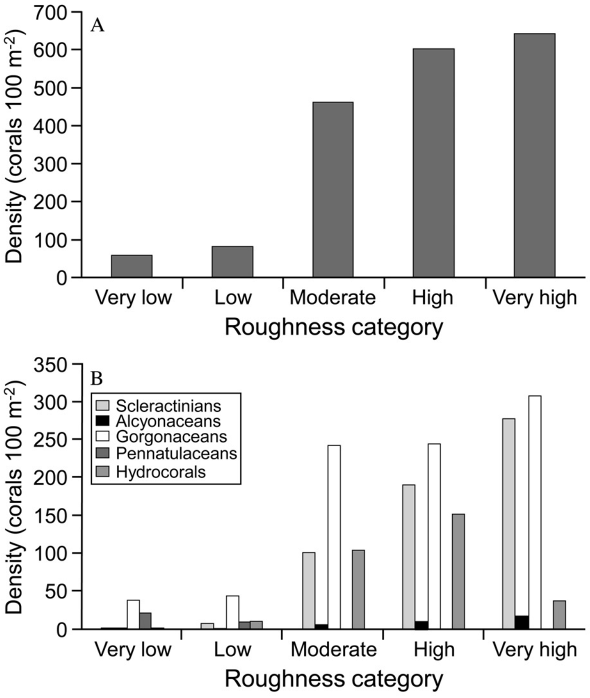

Figure 9

Absolute density (**A**) of all corals combined and (**B**) of 5 major taxa of corals per roughness category observed in frames sampled (*n*=33,719) from video collected along 29 transects with the submersible *Delta* and remotely operated vehicle *Jason II* in 2003 and 2004 in the central Aleutian Islands. Seafloor roughness was visually estimated and categorized into 5 hierarchal groups from very low to very high.

2). Antipatharians (black corals) were observed on only 6 transects and at depths between 464 and 1715 m (Table 2). They were represented by at least 2 species, including *Dendrobathypathes boutillieri* (depth range=859–2161 m) and *Parantipathes* sp. (depth range=690–1562 m). A single specimen of *Trissopathes pseudotristicha* was collected at a depth of 2828 m, but others were observed off transects as shallow as 2306 m.

Corals were found at fairly high densities in habitats dominated by all substrate types, but they were not distributed equally with substrate type (Table 4). Habitats dominated by bedrock, cobbles, and hexactinellid skeletons supported the highest densities of corals, while sand, silt, shell, and siltstone habitats supported the lowest densities (Table 4). Siltstone supported low densities of corals but was an important attachment substrate in deeper areas (depths >1000 m) that often lacked other exposed, consolidated substrates (e.g., bedrock and cobbles). Sand and bedrock habitats supported the highest number of coral taxa (Table 4). The high species richness observed in sand habitat was likely in part a result of the high rate at which this habitat was sampled (e.g., almost 8 times more sand than bedrock habitat was sampled) and the regular presence of minor substrates important for coral attachment.

The density of corals was lowest in areas where the seafloor was unstructured (i.e., lowest roughness) and increased steadily in density as the seafloor became rougher (Fig. 9A). There was a marked increase in coral density between areas with a seafloor roughness of 2 (low) and areas with a seafloor roughness of 3 (medium) on the 5-point scale. In general, most corals were more abundant in areas where the seafloor was rough; the exceptions were pennatulaceans, which were more abundant in areas with a smooth seafloor (Fig. 9B). Hydrocorals had the highest density in rough and moderately rough habitats but lower densities in very rough habitat (Fig. 9B).

The density of corals was lowest in areas where the seafloor was flat and increased as the seafloor became more sloped (Fig. 10A). The highest densities of corals were found where the seafloor slope was medium, or between 10° and 30° (Fig. 10A). In general, most corals were more abundant in areas where the seafloor was more steeply sloped, except pennatulaceans, which were found in all areas but were more common where there was essentially no slope (<1°), and alcyonaceans, which seemed to be equally abundant in all areas with regard to the slope of the seafloor (Fig. 10B).

Sponges

Demosponges (*n*=15,866) were almost 6 times more abundant than were hexactinellid sponges (*n*=2708) in the frames sampled with the *Jason II* (*n*=24,178). Demosponges were observed to a depth of 2911 m but were

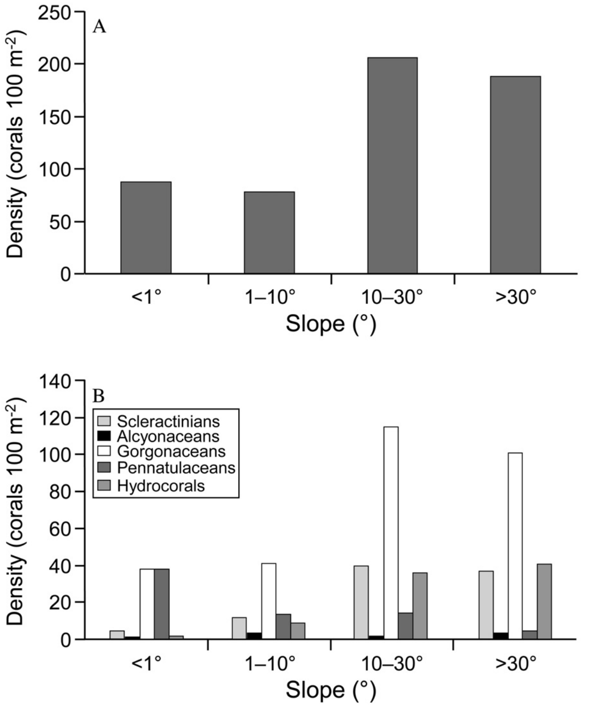

Figure 10

Absolute density of (**A**) all corals combined and (**B**) of 7 major taxa of corals per slope category observed in frames sampled (n=33,719) from video collected along 29 transects with the submersible *Delta* and remotely operated vehicle *Jason II* in 2003 and 2004 in the central Aleutian Islands. Seafloor slope was visually estimated and categorized into 4 hierarchal groups.

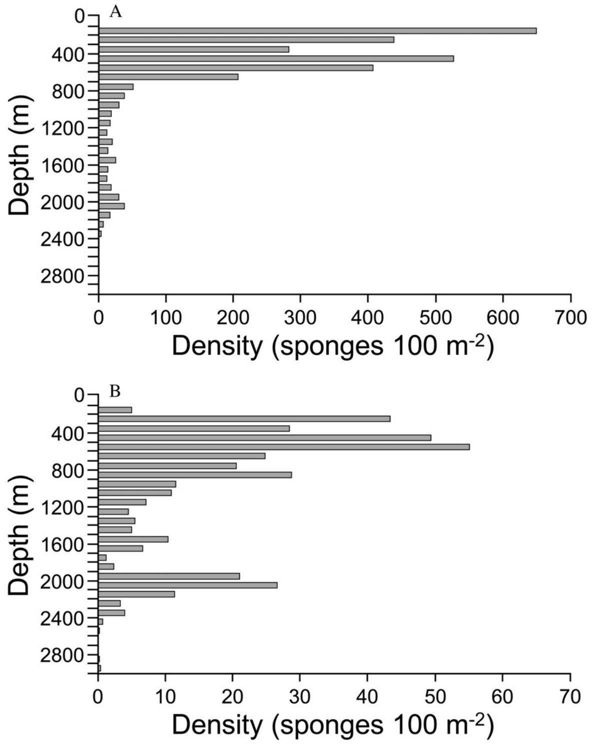

Figure 11

Absolute density of (**A**) demosponges and (**B**) hexactinellid sponges (sponges 100 m^{-2}) per depth strata (100-m) observed in analysis of video collected along transects with the remotely operated vehicle *Jason II* in 2004 in the central Aleutian Islands.

not distributed uniformly with depth (Fig. 11A). Demosponge density was highest at depths <700 m, particularly between 100 and 300 m and between 400 and 600 m (Fig. 11A). A few small areas of higher density observed at depths of 1900–2100 m were dominated principally by 3 carnivorous species: *Chondrocladia concrescens*, *Cladorhiza bathycrinoides*, and *Cladorhiza corona*. Hexactinellid sponges were observed to a depth of 2947 m and were most abundant at depths of 200–900 m and 1900–2200 m (Fig. 11B). Sponges in deeper water generally were restricted to exposed bedrock and siltstone in habitats with steep canyon walls. In general, hexactinellid sponges had a broader depth distribution than did demosponges, and a higher percentage of total individuals (34.7% compared to 13.9%) was found at depths >1000 m.

Vertical relief and coverage of emergent epifauna

Almost 49% of the video frames sampled contained emergent epifauna. Corals were present in 10,768 of the sampled frames (31.9% of total) and provided more vertical relief to the seafloor than did either sponges or other emergent epifauna (Fig. 12). Of those frames, 52% contained corals with vertical relief ≤15 cm, 23% had corals between 15 and 29 cm high, and 25% contained corals ≥30 cm in height (Fig. 12). Sponges were present in 11,073 of the frames sampled (32.8% of total). The majority of those frames contained sponges with vertical relief ≤15 cm (85%), but only 4% contained sponges ≥30 cm in height (Fig. 12). Other emergent epifauna were present in only 8555 of the frames sampled (25.4% of total). Only 8% of those frames contained sedentary invertebrates that provided relief >15 cm above the seafloor (Fig. 12).

In contrast to the difference in vertical relief between the 2 groups, sponges provided more coverage of the seafloor than did corals (Table 5). Sponges covered >10% of the seafloor in more than 7% of the sampled video frames; however, only 2.2% and 2.7% of the seafloor was covered similarly by corals and other emergent epifauna, respectively (Table 5). In terms of biotic

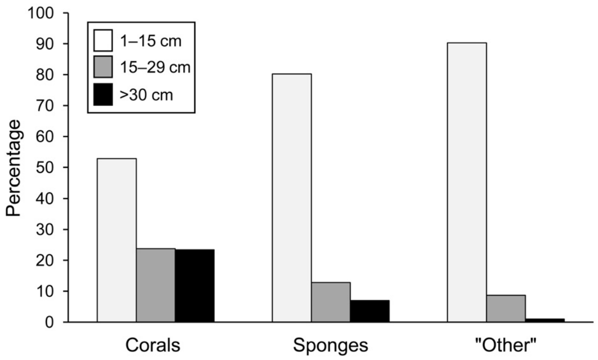

Figure 12

Vertical relief of corals, sponges, and "other" emergent epifauna observed in frames sampled (*n*=33,719) from video collected along 29 transects with the submersible *Delta* and remotely operated vehicle *Jason II* in 2003 and 2004 in the central Aleutian Islands. Data are presented as a percentage of the total area sampled within frames where corals (*n*=10,768), sponges (*n*=11,073), and "other" emergent epifauna (*n*=8555) were present.

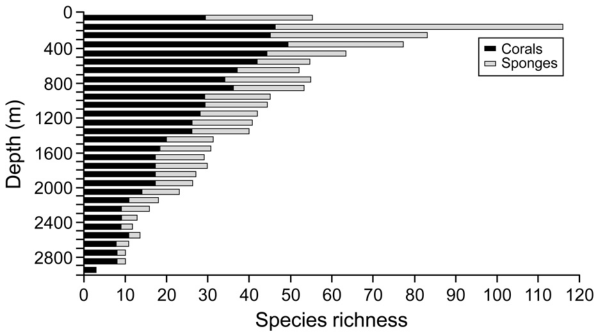

Figure 13

Species richness (number of species) of corals and sponges per depth strata (100-m) derived from the total depth range of published records, archived museum specimens, specimens collected during this study, and detailed analysis of video collected as part of this study with the submersible *Delta* and remotely operated vehicle *Jason II* in 2003 and 2004 in the central Aleutian Islands.

coverage of the seafloor, other emergent epifauna were the least important group with almost 72% of sampled frames containing no other emergent epifauna. Collectively, sedentary invertebrates—all 3 groups, corals, sponges, and other emergent epifauna—covered >10% of the seafloor in 32.5% of sampled frames but covered >50% of the seafloor in only about 3% of sampled frames (Table 5).

All 3 groups of invertebrates provide important biotic coverage of the seafloor, but the abundance and relative contribution of each group differed with respect to depth. Corals generally were present in more than 40% of the sampled frames collected at depths shallower than 1000 m, with isolated patches of high coverage below about 1250 m. Few frames contained corals that provided substantial coverage of the seafloor at depths between 1250 and 1650 m. More frames at depths between 1650 and 2500 m contained some corals (mostly *Radicipes verrilli* and the pennatulaceans *Anthoptilum grandiflorum* and *Halipteris* sp. B) that provided substantial vertical structure but little horizontal coverage of the seafloor. However, we observed that these corals served as important obstacles that accumulated drifting debris (e.g., macroalgae and dying jellyfish) that in turn served as a source of habitat or forage to other biota. Most sampled frames collected at depths below 2550 m contained few corals that provided coverage of the seafloor.

Sponges were generally present in more than 50% of sampled frames collected at depths <1050 m, with more than 10% of sampled frames collected below 650 m containing >10% cover of sponges. Sponges were less important as providers of seafloor coverage below a depth of about 1050 m, with isolated patches of higher coverage between 1900 and 2150 m. These deeper patches were attributable mostly to a few species of hexactinellids (principally *Farrea* spp.). Other emergent epifauna were most important in providing coverage of the seafloor at depths <100 m, with subsequent decreases in percent cover at depths of 300 m and 750 m. Generally, other emergent epifauna were not important in providing biotic coverage of the seafloor below a depth of 950 m, with the exception of a few patches of actiniarians, crinoids, and hydroids. All groups combined, emergent epifauna were an important component of seafloor coverage to a depth of about 2500 m but were most important at depths shallower than 1000 m. Marked changes in percent cover of emergent epifauna were observed at depths of about 650 m and 1050 m. There was a relatively small "pulse" of coverage at depths between about 1850 and 2100 m, but very little coverage was seen below that depth.

Species richness

On the basis of published records, archived museum specimens, specimens collected during this study, and confirmed identifications made during detailed examination of video footage collected during this study, the depth range for 77 species (or distinct taxa) of corals and 100 species (or distinct taxa) of sponges from the study area can be confirmed. Species richness for corals was greatest at depths between 100 and 900 m and greatest for sponges at depths

Table 5

Percent cover of corals, sponges, and other sedentary invertebrates within frames sampled (*n*=33,719) from video collected along transects with the submersible *Delta* and remotely operated vehicle *Jason II* in 2003 and 2004. Values are the total area (m^2) of the seafloor within frames sampled for each category, and values in parentheses are percentages of the total area sampled. The "other" category includes sedentary and principally sessile invertebrates, other than corals and sponges, that provided 3-D structure to the seafloor.

Cover (%)	Corals	Sponges	Other	All combined
0	31,927 (65.2)	31,250 (63.8)	35,144 (71.7)	23,662 (48.3)
<10	15,968 (32.6)	14,099 (28.8)	12,537 (25.6)	9412 (19.2)
10–20	834 (1.7)	1588 (3.2)	797 (1.6)	7087 (14.5)
20–30	207 (0.4)	1101 (2.2)	285 (0.6)	4930 (10.1)
30–40	35 (<0.1)	515 (1.1)	122 (0.2)	1412 (2.9)
40–50	8 (<0.1)	288 (0.6)	52 (0.1)	989 (2.0)
50–60	3 (<0.1)	95 (0.2)	34 (0.1)	576 (1.2)
60–70	3 (<0.1)	42 (0.1)	13 (<0.1)	432 (0.9)
70–80	0	5 (<0.1)	1 (<0.1)	331 (0.7)
80–90	0	2 (<0.1)	0	120 (0.2)
>90	0	0	0	34 (<0.1)
Total	48,985 (100.0)	48,985 (100.0)	48,985 (100.0)	48,985 (100.0)

between 50 and 400 m (Fig. 13). Species richness stead-ily declined with depth, with changes at depths of 500 m, 900 m, and 1400 m (Fig. 13). Additional collection and taxonomic identification of specimens from the region, particularly for demosponges, which appear to be particularly diverse and still largely unknown, will help to further elucidate these patterns of species richness with depth.

Damaged corals and sponges

Damage observed to corals and sponges on transects was previously reported for a subset of the data presented here (Heifetz et al., 2009). That report indicated that 14% of corals and 21% of sponges overall were damaged and that disturbance to the seafloor from fishing gear was widespread and evident on most transects. Analyses for this study indicate that 6.5% of the corals and 18.1% of the sponges enumerated on transects were damaged (Table 6). Antipatharians had the highest incidence of damage (14.9%), followed by hydrocorals (9.0%), gorgonians (6.0%), and pennatulaceans (5.0%) (Table 6). All coral groups and all coral taxa combined had a much higher incidence of damage in water shallower than 1000 m than in deeper water (Table 6). Among the sponges, hexactinellids (18.0%) and demosponges (18.1%) had similar incidences of disturbance, and both groups of sponges had proportions of damaged specimens (28% and 21%) that were much higher at depths shallower than 1000 m than in deeper water (Table 6).

Predation on corals and sponges

Deep-sea corals and sponges in the Aleutian Islands appear to have few predators (Fig. 14). Blood stars (*Henricia* spp.) that displayed a typical feeding posture on

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Figure 14 (opposite page)

Images of taxa from sampled frames of video collected along 29 transects with the submersible *Delta* and remotely operated vehicle *Jason II* in 2003 and 2004 in the central Aleutian Islands: (**A**) A sea star (*Hippasteria* sp.) preys on the soft flesh of a bamboo coral (*Isidella tentaculum*) at a depth of 926 m. (**B**) A sea star (*Hippasteria* sp.) preys on the soft flesh of a gorgonian (*Plumarella echinata*) at a depth of 1615 m. (**C**) Calliostomatid snails (genus *Otukaia*) prey on the soft flesh of a bamboo coral (*I. tentaculum*) at a depth of 1227 m. (**D**) Calliostomatid snails (genus *Otukaia*), shown preying on the soft flesh of a large bamboo coral (*I. tentaculum*) at a depth of 1181 m, had almost totally denuded the colony at the time this photo was taken. (**E**) A sea star (*Hippasteria californica*) preys on the soft flesh of a bamboo coral (*I. tentaculum*) at a depth of 1378 m. Note that the calliostomatid snail (*Otukaia* sp.) is laying its egg cases on the denuded coral skeleton. (**F**) An unknown sea star, apparently a species of *Solaster* (possibly *S. borealis*), preys on the pennatulacean *Halipteris* sp. B at a depth of 2235 m. The 2 red laser marks at the bottom of the image are separated by 10 cm, providing a scaling tool for the measurement of fauna. (**G**) An unknown nudibranch, probably a *Tritonia* sp., also appears to prey on bamboo corals, particularly *I. tentaculum*, at depths between 720 and 1178 m. (**H**) An unknown nudibranch, probably a *Tritonia* sp., lays its egg case on the base of a denuded bamboo coral (*I. tentaculum)* at a depth of 1173 m.

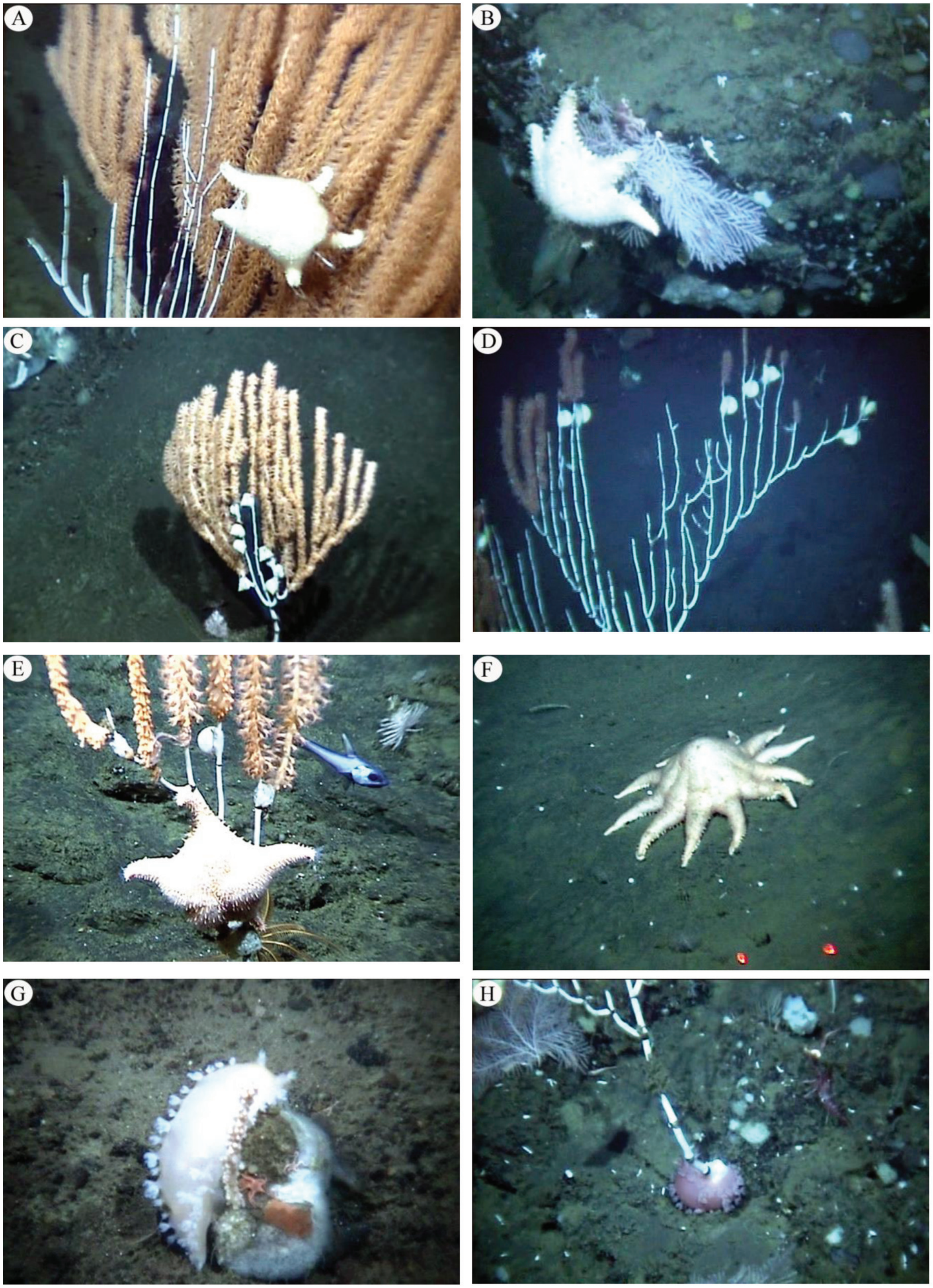
A
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Table 6

Percentage of corals (antipatharians, gorgonians, pennatulaceans, and hydrocorals) and sponges damaged, percentage of corals and sponges observed at depths <1000 m and damaged, and percentage of corals and sponges seen at depths ≥1000 m and damaged. Corals were enumerated on 29 transects surveyed with the submersible *Delta* and remotely observed vehicle *Jason II* in 2003 and 2004. Sponges were enumerated only on 7 transects surveyed with the ROV *Jason II* in 2004. Note that the gorgonian group excludes *Radicipes verrilli* and Gorgonacea (unidentified).

	Percentage damaged		
Taxon	Total	<1000 m	≥1000 m
Antipatharians	14.9% (13/87)	34.6% (9/26)	6.6% (4/61)
Gorgonians	6.0% (1427/23,787)	6.3% (1374/21,804)	2.7% (54/1977)
Acanthogorgia sp.	0% (0/40)	0	0% (0/40)
Alaskagorgia aleutiana	0.9% (2/231)	0.9% (2/231)	0%
Arthrogorgia spp.	2.3% (45/1983)	2.5% (43/1709)	0.7% (2/274)
Calcigorgia beringi	0% (0/63)	0% (0/56)	0% (0/7)
Calcigorgia spiculifera	2.8% (13/457)	2.8% (13/457)	0
Cryogorgia koolsae	1.0% (1/96)	1.0% (1/96)	0
Fanellia spp.	7.4% (96/1295)	7.1% (89/1248)	14.9% (7/47)
Isididae	7.6% (199/2625)	9.0% (171/1902)	3.9% (28/723)
Muriceides nigra	0.9% (7/795)	0.9% (7/795)	0
Paragorgia arborea	1.1% (2/178)	1.2% (2/166)	0% (0/12)
Plumarella spp.	4.3% (438/10,173)	4.4% (425/9577)	2.2% (13/596)
Primnoa pacifica	0% (0/23)	0% (0/23)	0
Primnoa wingi	0% (0/24)	0% (0/24)	0
Swiftia sp.	4.7% (7/148)	4.7% (7/148)	0
Swiftia pacifica	3.0% (10/331)	3.7% (10/268)	0% (0/63)
Thouarella spp.	11.4% (608/5325)	11.8% (604/5110)	1.9% (4/215)
Pennatulaceans	5.0% (351/7083)	10.5% (260/2483)	2.0% (91/4600)
Anthoptilum grandiflorum	0.7% (6/866)	0	0.7% (6/866)
Halipteris willemoesi	17.2% (221/1282)	17.2% (221/1282)	0
Halipteris sp. A	13.1% (57/435)	19.0% (39/205)	7.8% (18/230)
Halipteris sp. B	2.0% (67/3305)	0	2.0% (67/3305)
Pennatulidae (unidentified species)	0% (0/122)	0	0% (0/122)
Ptilosarcus gurneyi	0% (0/996)	0% (0/996)	0
Umbellula lindahli	0% (0/77)	0	0% (0/77)
Hydrocorals	9.0% (858/9534)	11.6% (837/7201)	0.9% (21/2333)
All corals	6.5% (2649/40,549)	7.9% (2480/31,572)	1.9% (170/8977)
Class Hexactinellida	18.0% (443/2467)	28.2% (433/1534)	1.1% (10/933)
Class Demospongiae*	18.1% (2913/16,108)	20.7% (2878/13,891)	1.6% (35/2217)
All sponges	18.1% (3356/18,575)	21.5% (3311/15,425)	1.4% (45/3150)

*This group also includes a few sponges in the Class Calcarea.

several demosponges (e.g., *Artemisina* sp., *Monanchora pulchra*, *Semisuberites cribrosa*, and *Haliclona* sp.) were observed at relatively shallow depths (80 to 300 m). In deeper water (depths of 448–1615 m), the sea stars *Hippasteria phrygiana*, *H. heathi*, *and H. californica* appeared to prey on several species of sponges, bamboo corals (especially *Isidella tentaculum*), and the gorgonians *Plumarella* spp., *Arthrogorgia* spp., and *Calcigorgia beringi* (Figs. 14A and 14B). Calliostomatid snails (*Otukaia* sp.) also preyed en masse on the bamboo coral *I. tentaculum* at depths between 926 and 1398 m (Figs. 14C and 14D). These sea stars and snails appeared to often prey on *I. tentaculum* in tandem, and the snails laid their egg cases on the denuded coral skeletons (Fig. 14E).

An unknown sea star, apparently a species of *Solaster*, was observed in deep water (>1460 m) preying on the pennatulacean *Halipteris* sp. B and the demosponge *Chondrocladia concrescens* (Fig. 14F). The demosponge *Cladorhiza corona* also appeared to have been preyed upon in deep water by an unknown predator, possibly the same *Solaster* sea star. An unknown nudibranch, probably a *Tritonia* sp., also appeared to prey on bamboo corals, particularly *I. tentaculum*, at depths between 720 and 1178 m (Fig. 14G). The nudibranch laid eggs on the exposed skeletons of *I. tentaculum* (Fig. 14H). The incidence of predation on deep-sea corals and sponges in the Aleutian Islands, however, appears to be relatively low and limited to only a few species of sea stars, snails, and nudibranchs.

Table 7

Characteristics for 18 new coral and sponge gardens identified from analysis of video footage of the seafloor collected with the submersible *Delta* and remotely operated vehicle *Jason II* in 2003 and 2004. Latitude and longitude coordinates are provided in decimal degrees. Disturbances were rated on a 4-point scale with 1) none, 2) very light, 3) light, and 4) heavy. HAPC=Habitat Area of Particular Concern.

Transect	Start coordinates	End coordinates	Depth range (m)	Habitat	Disturbance
Delta 6203–6206	51.8664, –176.2526	51.8706, –176.2665	97–120	Sponge garden	Light; longlines
Delta 5597*	52.7550, –179.3074	52.7551, –179.3139	153–164	Sponge garden	Heavy; bottom trawls
Delta 5612*	51.5985, –177.0207	51.5994, –177.0071	98–336	Sponge garden (in existing HAPC but nonoverlapping)	Light; longlines
Delta 5988	51.9820, –176.7337	51.9814, –176.7311	93–200	Sponge garden	Light; longlines
Delta 5991	51.9066, –177.2190	51.9062, –177.2161	112–235	Sponge garden	Very light; longlines
Delta 5993	51.4055, –178.5771	51.4015, –178.5749	104–165	Sponge garden	Very light; longlines
Delta 5994	51.3932, –178.5615	51.3963, –178.5622	106–115	Sponge and coral gardens in patches	None
Delta 5997	51.3647, –179.4833	51.3632, –179.4930	95–222	Sponge and coral gardens	None
Delta 6004	52.7686, –179.3253	52.7635, –179.3311	130–225	Sponge and coral gardens	Heavy patches; bottom trawls
Delta 6216	51.8565, –177.4714	51.8609, –177.4764	115–250	Sponge garden	Very light; derelict longlines present
Delta 6220	51.9150, –175.2915	51.9196, –175.2939	116–120	Sponge gardens in patches	Very light; derelict longlines present
Delta 6221	51.9125, –173.8872	51.9137, –173.8886	121–122	Sponge garden	None
Delta 6222	51.8577, –173.9094	51.8589, –173.9102	192–199	Sponge garden	None
Delta 6223	51.9462, –173.9363	51.9461, –173.9272	83–101	Sponge gardens in patches	None
Jason II 104	51.7232, –179.5834	51.7211, –179.5831	700–726	Coral garden	Light; longlines
Jason II 104	51.6410, –179.5788	51.6382, –179.5777	395–460	Coral garden	Light; derelict longlines present
Jason II 107	52.0084, –176.7719	52.0044, –176.7724	810–937	Coral garden	Light; longlines
Jason II 107	51.9883, –176.7724	51.9861, –176.7705	130–268	Sponge garden	Light; derelict longlines present

*Sponge gardens identified from archived video footage collected with the submersible *Delta* in 2002.

New coral and sponge gardens

Six areas that support coral gardens (with a total seafloor habitat of 377 km^2) discovered in the central Aleutian Islands in 2002 (Stone, 2006) are closed to the use of all bottom-contact fishing gear as part of the AIHCA (Fig. 2). Video footage collected from the 71 submersible and ROV dives conducted during this study (Appendix I) was qualitatively examined, and previously collected video footage from the 2002 submersible dives was reexamined; as a result, the locations of an additional 18 coral and sponge gardens were identified (Fig. 15). The majority (83%) of these newly discovered coral and sponge gardens are located in areas that remain open to bottom trawling and other fishing activities (Fig. 15). The new gardens range in depth from 83 to 937 m (Table 7). Disturbance from fishing activities was evident at 72% of these gardens and ranged from very light disturbance, likely from longline gear, to heavy disturbance, likely caused by bottom trawls (Table 7). Derelict longline gear was observed at 4 of the garden sites (Table 7).

Fish, crab, and octopod taxa (or life history groups)

In the sampled video frames, 3029 fishes (25 taxa total), crabs (7 taxa total), and octopods (1 taxon) were enumerated (Table 8). Fishes were observed at depths from 54 to 2944 m, crabs were recorded at depths from 102 to 2838 m, and octopods were seen at depths from 93 to 2922 m. Collectively, fishes, crabs, and octopods were present in 6.6% of the frames sampled and were observed on all 29 transects. Juvenile rockfishes (*Sebastes* spp.) were the most abundant taxa observed in sampled video frames, followed by grenadiers and Pacific Ocean Perch. Crabs were not as abundant as fishes and were represented by 7 taxa. Among those taxa, deep-sea Tanner crabs were collectively the most abundant, followed by Verrill's *Paralomis* crab and southern Tanner crab. The majority of taxa (18 of 33) enumerated in sampled video frames were found exclusively at depths <1000 m, putting them within the approximate depth range of current fishing activities. More than 71% of the individuals enumerated were found at depths <500 m, but only

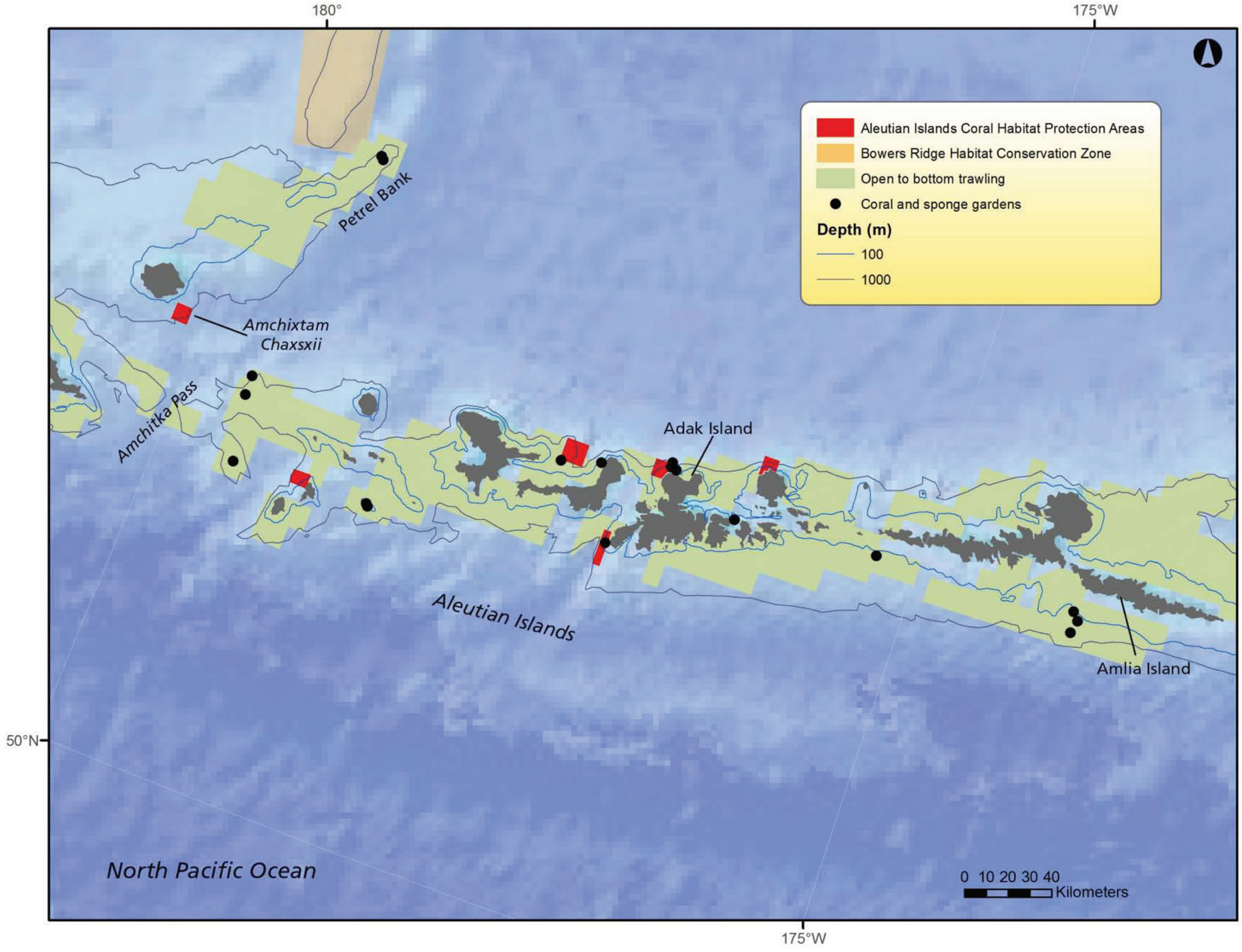

Figure 15

Map of locations of coral and sponge gardens newly discovered in 2003 and 2004 during surveys conducted with the submersible *Delta* and remotely operated vehicle *Jason II* in the central Aleutian Islands.

Table 8

Total number, frequency of occurrence (percentage of transects), mean depth, and depth range of fishes, crabs, and octopods observed on 29 transects surveyed through collection of video with the submersible *Delta* and remotely operated vehicle *Jason II* in 2003 and 2004. Depth range observed on all video footage in this study (i.e., including footage not quantitatively analyzed) is noted in parentheses if it differs from range of transect observations. Taxa are arranged from most to least abundant.

			Depth (m)	
Taxon	Total number	Frequency	Mean	Range
Rockfishes—juveniles	744	41	127	87–535
Grenadiers	462	24	1397	(236) 379–2944
Pacific Ocean Perch	336	52	216	102–325
Ronquils	187	48	123	70–216
Sculpins	181	79	213	63–2734
Northern Rockfish	130	28	102	74–131 (160)
Blackspotted Rockfish	113	31	285	101–473
Shortspine Thornyhead	85	35	483	199–1132 (1322)
Shortraker Rockfish	76	21	368	171–675
Deep-sea Tanner crabs	67	21	1710	684–2526
Snailfishes	58	31	1304	253–2929
Verrill's *Paralomis* crab	56	21	1591	1092–2389
Octopods	52	55	1009	93–2922
Pleuronectids	50	45	226	63–827
Southern Tanner crab	49	11	109	102–128
Atka Mackerel	48	17	115	54–174
Eelpouts	41	35	1278	67–2935
Golden king crab	40	21	394	174–1041
Spiny *Paralomis* crab	37	14	2387	1185–2838
Pleuronectids—juveniles	36	17	118	104–273
Poachers	28	38	450	91–874
Lanternfishes	27	17	1331	(697) 801–2520
Skates	25	28	1162	(95) 124–2852
Light Dusky Rockfish	23	14	95	57–112 (131)
Pacific Flatnose	19	21	1470	836–2451
Sharpchin Rockfish	13	17	154	93–330
Longnose Tapirfish	11	10	2544	(1532) 1585–2855
Prowfish	10	17	115	95–194
Pacific Cod	8	14	129	63–351
Deep-sea lithodid crabs	7	7	1025	(713) 892–1286
Pricklebacks	5	10	188	115–288
Hair crab	4	10	128	104–176 (224)
Sablefish	1	3	895	(287) 895
All taxa	3029	100	704	54–2944

21.6% of the individuals were found at depths >1000 m.

Overall, 63% of the individual fishes, crabs, and octopods enumerated on transects were found in sampled frames with corals, 69% of them were observed in sampled frames with sponges, and 55% of them were seen in sampled frames with other emergent epifauna (Table 9). Association with corals ranged from 100% for Sharpchin Rockfish to only 16% for skates. The majority of individuals for 50% of all taxa were observed in sampled frames in which corals were present (Table 9). Association with sponges ranged from 100% for 4 taxa (Sharpchin Rockfish, juvenile rockfishes, Prowfish, and Light Dusky Rockfish) to 0% for Longnose Tapirfish. The majority of individuals for 54% of all taxa were observed in sampled frames in which sponges were present. Association with other emergent epifauna ranged from 100% for Light Dusky Rockfish to 0% for Pacific Flatnose and Longnose Tapirfish. The majority of individuals for 46% of all taxa were observed in sampled frames in which other emergent epifauna were present (Table 9).

Of all taxa observed in sampled frames, 52% had greater odds of being found in a video frame with coral than without (Table 10). The proportion of sampled frames with Sharpchin Rockfish, juvenile rockfishes, or Northern Rock-

Table 9

Percentage of fishes, crabs, and octopods that were observed in the same video frame with corals, sponges, and other emergent epifauna. Frames were sampled from video collected along 29 transects surveyed with the submersible *Delta* and remotely operated vehicle *Jason II* in 2003 and 2004. Analysis was not performed for rare species (i.e., ≤10 observations). Taxa are arranged per Table 8.

	Percentage with		
Taxon	corals	sponges	other
Rockfishes—juveniles	97	100	70
Grenadiers	32	23	11
Pacific Ocean Perch	59	89	86
Ronquils	77	91	58
Sculpins	41	59	62
Northern Rockfish	90	97	91
Blackspotted Rockfish	74	90	84
Shortspine Thornyhead	67	75	48
Shortraker Rockfish	72	89	84
Deep-sea Tanner crabs	49	16	12
Snailfishes	36	50	50
Verrill's *Paralomis* crab	57	46	18
Octopods	40	54	44
Pleuronectids	32	38	38
Southern Tanner crab	27	14	22
Atka Mackerel	88	96	77
Eelpouts	51	34	27
Golden king crab	60	93	70
Spiny *Paralomis* crab	22	8	8
Pleuronectids—juveniles	17	14	19
Poachers	21	32	29
Lanternfishes	30	19	22
Skates	16	32	28
Light Dusky Rockfish	78	100	100
Pacific Flatnose	32	32	0
Sharpchin Rockfish	100	100	92
Longnose Tapirfish	18	0	0
All taxa	63	69	55

Table 10

Odds ratios and 95% confidence intervals (CIs) for fishes, crabs, and octopods being observed in the same video frame with corals. Frames were sampled from video collected along 29 transects surveyed with the submersible *Delta* and remotely operated vehicle *Jason II* in 2003 and 2004. Analysis was not performed for rare species (i.e., species with ≤10 observations). The 95% CIs were calculated with 10,000 boot strappings (Rice, 1995). Taxa are arranged per Table 8.

Taxon	Odds ratio	95% CI
Rockfishes—juveniles	26.2	17.6–45.2*
Grenadiers	1.2	1.0–1.4*
Pacific Ocean Perch	2.1	1.6–2.7*
Ronquils	5.5	4.0–8.0*
Sculpins	1.3	0.9–1.7
Northern Rockfish	10.4	6.1–22.6*
Blackspotted Rockfish	3.5	2.3–5.8*
Shortspine Thornyhead	2.1	1.4–3.5*
Shortraker Rockfish	2.4	1.5–4.4*
Deep-sea Tanner crabs	1.7	1.0–2.8*
Snailfishes	1.3	0.7–2.3
Verrill's *Paralomis* crab	2.7	1.6–4.8*
Octopods	1.4	0.8–2.5
Pleuronectids	0.6	0.3–1.0
Southern Tanner crab	0.8	0.4–1.4
Atka Mackerel	8.4	4.0–29.1*
Eelpouts	2.1	1.1–4.1*
Golden king crab	1.3	0.7–2.7
Spiny *Paralomis* crab	1.0	0.4–2.0
Pleuronectids—juveniles	0.3	0.1–0.7*
Poachers	0.3	0.1–0.7*
Lanternfishes	0.8	0.3–1.7
Skates	0.4	0.1–1.0
Light Dusky Rockfish	4.2	1.6–23.5*
Pacific Flatnose	0.8	0.2–2.1
Sharpchin Rockfish	188.4	14.8–296.3*
Longnose Tapirfish	0.8	0.03–2.7

*The 95% CIs for these taxa do not include 1.

fish was more than 10 times higher among frames with the presence of corals than among frames without corals. Conversely, poachers and juvenile pleuronectids were less likely to be found in the same frames as corals. For 11 taxa, there was no difference in their odds of being found in the same frame as corals or in a frame without corals.

Among all taxa enumerated from video, 56% had greater odds of being found in a video frame with sponges than without (Table 11). The proportion of sampled frames with Light Dusky Rockfish, juvenile rockfishes, Sharpchin Rockfish, Northern Rockfish, or Atka Mackerel was more than 10 times higher among frames with the presence of sponges than among frames without sponges. In contrast, pleuronectids, juvenile pleuronectids, southern Tanner crab, and poachers were less likely to be found in the same frames as sponges. For 8 taxa, there was no difference in their odds of being found in the same frame as sponges or in a frame without sponges.

Of all taxa observed in sampled frames, 42% had greater odds of being found in a video frame with other emergent epifauna than without (Table 12). The proportion of sampled frames with Light Dusky Rockfish or Northern Rockfish was more than 10 times higher among frames with the presence of other emergent epifauna than among frames without other emergent epifauna. Pacific Flatnose, pleuronectids, juvenile pleuronectids, and poachers were less likely to be found in the same frames as other emergent epifauna. For 11 taxa, there was no difference in their odds of being found in the same frame as other emergent epifauna or in a frame without other emergent epifauna.

Table 11

Odds ratios and 95% confidence intervals (CIs) for fishes, crabs, and octopods being observed in the same video frame with sponges. Frames were sampled from video collected along 29 transects surveyed with the submersible *Delta* and remotely operated vehicle *Jason II* in 2003 and 2004. Analysis was not performed for rare species (i.e., species with ≤10 observations). The 95% CIs were calculated with 10,000 boot strappings (Rice, 1995). Taxa are arranged per Table 8.

Taxon	Odds ratio	95% CI
Rockfishes—juveniles	86.9	33.5–1820.1*
Grenadiers	1.4	1.1–1.7*
Pacific Ocean Perch	4.9	3.4–8.2*
Ronquils	7.0	4.5–12.9*
Sculpins	2.4	1.7–3.2*
Northern Rockfish	23.1	11.1–114.5*
Blackspotted Rockfish	4.3	2.4–11.0*
Shortspine Thornyhead	1.7	1.1–3.1*
Shortraker Rockfish	1.8	0.9–5.2
Deep-sea Tanner crabs	0.8	0.3–1.4
Snailfishes	2.8	1.7–4.9*
Verrill's *Paralomis* crab	4.4	2.6–7.6*
Octopods	2.4	1.3–4.2*
Pleuronectids	0.3	0.2–0.5*
Southern Tanner crab	0.4	0.1–0.8*
Atka Mackerel	10.5	4.2–303.9*
Eelpouts	1.0	0.4–1.9
Golden king crab	4.6	1.9–138.4*
Spiny *Paralomis* crab	1.0	0.03–2.4
Pleuronectids—juveniles	0.1	0.02–0.2*
Poachers	0.2	0.1–0.5*
Lanternfishes	1.0	0.2–2.4
Skates	0.9	0.3–2.1
Light Dusky Rockfish	264.9	21.8–396.2*
Pacific Flatnose	2.0	0.5–5.3
Sharpchin Rockfish	57.8	4.5–90.4*
Longnose Tapirfish	0.2	0.1–2.6

*The 95% CIs for these taxa do not include 1.

Table 12

Odds ratios and 95% confidence intervals (CIs) for fishes, crabs, and octopods being observed in the same video frame with "other" emergent epifauna. Frames were sampled from video collected along 29 transects surveyed with the submersible *Delta* and remotely operated vehicle *Jason II* in 2003 and 2004. Analysis was not performed for rare species (i.e., species with ≤10 observations). The 95% CIs were calculated with 10,000 boot strappings (Rice, 1995). Taxa are arranged per Table 8.

Taxon	Odds ratio	95% CI
Rockfishes—juveniles	2.3	1.8–2.9*
Grenadiers	1.3	0.9–1.7
Pacific Ocean Perch	3.4	2.5–4.9*
Ronquils	1.3	0.9–1.7
Sculpins	4.1	3.0–5.6*
Northern Rockfish	10.8	5.9–27.6*
Blackspotted Rockfish	3.2	2.0–5.8*
Shortspine Thornyhead	1.0	0.7–1.6
Shortraker Rockfish	2.8	1.6–7.0*
Deep-sea Tanner crabs	1.3	0.5–2.4
Snailfishes	4.8	2.8–8.2*
Verrill's *Paralomis* crab	2.6	1.1–4.8*
Octopods	2.4	1.3–4.1*
Pleuronectids	0.5	0.2–0.8*
Southern Tanner crab	0.6	0.3–1.1
Atka Mackerel	2.9	1.5–7.1*
Eelpouts	1.0	0.4–1.9
Golden king crab	1.8	0.9–4.1
Spiny *Paralomis* crab	2.0	0.1–5.0
Pleuronectids—juveniles	0.2	0.1–0.3*
Poachers	0.3	0.1–0.7*
Lanternfishes	2.8	0.8–6.5
Skates	1.2	0.4–2.7
Light Dusky Rockfish	168.3	14.1–250.5*
Pacific Flatnose	0.0	0.03–0.6*
Sharpchin Rockfish	7.2	1.8–103.4*
Longnose Tapirfish	0.6	0.4–8.5

*The 95% CIs for these taxa do not include 1.

When all emergent epifauna were combined into a single category, 59% of all taxa had greater odds of being found in a video frame with emergent epifauna than without (Table 13). The proportion of frames with Light Dusky Rockfish, juvenile rockfishes, Sharpchin Rockfish, Northern Rockfish, or Pacific Ocean Perch was more than 10 times higher among frames with the presence of emergent epifauna than among frames without them. Conversely, pleuronectids, juvenile pleuronectids, and poachers had lesser odds of being found in the same frames as emergent epifauna. Only 8 taxa (eelpouts, octopods, Pacific Flatnose, lanternfishes, southern Tanner crab, spiny *Paralomis* crab, Longnose Tapirfish, and skates) were not associated, positively or negatively, with emergent epifauna (Table 13). The results from the odds-ratios analysis for all 4 categories of emergent epifauna are summarized in Table 14. Eight taxa were positively associated with all types of emergent epifauna, 2 taxa (poachers and juvenile pleuronectids) had lesser odds of being found with any type of emergent epifauna, and 4 taxa (lanternfishes, spiny *Paralomis* crab, Longnose Tapirfish, and skates) were not associated, positively or negatively, with emergent epifauna (Table 14). Thirteen taxa showed preferences for some emergent epifauna groups and not others, but no taxon showed a positive association for one category of emergent epifauna and a negative association for another category of emergent epifauna (Table 14).

Table 13

Odds ratios and 95% confidence intervals (CIs) for fishes, crabs, and octopods being observed in the same video frame with "any" emergent epifauna, meaning corals, sponges, and other emergent epifauna combined. Frames were sampled from video collected along 29 transects surveyed with the submersible *Delta* and remotely operated vehicle *Jason II* in 2003 and 2004. Analysis was not performed for rare species (i.e., species with ≤10 observations). The 95% CIs were calculated with 10,000 boot strappings (Rice, 1995). Taxa are arranged per Table 8.

Taxon	Odds ratio	95% CI
Rockfishes—juveniles	50.3	19.6–1056.8*
Grenadiers	1.3	1.1–1.6*
Pacific Ocean Perch	14.9	7.4–73.9*
Ronquils	5.7	3.5–12.2*
Sculpins	2.5	1.8–3.8*
Northern Rockfish	29.3	10.6–652.5*
Blackspotted Rockfish	6.1	2.8–27.4*
Shortspine Thornyhead	2.0	1.2–4.4*
Shortraker Rockfish	3.7	1.3–82.0*
Deep-sea Tanner crabs	1.6	1.0–2.7*
Snailfishes	2.3	1.4–4.3*
Verrill's *Paralomis* crab	3.1	1.8–6.3*
Octopods	1.5	0.9–2.8
Pleuronectids	0.3	0.2–0.5*
Southern Tanner crab	0.7	0.4–1.3
Atka Mackerel	5.5	2.2–165.8*
Eelpouts	1.0	0.5–2.0
Golden king crab	7.6	2.1–95.0*
Spiny *Paralomis* crab	0.9	0.4–1.8
Pleuronectids—juveniles	0.1	0.1–0.3*
Poachers	0.2	0.1–0.4*
Lanternfishes	1.0	0.4–2.1
Skates	0.9	0.4–2.2
Light Dusky Rockfish	88.3	7.2–131.7*
Pacific Flatnose	1.1	0.4–2.8
Sharpchin Rockfish	35.0	2.8–55.1*
Longnose Tapirfish	0.6	0.02–2.4

*The 95% CIs for these taxa do not include 1.

Discussion

The first deepwater in situ observations in the central Aleutian Islands made with the ROV *Jason II* in 2004 confirmed the presence of abundant and diverse coral and sponge fauna to depths of almost 3000 m. Contrary to expectations, deepwater areas with soft sediment were not devoid of corals but were inhabited in some areas by extensive groves of pennatulaceans and the gorgonian *Radicipes verrilli*. Corals, sponges, and other emergent epifauna, however, were most abundant and diverse in shallower areas. Gradual changes in abundance and species richness of emergent epifauna and in their percent cover of the seafloor were evident at several depths, with major changes observed between 400 and 700 m for all measures. Also, all measures increased from deep to shallow water.

Prior to this study, we knew that the Aleutian Islands supported the most abundant and diverse coral assemblages in Alaska, but the results from this study and those from previous work in the region (Stone, 2006) clearly indicate that the Aleutian Islands support the most abundant deepwater, ahermatypic (i.e., non-reef-building) coral resources in high-latitude ecosystems reported anywhere in the world. Although there have been many studies initiated in the past decade on deep-sea coral habitat worldwide, few explicitly report density measurements, or even estimates; therefore, there are few studies with which to compare the results of this study.

A recent study in the nearby canyons of the Bering Sea slope estimated overall coral density at about one-fifth the density measured in this study over the same depth range (Miller et al., 2012), but otherwise study measurements for coral density were typically up to (and sometimes more than) 10 times greater than the levels reported for other areas along the coasts of North America (Mortensen and Buhl-Mortensen, 2004; Tissot et al., 2006; Du Preez and Tunnicliffe, 2011; Stierhoff et al., 2011); the mid-Atlantic Ridge (Mortensen et al., 2008); the Weddell Sea, Antarctica (Orejas et al., 2002); and the low-latitude ecosystems of the Hawaiian Islands (Parrish, 2007). The reason for the lack of comparable reports from the North Atlantic Ocean, and elsewhere, is that many of the coral habitats in those regions are dominated by hermatypic scleractinians that, because of their reef-like structure, are measured in percent cover rather than number of individual colonies per unit area.

As pointed out by Cairns (2011), previous inferences that the Aleutian Islands "may harbor the highest diversity and abundance of cold-water corals in the world" (Heifetz et al., 2005) were partially incorrect. The region does have a high rate of species endemism and abundance is likely among the world's greatest (Stone, 2006), but diversity is low relative to regions like the Hawaiian Islands and Sea of Japan (Cairns, 2011). A previous report indicated that 25 coral taxa were endemic to the region (Heifetz et al., 2005). Updated records, including new identifications from this study, indicate that 101 coral taxa occur in the Aleutian Islands with as many as 51 species endemic to the region (Stone and Shotwell, 2007). Gorgonians and stylasterids are the most diverse groups with 45 and 25 species or subspecies reported, respectively (Stone and Shotwell, 2007). Ongoing work on the taxonomy of collected gorgonian specimens will increase the total number of species for that group. Twelve species of true soft corals, 3 species of stoloniferans, 6 species of pennatulaceans, and 10 species of scleractinians also have been reported from the region (Stone and Shotwell, 2007). Additionally, 3 species of black corals,

Table 14

Summary of odds ratios significance for fishes, crabs, and octopods being observed in the same video frame with corals, sponges, "other" emergent epifauna, and "any" emergent epifauna (corals, sponges, and other emergent epifauna combined). Frames were sampled from video collected along 29 transects surveyed with the submersible *Delta* and remotely operated vehicle *Jason II* in 2003 and 2004. (+) indicates greater odds, (–) indicates lesser odds, and (0) indicates equal odds of being found in the same frame as the emergent epifauna group. Taxa are arranged per Table 8.

Taxon	Corals	Sponges	Other	Any
Rockfishes—juveniles	+	+	+	+
Grenadiers	+	+	0	+
Pacific Ocean Perch	+	+	+	+
Ronquils	+	+	0	+
Sculpins	0	+	+	+
Northern Rockfish	+	+	+	+
Blackspotted Rockfish	+	+	+	+
Shortspine Thornyhead	+	+	0	+
Shortraker Rockfish	+	0	+	+
Deep-sea Tanner crabs	+	0	0	+
Snailfishes	0	+	+	+
Verrill's *Paralomis* crab	+	+	+	+
Octopods	0	+	+	0
Pleuronectids	0	–	–	–
Southern Tanner crab	0	–	0	0
Atka Mackerel	+	+	+	+
Eelpouts	+	0	0	0
Golden king crab	0	+	0	+
Spiny *Paralomis* crab	0	0	0	0
Pleuronectids—juveniles	–	–	–	–
Poachers	–	–	–	–
Lanternfishes	0	0	0	0
Skates	0	0	0	0
Light Dusky Rockfish	+	+	+	+
Pacific Flatnose	0	0	–	0
Sharpchin Rockfish	+	+	+	+
Longnose Tapirfish	0	0	0	0

including *Dendrobathypathes boutillieri*, a species new to science (Opresko, 2005), were collected from the region with the *Jason II* in 2004.

All 7 major groups of corals found in Alaskan waters (scleractinians, black corals, true soft corals, stoloniferans, gorgonians, pennatulaceans, and hydrocorals) were observed on the survey transects. Gorgonians, particularly primnoids, were by far the most abundant corals observed, followed by scleractinians, hydrocorals, and pennatulaceans. These findings closely agree with previous observations made in shallower areas (<367 m) in the study area (Stone, 2006), with the exception that scleractinians were more abundant in the current study. Scleractinians were found over a broad depth range, but dense patches were observed at only a single site (at Amchixtam Chaxsxii, a submarine volcano in Amchitka Pass discovered in 2002; Stone, 2006) and within a narrow depth range (1200–1300 m), deeper than the observations of the previous study. True soft corals and stoloniferan corals, while not abundant overall, were locally abundant in areas where other corals were not. Black corals were not abundant except in small patches on a few transects where they formed relatively dense thickets.

Corals were not equally distributed with respect to substrate type or seafloor roughness and slope. Habitats dominated by bedrock and cobble supported the highest densities of corals, but sand and silt habitats supported the lowest. These findings agree closely with previous observations made in shallower waters (<367 m) in the central Aleutian Islands (Stone, 2006), where "scarp," "buttress," and "cobble field" habitats—habitats dominated by bedrock and cobble—supported the highest densities of corals. Additionally, in that study, "open habitat"—habitats dominated by unconsolidated sediments of pebbles, sand, and silt—generally had the lowest densities of corals. Density of corals was lowest in seafloor areas that were not very rough and increased steadily as the seafloor became rougher. Similarly, density of corals was lowest where the seafloor was flat and increased as the seafloor became more sloped. These findings agree closely with results from the use of a predictive model on a subset of these data (Woodby et al., 2009) that indicated that depth, slope, and rugosity were important variables that explain the distribution of corals in the region. These observations from this study clearly indicate the preference of most corals for hard, rough substrate in areas where the seafloor is sloped, and perhaps highlight the importance of localized water currents for many species of filter- and suspension-feeding biota (Bryan and Metaxas, 2007).

A novel observation made during this study was the use of hexactinellid sponge skeletons as attachment substrate by several species of corals. To my knowledge, this observation has not been reported before. Several large fields comprised mainly of hexactinellid sponge skeletons, both fragmented and apparently intact and attached to the seafloor, were observed in South Amchitka Pass at depths between 207 and 1308 m. The fields often were arranged linearly along an isobath, similar to beach windrows, possibly indicating that some of the material was deposited from upslope. The debris fields were up to 24 m wide and contained the skeletons of *Farrea* spp., *Tretodictyum amchitkensis*, *Aphrocallistes vastus*, and others. The bubble gum coral, *Fanellia* spp., *Plumarella* spp., and bamboo corals, all gorgonians, and the hydrocoral *Stylaster* sp. were observed growing directly on the hexactinellid skeletons. No corals were observed growing on live hexactinellid sponges. A diversity of corals growing on siltstone at depths below 1000 m was also found; an observation that points to the importance of "minor" substrate types where bedrock and cobbles are absent. Together, these observations indicate that the availability of appropriate settling substrate may be the most important factor that controls the distribution of corals, sponges, and other emergent epifauna in the region.

Corals clearly provide more vertical relief to the seafloor than do other emergent epifauna; however, both corals and sponges, particularly demosponges, appear to be equally important in providing structural coverage of the seafloor. Although corals, sponges, and other emergent epifauna provide important structural coverage of the seafloor, the abundance and relative contribution of each group differs with depth. Corals and sponges were most important in providing structural coverage of the seafloor at depths shallower than approximately 1000 m, but other emergent epifauna were most important at depths shallower than 100 m.

Observations from this study clearly indicate that much of the standing stock of corals (6.5%) and sponges (18.1%) in the study area were damaged and that a much higher proportion of individuals for all major taxa observed at depths <1000 m or within the depth zone of current fishing activities are damaged. Antipatharians, hydrocorals, demosponges, and hexactinellid sponges had the highest proportions of damaged individuals, particularly at depths shallower than 1000 m, indicating that they have little resistance to physical disturbance. The percentages of damaged corals and sponges reported here are considerably lower than the proportions previously reported for a subset of these data (14% and 21%, respectively) by Heifetz et al. (2009), but the values presented here for damaged corals (6.5% overall and 7.9% for corals seen at depths <1000 m) are consistent with the damage rate (8.5%) previously reported from the region (Stone, 2006).

Small numbers of damaged corals and sponges were observed at depths below 1000 m, and, as noted by Heifetz et al. (2009), these low levels could be considered background levels from natural events, such as swift currents and submarine landslides. There was isolated evidence of both mechanisms at depths >1000 m in this study. Predation on deep-sea corals is another natural event that is largely undocumented (Watling et al., 2011), except for predation by sea stars, principally Hippasterinae (Krieger and Wing, 2002; Mah et al., 2010). Observations from this study indicate that predation does occur at low levels in the central Aleutian Islands by a limited number of predators that are more diverse than previously reported and that it occurs principally at depths seldom observed in situ and beyond the depths of most current fishing activities. For example, predation on bamboo corals principally at depths below 1000 m by the sea star *Hippasteria* sp., calliostomatid snails (*Otukaia* sp.), and at least one species of nudibranch was noted. There is some evidence that these predators may be operating in tandem. Observations also were made that a large brittle star (*Asteronyx* sp.) was largely responsible for the damage noted on the pennatulacean *Halipteris* sp. B in deep water (1226–2400 m). This brittle star does not prey on the sea whip but uses it as an elevated perch, presumably for feeding in the current above the benthic boundary layer, and in that process abrades the tissue near the tip of the colony.

Most of the factors that control the degree to which corals and sponges provide habitat structure (their maximum size, growth form, intraspecific fine-scale distribution, and interaction with other structure-forming invertebrates) are the same factors that control the degree to which they are vulnerable to disturbance (Stone and Shotwell, 2007; Stone et al., 2011). For example, high proportions of damaged antipatharians and bamboo corals, which are large, upright, and have rigid skeletons, were observed. In contrast, low proportions of damaged plexaurid (*Alaskagorgia aleutiana*, *Cryogorgia koolsae*, *Muriceides nigra*, and *Swiftia* spp.) and acanthogorgiid gorgonians (*Calcigorgia* spp.), which are generally small and have relatively flexible skeletons, were observed. Primnoid gorgonians (*Thouarella* spp. and *Plumarella* spp.) are of similar size to the plexaurids and acanthogorgiids but generally have a more rigid skeleton and appear to be intermediately vulnerable to disturbance.

Previous in situ observations of fish and crab distribution in the central Aleutian Islands have been limited to depths shallower than 367 m (Stone, 2006; Rooper et al., 2007). Fisheries records and stock assessment surveys conducted in the region provide additional information on fish distribution in deeper waters (depths to ~1000 m), but provide only large-scale (i.e., kilometers) information on fish distribution relative to habitat and species associations with emergent epifauna. This study provides the first detailed habitat information for many species, including several deepwater species that may support important commercial fisheries (except for bottom trawling that is now prohibited at depths >1000 m) in the future (e.g., Alcorn and Stone, 2012). In general, observations made in this study of species' depth distributions agree closely with those in the published literature (Mecklenburg et al., 2002).

The majority of individuals for most fish, crab, and octopod taxa observed in this study were present in sampled frames in which corals, sponges, and other emergent epifauna were also present (Table 9). Although emergent epifauna are common (present in more than half of the video frames sampled) in the central Aleutian Islands, most fish, crab, and octopod taxa clearly aggregate where corals and other emergent epifauna are most abundant. Results from this study (Table 9) agree closely with fine-scale (i.e., meters) species-association work previously done in the central Aleutian Islands (Stone, 2006; Rooper et al., 2007). One notable exception between this study and Stone (2006) is that fewer Pacific Ocean Perch were associated with corals (59% compared to 85%). In this study, several schools of large (>35 cm) Pacific Ocean Perch were encountered over seafloor habitat composed of soft sediment without emergent epifauna. Large schools of Pacific Ocean Perch were not encountered during the Stone (2006) study, and the majority of fish observed were smaller (<35 cm) and likely subadults. These observations indicate that larger Pacific Ocean Perch may tend to school rather than use areas of emergent epifauna as structural refuge; the observations also highlight the importance of incorporating size classifications into studies of species associations where ontogenetic shifts in habitat use or behavior are known or suspected.

A relatively simple methodology—odds ratios—was employed to assess whether an individual is preferentially using a particular habitat type (Tables 10, 11, and 12 and summarized in Table 13). This fine-scale measure of association takes into account the availability of a particular habitat (i.e., emergent epifauna) type and provides insight into whether the habitat association is "active" or "passive." This measure could convey information as to whether these habitat types are "essential" when used in conjunction with observations of the behavior and activity of an individual. Clearly, many of the species observed in this study were actively associating with corals, sponges, and other emergent epifauna in a way consistent with that defined as facultative habitat use by Auster (2005).

Several distinct species associations with emergent epifauna were observed. For example, Shortspine Thornyhead and ronquils were associated with corals and sponges but not with other emergent epifauna. Deep-sea Tanner crabs and eelpouts were associated with corals only. These associations may indicate that some species associate with certain emergent epifauna for specific purposes, such as shelter seeking or feeding on associated microfauna. In general, corals and sponges appeared to be equally important to the species examined in this study. Other emergent epifauna were not used by fishes, crabs, and octopods to the same degree as corals and sponges, perhaps because they are not as abundant, particularly at depths >100 m, or because they generally do not provide as much vertical relief. Some associations may be passive and occur simply because certain fish, crab, and octopod species and emergent epifauna have similar habitat requirements.

Study observations of a high degree of association between fish, crab, and octopod taxa and emergent epifauna are noteworthy. These observations support previous ones made in the same study area (Rooper and Boldt, 2005; Stone, 2006; Rooper et al., 2007) and elsewhere in the northeast Pacific Ocean (Krieger and Wing, 2002; Du Preez and Tunnicliffe, 2011) that some species, particularly juvenile rockfishes (Family Scorpaenidae, *Sebastes* spp.), are much more abundant in habitats that support dense assemblages of corals, sponges, and other emergent epifauna. Similar observations have been made in deepwater habitats of the North Atlantic Ocean dominated by principally monotypic stands of the scleractinian *Lophelia pertusa* (Husebø et al., 2002; Costello et al., 2005; Ross and Quattrini, 2007) at the scale of delineated coral habitats (i.e., hundreds of square meters). However, studies in other regions of the United States (southern California and New England) did not find a high degree of association between fishes and emergent epifauna and indicate that the habitat provided by corals may be no more than functionally equivalent to abiotic components (i.e., rock without emergent epifauna) of the habitats (Auster, 2005; Tissot et al., 2006). The next step for researchers is to determine if the use of emergent epifauna provides those species with some benefit that contributes considerably to their development and survival—to determine if emergent epifauna provide essential fish habitat, which is defined as "those waters and substrate necessary to fish for spawning, breeding, feeding or growth to maturity" in the Magnuson-Stevens Act. Observations made during this study of the use of emergent epifauna as refuge by most juvenile rockfishes clearly indicate that emergent epifauna is essential fish habitat for this group of fishes at that life history stage.

Most shallow-water (depths <1000 m) fish, crab, and octopod taxa use emergent epifauna much more frequently than would be expected on the sole basis of its availability. Because most of these shallow-water species are currently targeted by commercial fisheries and because many are predictably associated with emergent epifauna, those habitats continue to be at high risk to disturbance from fishing gear. Conversely, few deepwater (depths >1000 m) species of fishes and crabs are presently targeted by commercial fisheries and most are not found in close proximity to and do not appear to actively associate with emergent epifauna. Therefore, fisheries that may develop in the future for deepwater species, such as grenadiers (Clausen and Rodgveller[2]), could have less interaction with coral and sponge habitat than the shallow-water fisheries currently operating in the central Aleutian Islands, especially because there is less emergent epifauna at those depths.

New coral and sponge gardens were discovered at 18 sites, and the majority (83%) of these sites are located in areas open to bottom trawling under the AIHCA regulations (Fig. 15). Most (more than 60%) of the seafloor habitat within the depth range (83–937 m) where gardens typically occur in the study area have been designated as open areas. Consequently, the majority of study submersible transects, the locations of which were determined before the closure boundaries of the AIHCA were designed, were simply by chance located in areas open to trawling. One of the new garden areas, dominated by demosponges rather than corals, is located within an existing HAPC but does not overlap with the existing garden there. Four other gardens are located very close to other existing HAPCs. Adjustment of the boundaries of existing HAPCs could in these particular cases provide protection to the newly discovered gardens.

The AIHCA was designed and implemented after this study was completed, so evaluation of the efficacy of the AIHCA closures to protect deep-sea coral and sponge habitat in the central Aleutian Islands was not a specific objective of the study. Because the majority of the seafloor habitat within the AIHCA remains otherwise unexplored, study observations provide important insights regarding the distribution of deep-sea coral resources in relation to the closure boundaries. Vast areas of seafloor habitat at depths below 1000 m are now off limits to bottom trawling. Dense groves of pennatulaceans and fields of the chrysogorgiid gorgonian *Radicipes verrilli* were observed in deepwater areas, but much of the habitat at those depths appears similar to abyssal plain that likely supports little deep-sea coral and sponge habitat. Furthermore, there appear to be few fish and crab species of potential commercial importance in these deepwater areas that would put the habitat at risk of immediate or future trawling activities. Nonetheless, the closure effectively freezes the current footprint of trawling activities until scientists can determine the full scope of deep-sea coral habitat and fisheries resources in the region and provides a *de facto* sanctuary for those coral species residing in deep water. Unfortunately, many coral species are found only within the depth range of current fishing activities (<1000 m); therefore, there may be no deepwater reserves to serve as a potential source of recruits to disturbed habitats at shallower depths for those species.

The majority of optimal coral and sponge habitats appear to occur at depths <1000 m, and approximately 40% of that habitat is now protected from bottom trawling. However, under provisions of the AIHCA, the majority of coral and sponge garden habitats appear to remain open to fishing activities. In the short term, the boundaries of the open and closed areas could be reconstructed to provide protection to the newly discovered gardens, but a long-term goal would be to conduct studies that expand the modeling effort of Woodby et al. (2009) and to focus on determination of the location of coral and sponge garden habitats. Efforts currently underway to increase the taxonomic resolution of fisheries bycatch data and improve the spatial resolution of seafloor bathymetry data will provide necessary inputs into models for the prediction of the location of the region's most important seafloor habitats.

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[2] Clausen, D. M., and C. J. Rodgveller. 2011. Assessment of the grenadier stock complex in the Gulf of Alaska, eastern Bering Sea, and Aleutian Islands. *In* Stock assessment and fishery evaluation report for the groundfish resources of the Bering Sea/Aleutian Islands regions, p. 1509–1511. [Available from North Pacific Fishery Management Council, 605 West 4th Ave., Suite 306, Anchorage, AK 99501.]

Acknowledgments

Major funding for this research was provided by the North Pacific Research Board, the West Coast and Polar Regions Center of NOAA's Undersea Research Center, and the NOAA Alaska Fisheries Science Center. J. Heifetz (National Marine Fisheries Service), D. Woodby (Alaska Department of Fish and Game), and J. Reynolds (University of Alaska Fairbanks) were co-principal investigators of the projects that contributed largely to this research. D. Alcorn contributed largely to this project by processing a massive amount of the video and coauthored the original report. D. Carlile (Alaska Department of Fish and Game), P. Rigby, P. Malecha, J. Orr, J. Hoff, and D. Courtney (National Marine Fisheries Service), S. France (University of Louisiana at Lafayette), L. Watling (University of Hawaii at Manoa), H. Lehnert (Freelance Sponge Taxonomy), L. Krutikov, S. Rooney, and D. Dove (University of Alaska Fairbanks), E. Brown (University of Western Australia), C. Kellogg (U.S. Geological Survey), S. Gerken (University Of Alaska Anchorage), G. Hendler, R. Clark, and J. McLean (Natural History Museum of Los Angeles County), G. Yogodzinski and C. Wyatt (University of South Carolina), D. Scholl and G. Greene (Moss Landing Marine Laboratories), B. Jicha (University of Wisconsin), S. Cairns and M. Vecchione (Smithsonian National Museum of Natural History), G. Williams (California Academy of Sciences), D. Opresko (Oak Ridge National Laboratory), S. Brooke (Florida State University), H. Reiswig (University of Victoria and Royal British Columbia Museum), A. Simpson (University of Maine), B. Horvath (Westmont College), M. Love (University of California, Santa Barbara), and A. Lindner (Duke University) are all gratefully acknowledged for their contributions to this research. I thank M. Masuda (National Marine Fisheries Service) for providing assistance with the odds-ratio analysis, J. Olson (National Marine Fisheries Service) for constructing figures 2, 3, and 15, J. Guinotte (Marine Conservation Institute) for analysis with graphical information systems, and J. Heifetz and K. Echave (National Marine Fisheries Service) for reviewing an earlier version of this manuscript. I thank Delta Oceanographics, Captain D. Minks and the crew of the RV *Velero IV*, the Deep Submergence Laboratory of the Woods Hole Oceanographic Institution, Scripps Institution of Oceanography, and Captain D. Murline and the crew of the RV *Roger Revelle* for their assistance and support.

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Appendix I. Dive parameters

Parameters for 71 dives made with the submersible *Delta* and remotely operated vehicle *Jason II* along 29 transects in 2003 and 2004 as part of this in situ exploration of deep-sea coral and sponge habitats in the central Aleutian Islands. Depth ranges represent the total depth range from the start to the end of each transect while the vehicle was in visual contact with the seafloor. Latitude and longitude coordinates are provided in decimal degrees.

Dive number	Date	Start coordinates	End coordinates	Depth range (m)
Delta 5985	28 June 2003	52.1750, –173.8353	52.1800, –173.8345	101–120
Delta 5986	29 June 2003	52.2338, –173.8361	52.2394, –173.8379	97–100
Delta 5987	29 June 2003	52.2300, –173.8382	52.2857, –173.8414	100–110
Delta 5988	1 July 2003	51.9844, –176.7359	51.9797, –176.7319	70–350
Delta 5989*	1 July 2003	51.9580, –176.8309	51.9440, –176.8362	104–167
Delta 5991	1 July 2003	51.9084, –177.2219	51.9040, –177.2137	60–355
Delta 5992	1 July 2003	51.9179, –177.4096	51.9118, –177.4144	65–350
Delta 5993	3 July 2003	51.4143, –178.5945	51.4011, –178.5735	100–295
Delta 5994	3 July 2003	51.3895, –178.5616	51.3965, –178.5619	103–130
Delta 5995	3 July 2003	51.5491, –177.9720	51.5544, –177.9554	115–352
Delta 5996	4 July 2003	51.3501, –179.4731	51.3553, –179.4909	110–347
Delta 5997	4 July 2003	51.3682, –179.4647	51.3630, –179.4934	95–355
Delta 5998	4 July 2003	51.3299, –179.5119	51.3385, –179.5202	169–238
Delta 5999*	4 July 2003	51.3505, –179.5073	51.3503, –179.5082	115–120
Delta 6000	5 July 2003	51.8423, 179.8144	51.8459, 179.8245	117–369
Delta 6001	5 July 2003	51.8988, 179.8121	51.9014, 179.7967	199–300
Delta 6002	5 July 2003	51.8787, 179.7774	51.8711, 179.7672	235–331
Delta 6003	5 July 2003	51.8982, 179.7629	51.9000, 179.7499	84–107
Delta 6004	6 July 2003	52.7736, –179.3169	52.7632, –179.3312	130–244
Delta 6005	6 July 2003	52.7325, –179.3107	52.7343, –179.3256	119–347
Delta 6006	7 July 2003	51.8814, –178.2380	51.8825, –178.2296	91–361
Delta 6007*	7 July 2003	51.9195, –178.4732	51.9223, –178.4702	120–151
Delta 6010	8 July 2003	52.2464, –174.8011	52.2379, –174.7985	121–133
Delta 6011	8 July 2003	52.2775, –174.8173	52.2705, –174.7989	175–346
Delta 6013	9 July 2003	52.4343, –173.8333	52.4268, –173.8268	156–351
Delta 6014*	9 July 2003	52.4640, –173.6105	52.4647, –173.6066	200–212
Delta 6199	26 June 2004	51.6199, –177.2343	51.6284, –177.2493	135–175
Delta 6200	26 June 2004	51.9868, –176.7552	51.9806, –176.7482	80–245
Delta 6201*	26 June 2004	51.9613, –176.8335	51.9614, –176.8332	110–150
Delta 6202*	27 June 2004	51.9622, –176.8364	51.9642, –176.8364	170–230
Delta 6203*	28 June 2004	51.8700, –176.2640	51.8706, –176.2665	138–159
Delta 6204*	28 June 2004	51.8716, –176.2626	51.8704, –176.2662	138–148
Delta 6205*	28 June 2004	51.8639, –176.2511	51.8679, –176.2541	99–113
Delta 6206*	29 June 2004	51.8671, –176.2521	51.8661, –176.2519	98–108
Delta 6207	30 June 2004	51.6156, –176.2755	51.6214, –176.2634	300–316
Delta 6208	30 June 2004	51.6761, –176.2730	51.6796, –176.2561	152–162
Delta 6209	30 June 2004	51.7183, –176.2990	51.7352, –176.2814	52–109
Delta 6211	2 July 2004	51.6004, –177.2721	51.5294, –177.2536	284–364
Delta 6212	2 July 2004	51.5951, –177.1671	51.6031, –177.1855	230–342
Delta 6213	3 July 2004	51.8647, –178.2373	51.8672, –178.2354	103–274
Delta 6214	3 July 2004	51.5966, –178.0229	51.6065, –177.9962	83–104
Delta 6215	3 July 2004	51.5727, –177.9683	51.5726, –177.9531	89–121
Delta 6216	4 July 2004	51.8553, –177.4711	51.8641, –177.4800	115–272
Delta 6217	4 July 2004	51.8956, –177.2384	51.8978, –177.2269	100–330
Delta 6218	5 July 2004	51.7784, –175.2195	51.7870, –175.2151	309–323
Delta 6219	5 July 2004	51.8601, –175.2613	51.8726, –175.2617	154–165
Delta 6220	5 July 2004	51.9062, –175.2892	51.9261, –175.2971	112–136
Delta 6221	6 July 2004	51.8983, –173.8720	51.9135, –173.8883	119–227
Delta 6222	6 July 2004	51.8493, –173.9090	51.8592, –173.9102	187–210
Delta 6223	6 July 2004	51.9465, –173.9405	51.9458, –173.9186	80–107
Delta 6224	6 July 2004	51.9703, –173.9470	51.9865, –173.9473	80–99
Delta 6226	7 July 2004	52.1838, –175.6083	52.1744, –175.6153	198–366
Delta 6227	7 July 2004	52.1419, –175.6272	52.1291, –175.6457	115–267
Delta 6228	7 July 2004	52.1069, –175.6410	52.0971, –175.6210	100–131
Delta 6229*	7 July 2004	52.1824, –175.5342	52.1808, –175.5319	56–182

Appendix I (cont.)

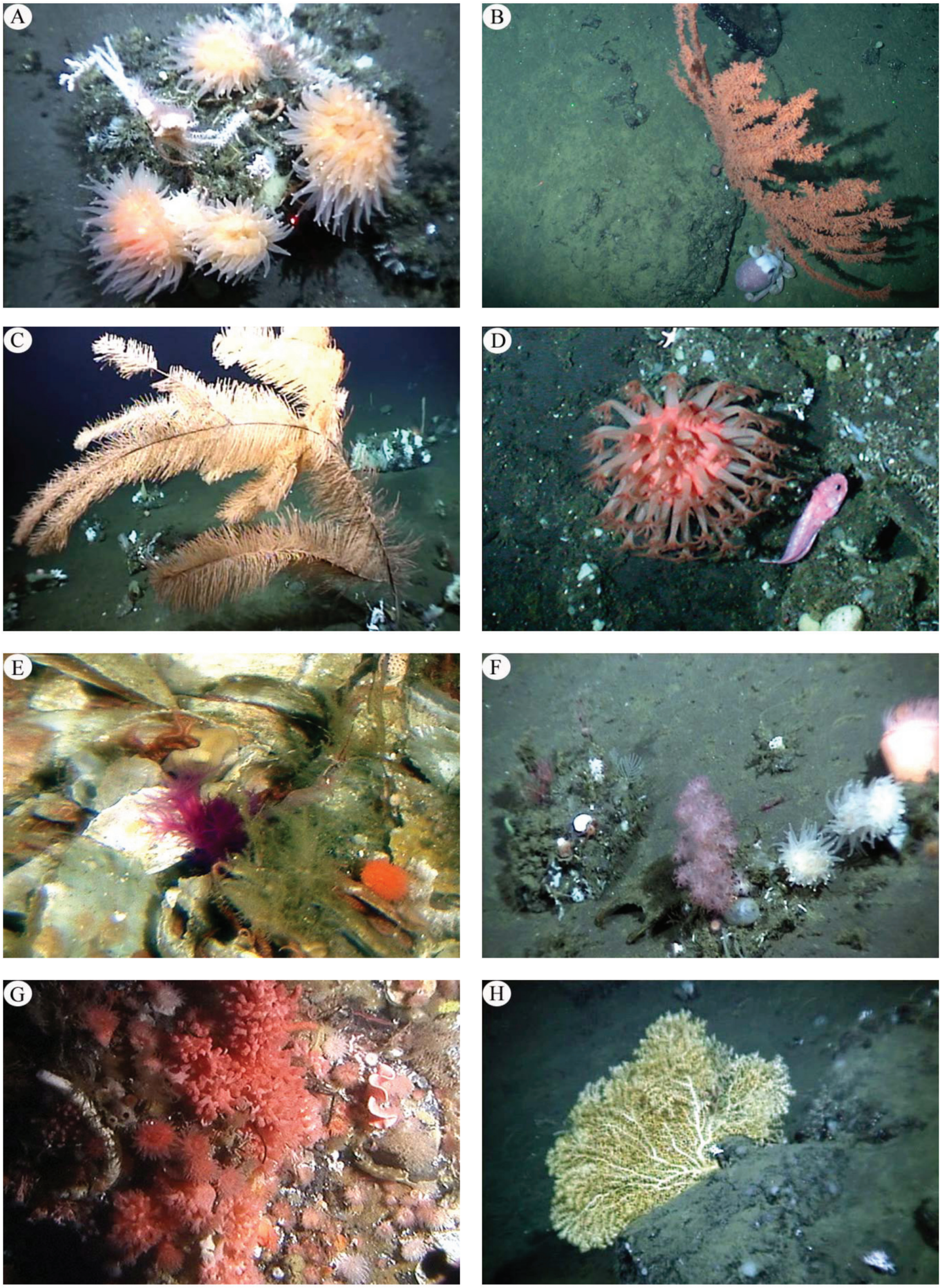
Dive number	Date	Start coordinates	End coordinates	Depth range (m)
Delta 6230*	8 July 2004	52.4690, –175.5980	52.4691, –175.5978	194–195
Delta 6231	8 July 2004	52.2175, –173.8305	52.2284, –173.8405	110–185
Jason II 095	25 July 2004	51.7219, –173.7813	51.8114, –173.8345	843–2828
Jason II 096	27 July 2004	52.4981, –174.9232	52.3929, –174.8840	2141–2947
Jason II 097	28 July 2004	51.4622, –176.2398	51.4930, –176.2329	1222–1734
Jason II 098	29 July 2004	51.3983, –177.0844	51.3770, –177.0604	1712–2852
Jason II 099	29 July 2004	51.4434, –177.0593	51.5092, –177.0367	1257–2533
Jason II 100	1 Aug 2004	51.5267, –177.0910	51.5310, –177.0985	1518–1811
Jason II 101	2 Aug 2004	51.4532, –177.8657	51.5254, –177.9597	485–1537
Jason II 102	3 Aug 2004	51.2782, –179.5686	51.3324, –179.5027	170–1846
Jason II 103	4 Aug 2004	51.7959, 179.9570	51.8480, 179.8387	396–1351
Jason II 104	5 Aug 2004	51.7309, –179.5846	51.6382, –179.5777	395–1011
Jason II 105	6 Aug 2004	51.9046, –178.3881	51.8711, –178.2619	870–2311
Jason II 106A	7 Aug 2004	51.9310, –177.3376	51.9120, –177.4025	354–1347
Jason II 106B	7 Aug 2004	51.8895, –177.3187	51.8926, –177.2762	889–1247
Jason II 107	8 Aug 2004	52.0325, –176.7679	51.9847, –176.7746	129–1556

*Dives made specifically to collect biological specimens only.

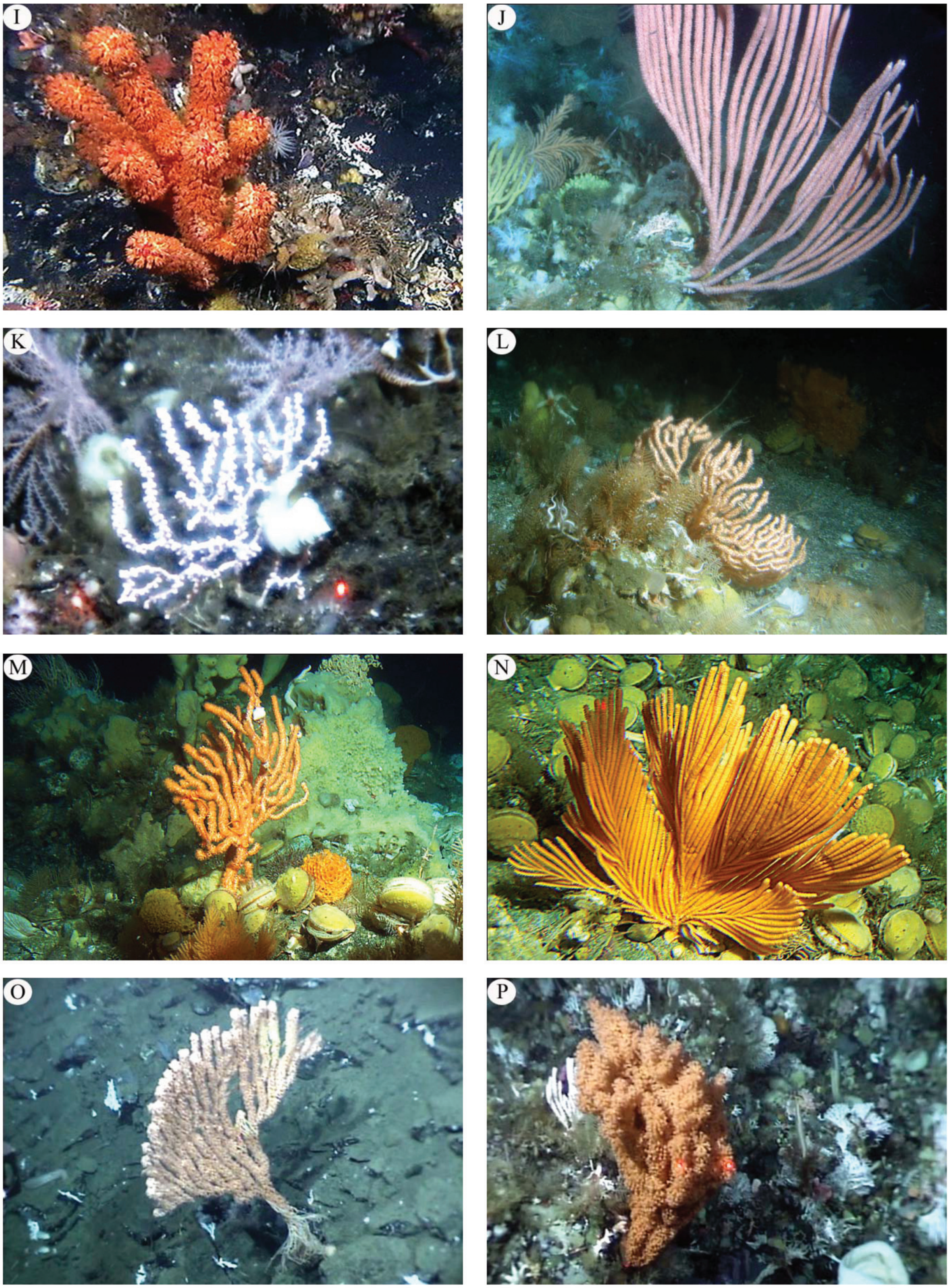
Appendix II. Coral taxa

Coral taxa observed and enumerated from analysis of video collected during dives made with the submersible *Delta* and remotely operated vehicle *Jason II* along 29 transects in 2003 and 2004 in the central Aleutian Islands. The separation between red laser marks present in some photos is 10 cm, providing a scaling tool for the measurement of fauna. (**A**) Scleractinians at a depth of 1196 m, (**B**) a black coral (*Dendrobathypathes boutillieri*) at a depth of 2019 m, (**C**) a black coral (*Parantipathes* sp.) at a depth of 1003 m, (**D**) a true soft coral (*Anthomastus* sp.) at a depth of 1332 m, (**E**) a true soft coral (*Anthothela* cf. *grandiflora*) at a depth of 100 m (see center of image), (**F**) a true soft coral (unknown Nephtheidae) at a depth of 1199 m (see center of image), (**G**) a stoloniferan coral (*Clavularia* sp.) at a depth of 205 m (see center of image), (**H**) a gorgonian (*Acanthogorgia* sp.) at a depth of 1894 m, (**I**) a gorgonian (*Alaskagorgia aleutiana*) at a depth of about 170 m, (**J**) a gorgonian (*Arthrogorgia* sp.) at a depth of about 200 m, (**K**) a gorgonian (*Calcigorgia beringi*) at a depth of 1247 m, (**L**) a gorgonian (*Calcigorgia spiculifera*) at a depth of about 160 m, (**M**) a gorgonian (*Cryogorgia koolsae*) at a depth of 100 m, (**N**) a gorgonian (*Fanellia fraseri*) at a depth of 98 m, (**O**) a bamboo coral (*Isidella tentaculum*) at a depth of 1348 m, (**P**) a bamboo coral (*Keratoisis* sp.) at a depth of 579 m, (**Q**) a gorgonian (*Muriceides nigra*) at a depth of 160 m, (**R**) a gorgonian, the bubble gum coral (*Paragorgia arborea*), at a depth of 150 m, (**S**) a gorgonian (*Plumarella aleutiana*) at a depth of 2828 m, (**T**) a gorgonian (*Plumarella echinata*) at a depth of 919 m, (**U**) a gorgonian (*Plumarella robusta*) at a depth of 711 m, (**V**) a gorgonian (*Plumarella superba*) at a depth of 105 m, (**W**) a gorgonian (*Primnoa pacifica willeyi*) at a depth of 863 m, (**X**) a gorgonian (*Primnoa wingi*) at a depth of 354 m, (**Y**) a gorgonian (*Radicipes verrilli*) at a depth of 2479 m, (**Z**) a gorgonian (*Swiftia pacifica*) at a depth of 726 m, (**AA**) a gorgonian (*Thouarella cristata*) at a depth of 150 m, (**BB**) a gorgonian (*Thouarella trilineata*) at a depth of 889 m, (**CC**) a pennatulacean (*Anthoptilum grandiflorum*) at a depth of 2284 m, (**DD**) pennatulaceans (*Halipteris willemoesi*) at a depth of 133 m, (**EE**) a pennatulacean (*Halipteris* sp. A) at a depth of 2150 m (see center of image), (**FF**) an unidentified pennatulacean at a depth of 2930 m, (**GG**) pennatulaceans (*Ptilosarcus gurneyi*) at a depth of 75 m, (**HH**) a pennatulacean (*Umbellula lindahli*) at a depth of 2846 m, (**II**) a hydrocoral (*Distichopora borealis*) at a depth of 720 m, (**JJ**) a hydrocoral (*Cyclohelia lamellata*) at a depth of 498 m, (**KK**) a hydrocoral (*Errinopora zarhyncha*) at a depth of 862 m (see center of image), (**LL**) a hydrocoral (*Stylaster campylecus*) at a depth of 681 m, (**MM**) a hydrocoral (*Stylaster* sp.) at a depth of 1280 m, and (**NN**) a hydrocoral (*Crypthelia trophostega*) at a depth of 1247 m.

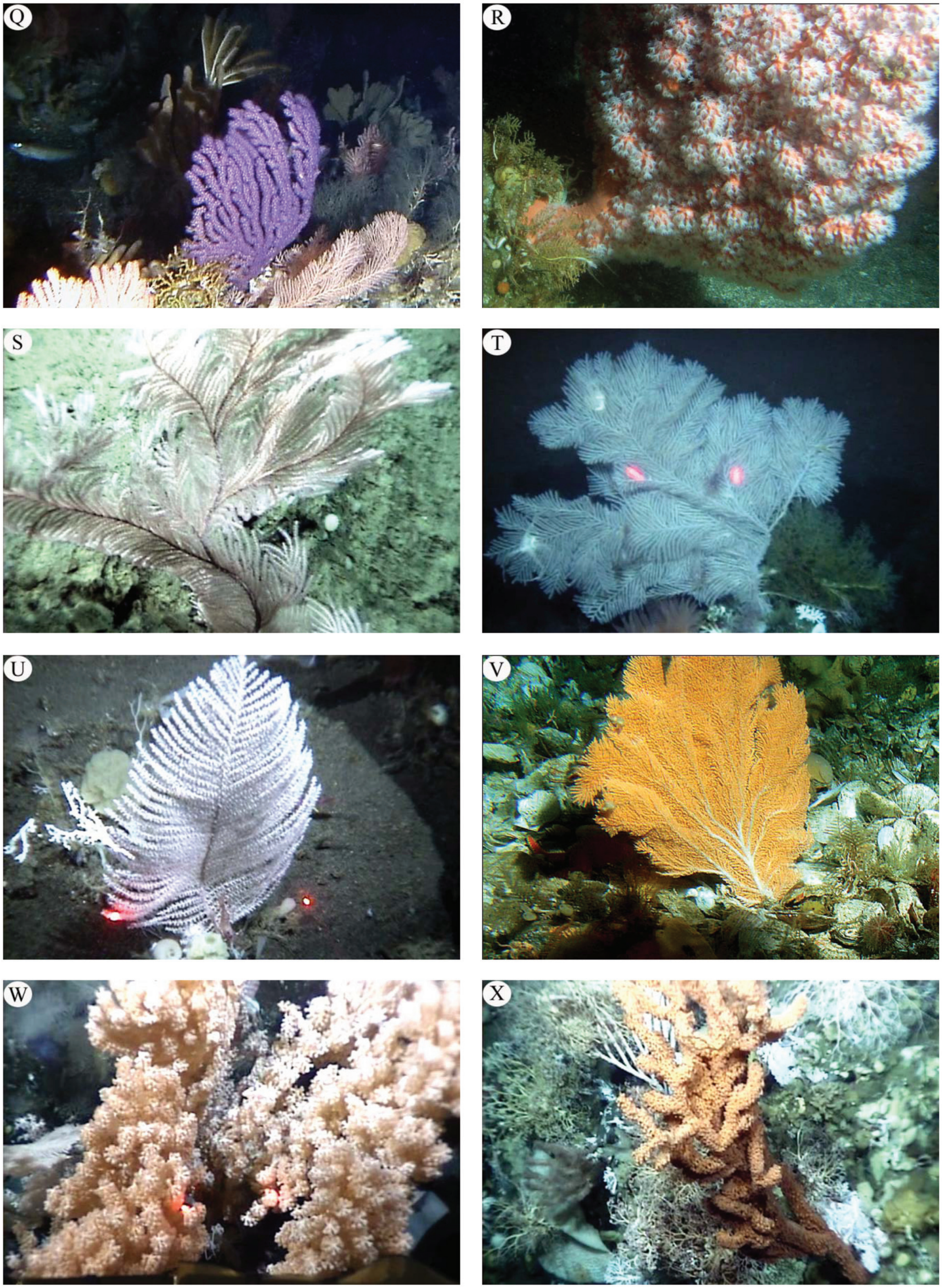
Appendix II, (A)–(H)



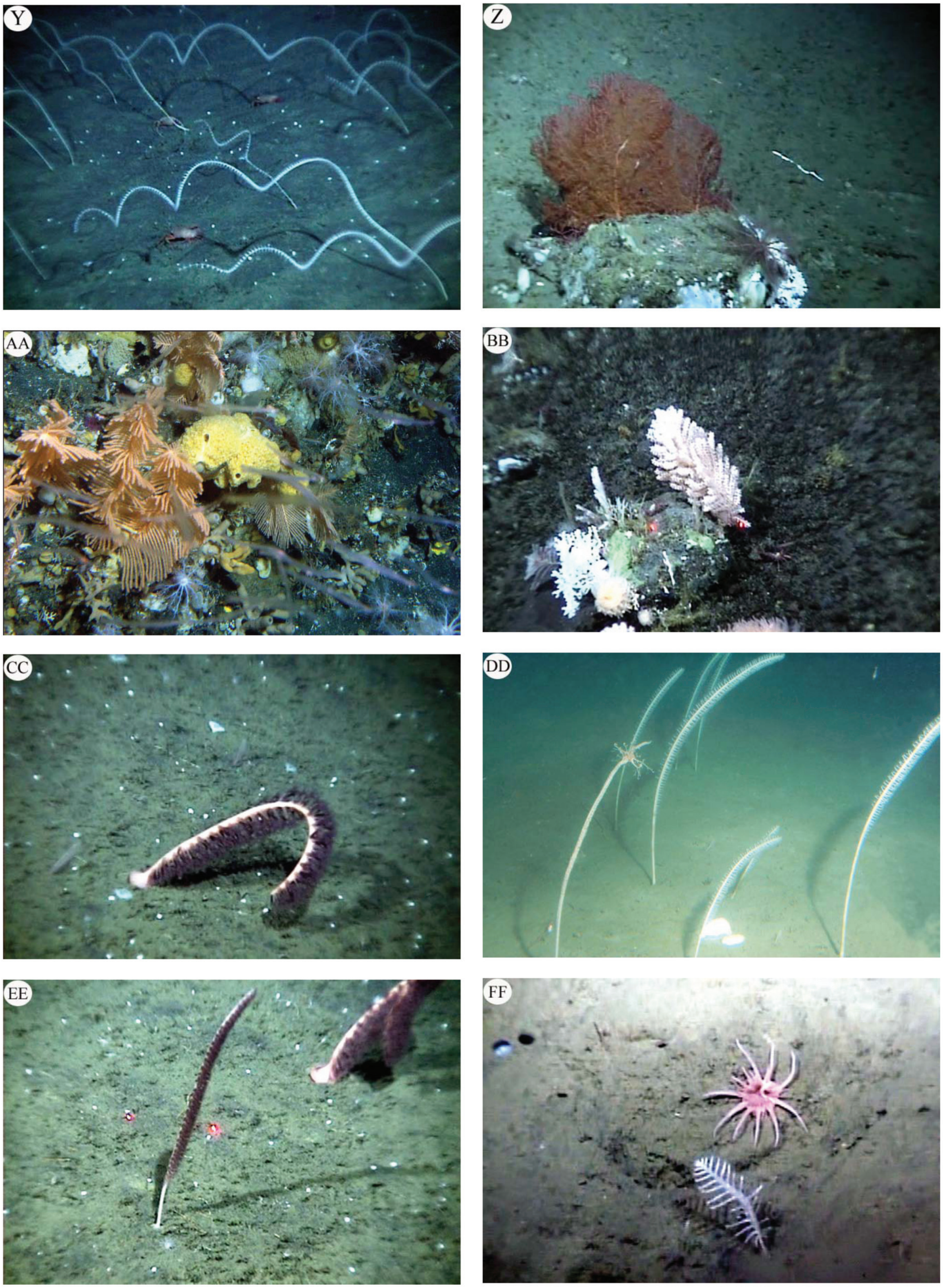
Appendix II, (I)–(P)



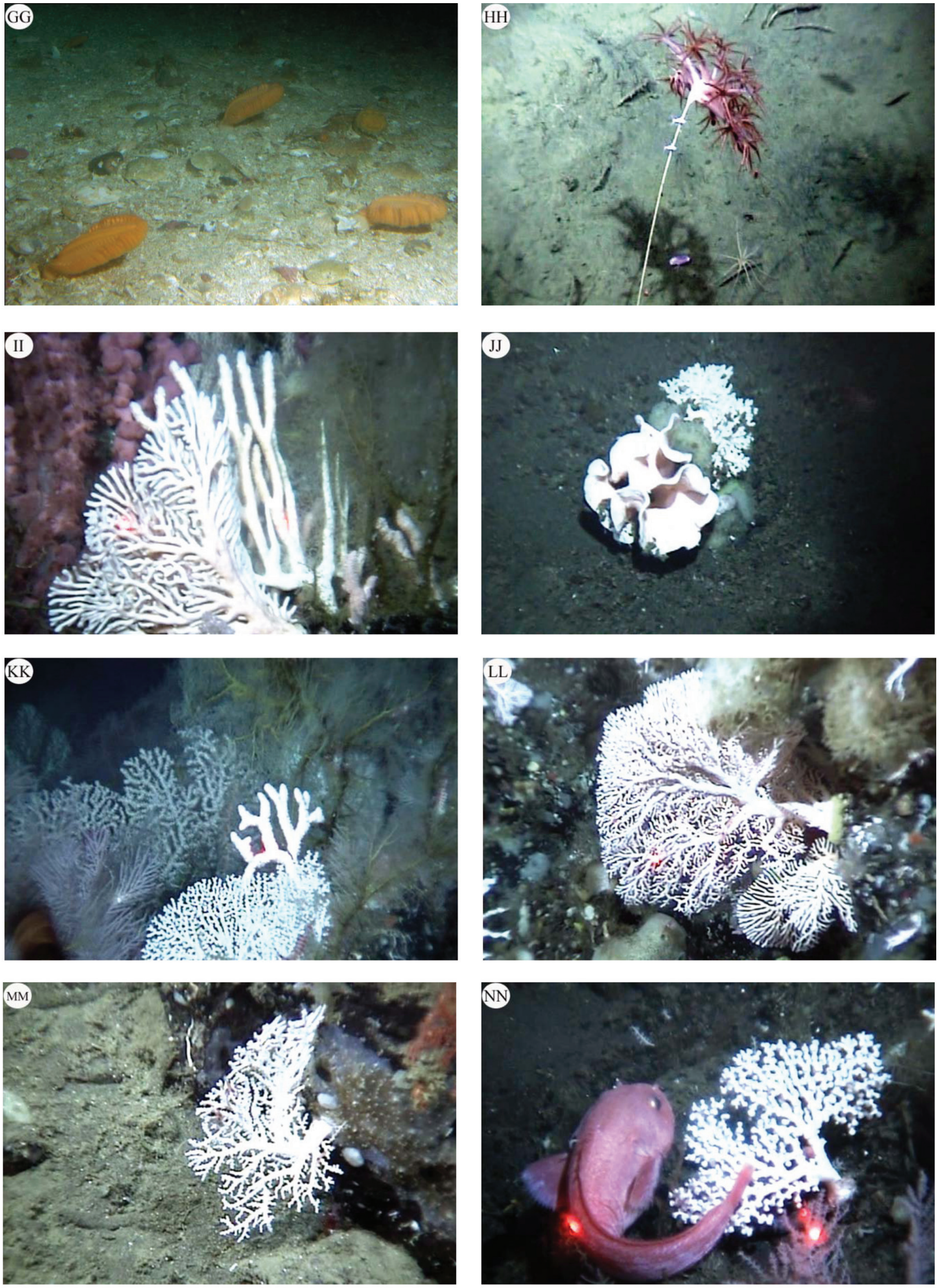
Appendix II, (Q)–(X)



Appendix II, (Y)–(FF)



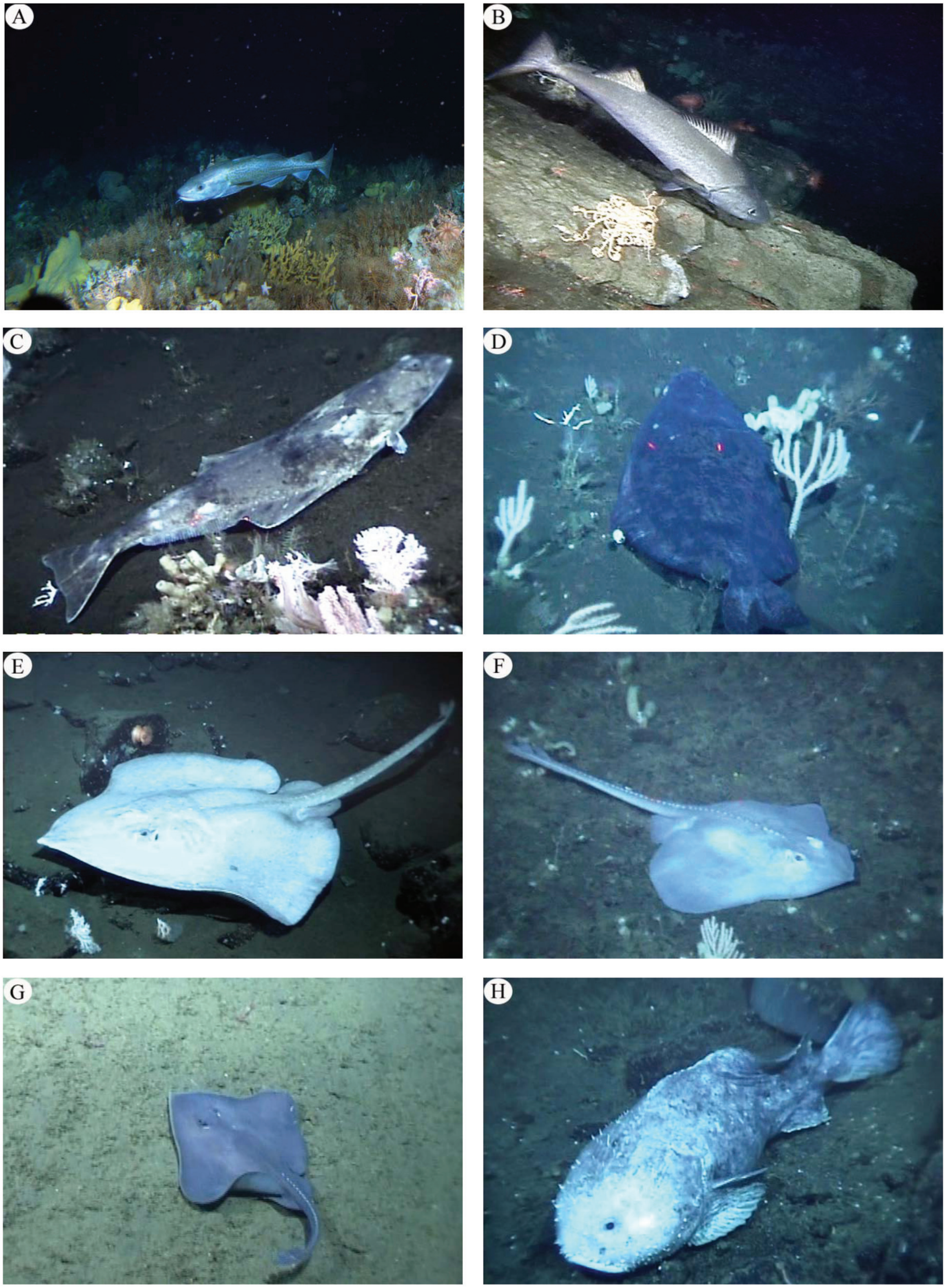
Appendix II, (GG)–(NN)



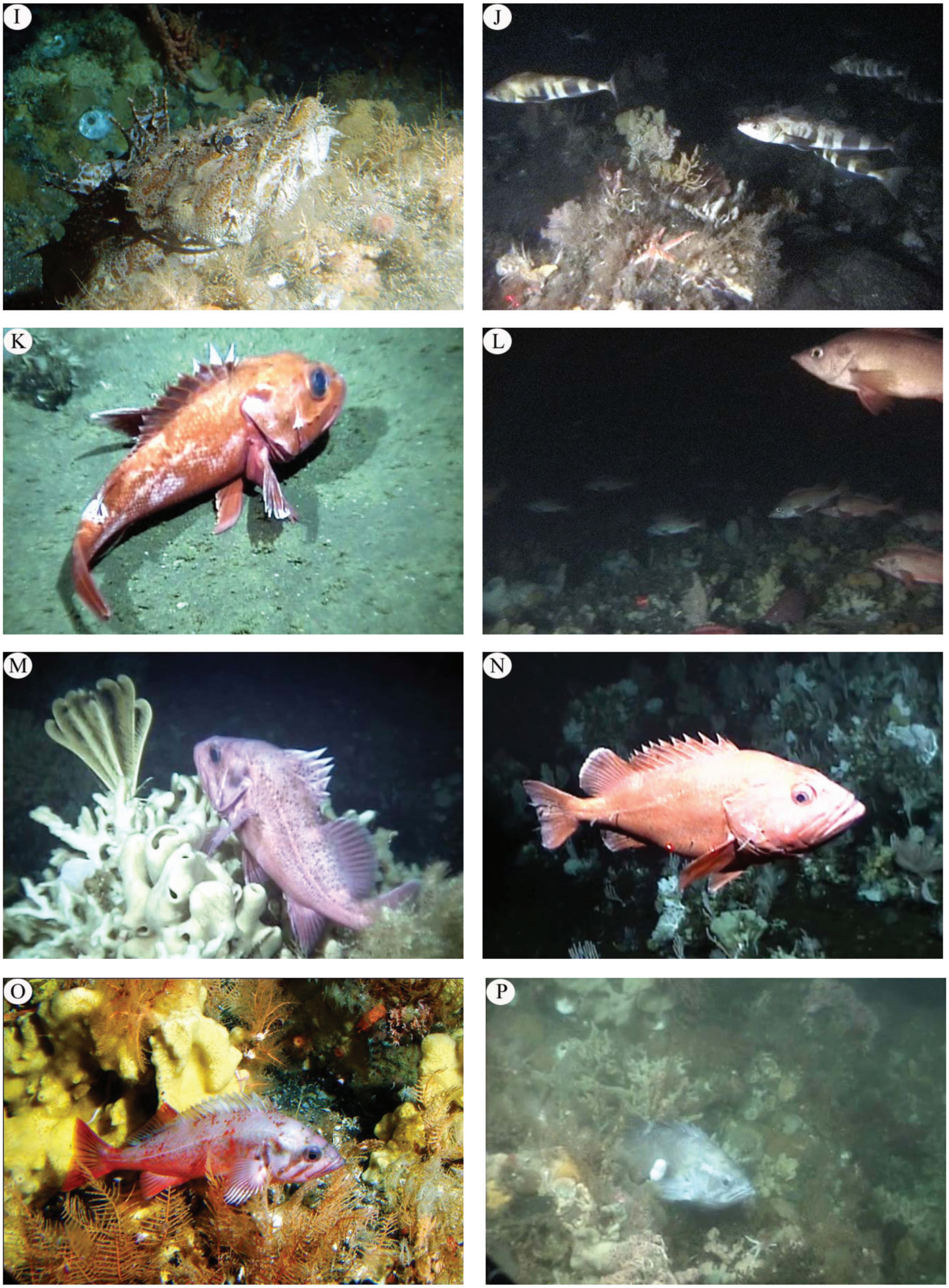
Appendix III. Fish, crab, and octopod taxa

Fish, crab, and octopod taxa observed and enumerated from analysis of video collected during dives made with the submersible *Delta* and remotely operated vehicle *Jason II* along 29 transects in 2003 and 2004 in the central Aleutian Islands. The separation between red laser marks present in some photos is 10 cm, providing a scaling tool for the measurement of fauna. Fish: (**A**) a Pacific Cod (*Gadus macrocephalus*) at a depth of about 150 m, (**B**) a Sablefish (*Anoplopoma fimbria*) at a depth of 607 m, (**C**) a Pacific Halibut (*Hippoglossus stenolepis*) at a depth of 519 m, (**D**) a Greenland Halibut (*Reinhardtius hippoglossoides*) at a depth of 773 m, (**E**) a Deepsea Skate (*Bathyraja abyssicola*) at a depth of 1474 m, (**F**) a Commander Skate (*Bathyraja lindbergi*) at a depth of 744 m, (**G**) a Roughtail Skate (*Bathyraja trachura*) at a depth of 978 m, (**H**) a Giant Blobsculpin (*Psychrolutes phrictus*) at a depth of 2466 m, (**I**) a Bigmouth Sculpin (*Hemitripterus bolini*) at a depth of about 100 m, (**J**) a school of Atka Mackerel (*Pleurogrammus monopterygius*) at a depth of about 130 m, (**K**) a Shortspine Thornyhead (*Sebastolobus alascanus*) at a depth of 1254 m, (L) a school of Pacific Ocean Perch (*Sebastes alutus*) at a depth of 154 m, (**M**) a Blackspotted Rockfish (*S. melanostictus*) at a depth of 217 m, (**N**) a Shortraker Rockfish (*S. borealis*) at a depth of 529 m, (**O**) a Northern Rockfish (*S. polyspinis*) at a depth of 150 m, (**P**) a Light Dusky Rockfish (*S. variabilis*) at a depth of 131 m, (**Q**) a Prowfish (*Zaprora silenus*) at a depth of about 120 m, (**R**) an eelpout (probably *Puzanovia rubra*) at a depth of 746 m, (**S**) a snailfish (Liparidae) at a depth of 859 m, (**T**) a ronquil, the Searcher (*Bathymaster signatus*), at a depth of about 100 m, (**U**) a Giant Grenadier (*Coryphaenoides pectoralis*) at a depth of 507 m, (**V**) a Pacific Flatnose (*Antimora microlepis*) at a depth of 1674 m, and (**W**) a Longnose Tapirfish (*Polyacanthonotus challengeri*) at a depth of 2822 m. Crabs: (**A**) a golden king crab (*Lithodes aequispinus*) at a depth of about 210 m, (**B**) a pair of deep-sea lithodid crabs at a depth of 1197 m, (**C**) a spiny *Paralomis* crab (*Paralomis multispina*) at a depth of 2180 m, (**D**) Verrill's *Paralomis* crab (*P. verrilli*) at a depth of 1323 m, and (**E**) a deep-sea Tanner crab (probably *Chionoecetes angulatus*) at a depth of 743 m. Octopods: (**A**) a North Pacific giant octopus (*Enteroctopus dofleini*) at a depth of about 150 m, (**B**) *Benthoctopus sibiricus* (924-m depth), (**C**) *Graneledone boreopacifica* (1706-m depth), (**D**) *Cirrothauma* cf. *murrayi* (2161-m depth), (**E**) *Opisthoteuthis* sp. (764-m depth), and (**F**) *Grimpoteuthis* sp. (2295-m depth).

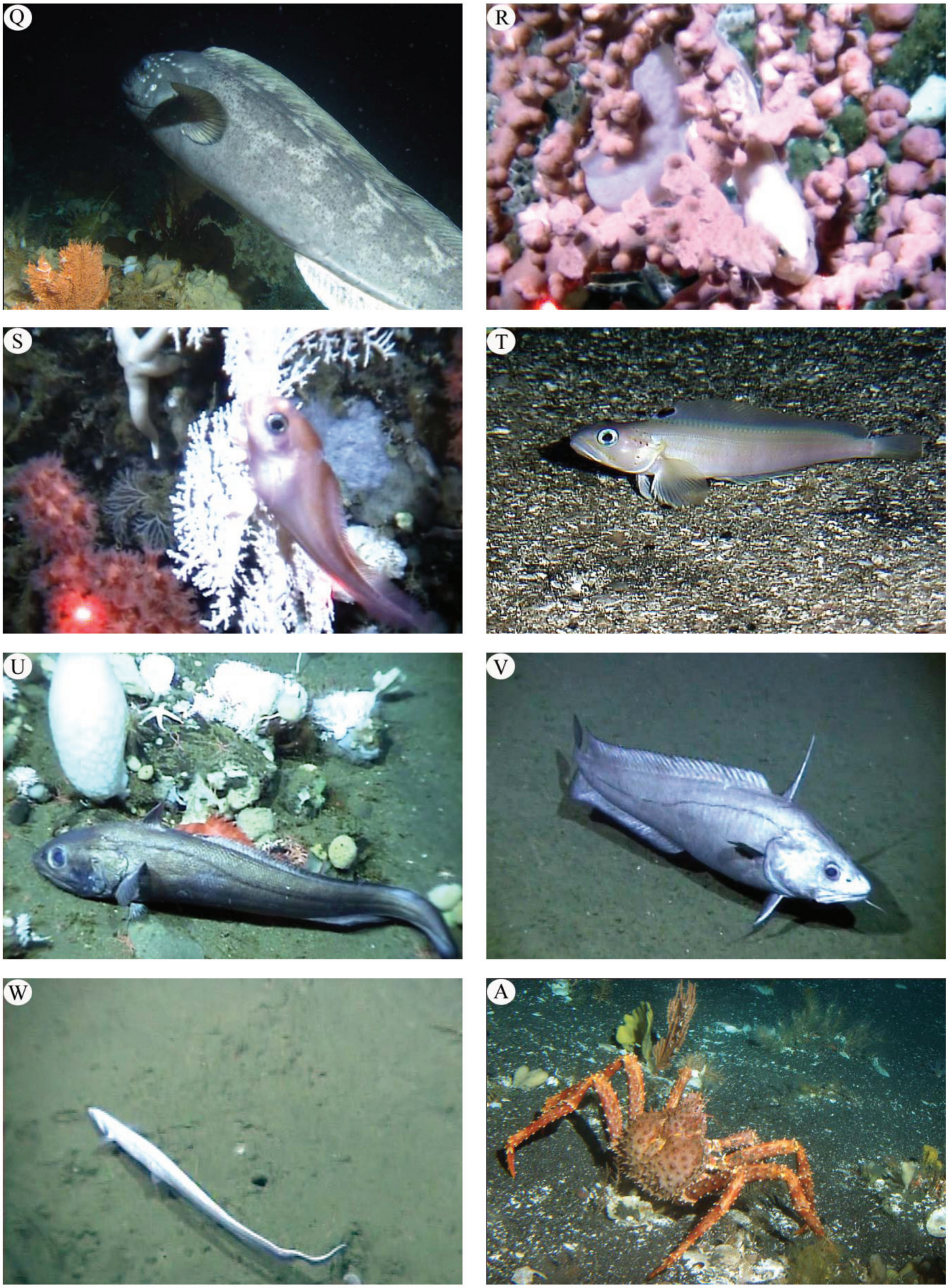
Appendix III, Fish: (A)–(H)



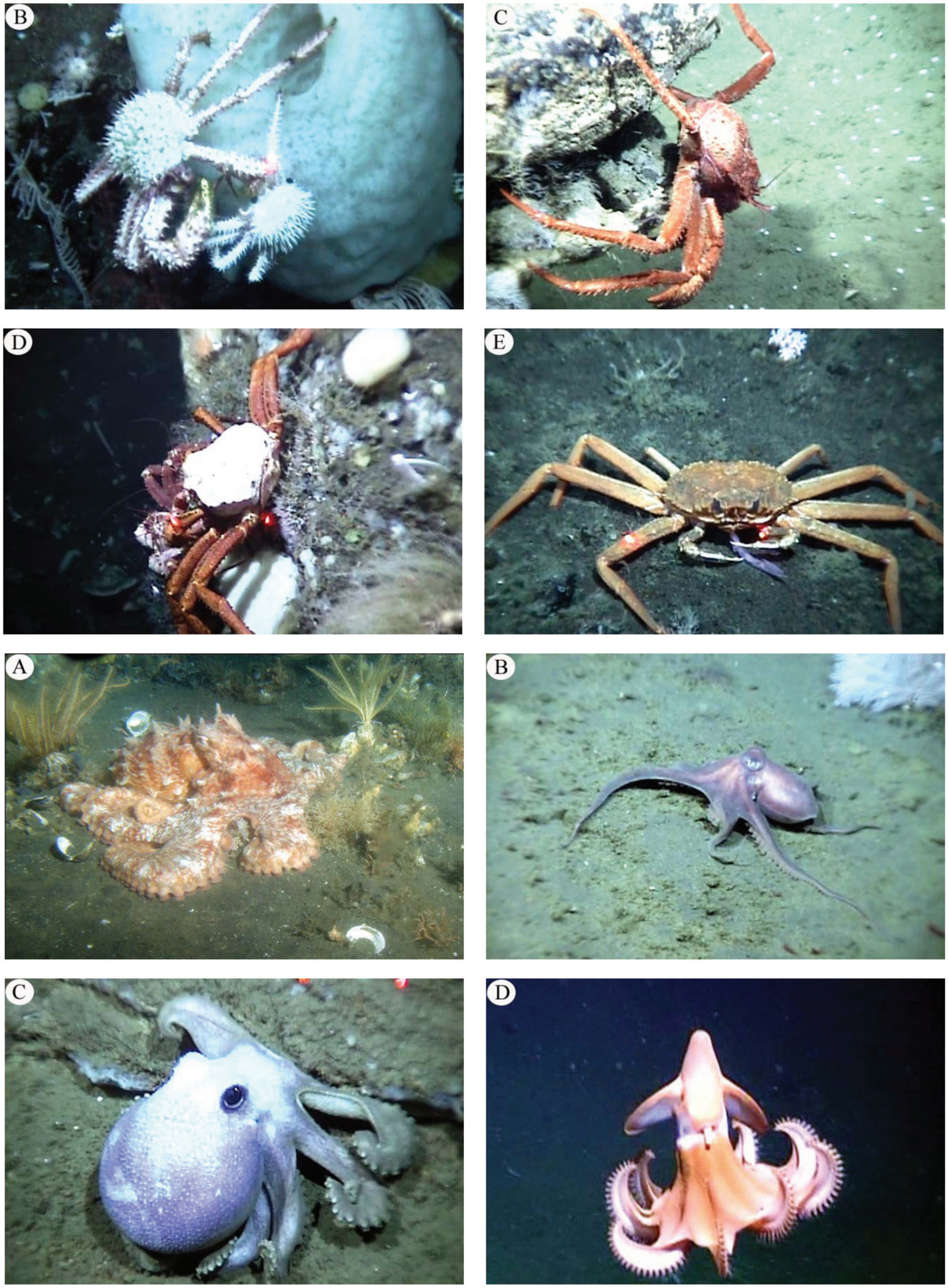
Appendix III, Fish: (I)–(P)



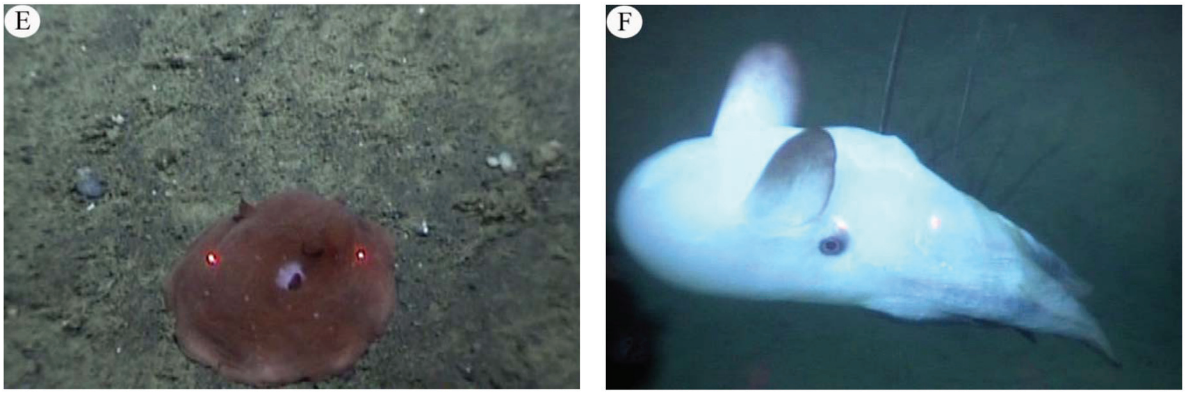
Appendix III, Fish: (Q)–(W); Crabs: (A)



Appendix III, Crabs: (B)–(E); Octopods: (A)–(D)



Appendix III, Octopods: (E)–(F)



Appendix IV. Sampling effort by substrate type

Sampling effort (numbers of frames and transects and area of seafloor) by substrate type of surveys conducted along 29 transects with the submersible *Delta* and remotely operated vehicle *Jason II* in 2003 and 2004 in central Aleutian Islands. Substrates were visually classified through the use of the Wentworth classification scale (Holme and McIntyre, 1971) and a hierarchy of up to 4 sediment types. Hexactinellid equals hexactinellid skeleton. Substrates with 4 sediment types are lumped together in a single category (e.g., bedrock/xxxx/xxxx/xxxx).

Substrate type	Number of frames	Number of transects	Area (m^2)	Depth range (m)
Bedrock	246	11	443.4	52–1929
Bedrock/Hexactinellid	2	1	3.6	811
Bedrock/Boulder	16	4	26.8	91–1349
Bedrock/Cobble	17	6	35.5	101–1332
Bedrock/Pebble	12	2	60.4	111–1775
Bedrock/Sand	461	12	813.3	52–2335
Bedrock/Silt	105	6	164.8	103–1588
Bedrock/Shell	7	3	22.0	83–110
Bedrock/Hexactinellid /Cobble	2	1	2.2	818
Bedrock/Hexactinellid /Sand	3	1	6.1	811–813
Bedrock/Boulder/Cobble	2	2	4.1	105–1346
Bedrock/Boulder/Sand	80	7	242.1	99–2093
Bedrock/Boulder/Silt	9	1	15.3	1340–1347
Bedrock/Boulder/Shell	1	1	3.2	103
Bedrock/Cobble/Pebble	1	1	1.4	1339
Bedrock/Cobble/Sand	100	8	155.7	85–1818
Bedrock/Cobble/Silt	3	1	5.7	1334–1346
Bedrock/Cobble/Shell	1	1	1.3	106
Bedrock/Pebble/Sand	1	1	3.3	121
Bedrock/Sand/Siltstone	1	1	2.2	1095
Bedrock/Sand/Hexactinellid	2	1	2.3	904–905
Bedrock/Sand/Boulder	58	3	183.4	101–2297
Bedrock/Sand/Cobble	143	11	209.5	83–2313
Bedrock/Sand/Pebble	44	7	69.3	66–2316
Bedrock/Sand/Silt	68	4	121.6	197–1641
Bedrock/Sand/Shell	20	3	52.0	58–112
Bedrock/Silt/Boulder	2	1	2.9	889–1562
Bedrock/Silt/Cobble	5	3	6.7	151–1586
Bedrock/Silt/Sand	166	3	253.1	777–1651
Bedrock/Silt/Shell	23	1	69.7	103–127
Bedrock/Shell/Sand	1	1	3.3	80
Bedrock/xxxx/xxxx/xxxx	41	10	121.0	84–1867
Total (Bedrock)	1643	16	3107.2	52–2335
Siltstone/Sand	25	3	45.2	1087–2579
Siltstone/Silt	126	2	296.1	1192–2918
Siltstone/Bedrock/Silt	4	1	5.6	2882–2883
Siltstone/Sand/ Hexactinellid	1	1	1.2	947
Siltstone/Sand/Pebble	3	1	4.1	1561–1681
Siltstone/Sand/Silt	2	2	2.6	895–1250
Siltstone/Silt/Boulder	1	1	1.2	1561
Siltstone/Silt/Sand	1	1	1.1	1543
Total (Siltstone)	163	2	357.1	895–2918
Hexactinellid	6	2	4.3	341–957
Hexactinellid/Sand	18	2	21.3	275–964
Hexactinellid/Silt	14	1	19.3	753–758
Hexactinellid/Siltstone/Sand	3	1	3.4	954
Hexactinellid/Cobble/Bedrock	1	1	.5	819
Hexactinellid/Cobble/Sand	13	1	17.4	258–827
Hexactinellid/Cobble/Silt	3	1	4.9	797
Hexactinellid/Sand/Cobble	48	1	61.6	289–1015

Appendix IV (cont.)

Substrate type	Number of frames	Number of transects	Area (m²)	Depth range (m)
Hexactinellid/Sand/Pebble	27	1	34.9	248–632
Hexactinellid/Sand/Silt	33	1	42.6	972–1038
Hexactinellid/Silt/Pebble	1	1	1.2	753
Total (Hexactinellid)	159	1	211.4	248–1038
Boulder	19	5	31.9	99–2486
Boulder/Bedrock	11	4	17.0	102–1423
Boulder/Cobble	2	2	3.3	162-2263
Boulder/Pebble	1	1	1.4	2223
Boulder/Sand	35	7	70.5	98–2493
Boulder/Silt	13	1	29.0	102–157
Boulder/Bedrock/Cobble	1	1	1.2	1361
Boulder/Bedrock/Pebble	2	2	3.8	1340–1713
Boulder/Bedrock/Sand	13	3	21.6	106–2198
Boulder/Bedrock/Silt	3	1	4.9	1337
Boulder/Cobble/Pebble	1	1	1.7	1323
Boulder/Cobble/Sand	49	11	94.2	99–2427
Boulder/Cobble/Silt	3	2	4.5	102–1346
Boulder/Pebble/Sand	11	5	19.7	106–2366
Boulder/Pebble/Silt	1	1	1.6	1337
Boulder/Sand/Bedrock	12	2	17.7	543–1870
Boulder/Sand/Hexactinellid	2	1	2.8	438–486
Boulder/Sand/Cobble	40	9	79.8	100–2407
Boulder/Sand/Pebble	16	7	33.3	185–2403
Boulder/Sand/Silt	14	2	32.2	205–2511
Boulder/Sand/Shell	1	1	1.5	349
Boulder/Silt/Siltstone	3	1	4.8	1197–1523
Boulder/Silt/Cobble	2	2	3.8	140–1337
Boulder/Silt/Sand	2	2	2.7	114–116
Boulder/Silt/Shell	3	1	5.0	106–125
Boulder/xxxx/xxxx/xxxx	114	11	289.0	101–2466
Total (Boulder)	374	19	778.9	98–2511
Cobble/Bedrock	1	1	.8	1375
Cobble/Boulder	1	1	1.4	1339
Cobble/Pebble	1	1	1.2	399
Cobble/Sand	20	3	30.6	99–2354
Cobble/Silt	1	1	1.2	101
Cobble/Bedrock/Sand	11	2	11.1	411–1902
Cobble/ Hexactinellid /Boulder	2	1	3.4	349–350
Cobble/ Hexactinellid /Sand	5	1	7.4	330–357
Cobble/ Hexactinellid /Silt	17	1	32.5	796–807
Cobble/Boulder/Pebble	9	2	20.5	177–2350
Cobble/Boulder/Hexactinellid	1	1	1.3	247
Cobble/Boulder/Sand	3	1	4.6	2098–2358
Cobble/Boulder/Silt	1	1	1.4	1345
Cobble//Pebble/Bedrock	1	1	6.1	290
Cobble/Pebble/Boulder	5	1	9.6	179–182
Cobble/Pebble/Sand	172	10	283.9	100–1324
Cobble/Pebble/Silt	6	1	8.4	1345–1346
Cobble/Pebble/Shell	4	1	5.5	442–481
Cobble/Sand/Bedrock	18	2	19.9	410–1813
Cobble/Sand/Hexactinellid	13	1	17.5	324–621
Cobble/Sand/Boulder	11	3	17.3	173–2351
Cobble/Sand/Pebble	56	7	100.3	123–2354
Cobble/Sand/Shell	2	2	2.9	88–99
Cobble/Silt/Boulder	1	1	1.0	101
Cobble/xxxx/xxxx/xxxx	52	10	105.0	93–1374
Total (Cobble)	414	17	694.8	88–2358

Appendix IV (cont.)

Substrate type	Number of frames	Number of transects	Area (m^2)	Depth range (m)
Pebble	3	2	3.0	343–420
Pebble/Boulder	2	1	3.2	2179–2365
Pebble/Cobble	6	2	7.4	696–2216
Pebble/Sand	128	9	145.0	68–1691
Pebble/Silt	1	1	2.5	298
Pebble/Shell	47	2	64.8	90–467
Pebble/Bedrock/Boulder	3	1	24.4	289
Pebble/ Hexactinellid/Sand	5	1	6.6	346–347
Pebble/Boulder/Bedrock	1	1	7.3	290
Pebble/Boulder/Sand	2	2	3.8	473
Pebble/Boulder/Shell	1	1	1.6	371
Pebble/Cobble/Bedrock	1	1	3.5	289
Pebble/Cobble/Boulder	3	1	21.9	289–290
Pebble/Cobble/Sand	88	11	146.5	122–478
Pebble/Cobble/Shell	49	2	64.5	89–499
Pebble/Sand/Bedrock	5	2	7.8	1262–2088
Pebble/Sand/Boulder	5	3	12.6	69–290
Pebble/Sand/Cobble	134	13	212.8	67–417
Pebble/Sand/Shell	30	3	37.9	68–476
Pebble/Silt/Boulder	2	1	4.6	297–298
Pebble/Shell/Boulder	1	1	2.5	90
Pebble/Shell/Cobble	35	2	46.3	279–476
Pebble/Shell/Sand	11	2	15.8	90–417
Pebble/xxxx/xxxx/xxxx	84	7	153.6	71–2024
Total (Pebble)	647	18	999.9	67–2365
Sand	4164	19	5976.5	63–2583
Sand/Bedrock	446	10	717.2	71–2347
Sand/Siltstone	197	4	272.7	777–2578
Sand/Hexactinellid	83	2	103.1	275–985
Sand/Boulder	319	11	717.7	95–2431
Sand/Cobble	547	14	941.3	86–2431
Sand/Pebble	3552	20	4826.6	63–2426
Sand/Silt	5827	12	7828.8	104–2528
Sand/Shell	27	6	47.9	80–398
Sand/Bedrock/Boulder	31	3	50.7	543–2347
Sand/Bedrock/Hexactinellid	3	1	2.9	933–934
Sand/Bedrock/Cobble	111	6	153.1	106–2346
Sand/Bedrock/Pebble	125	7	189.0	154–2340
Sand/Bedrock/Silt	38	3	53.7	777–1640
Sand/Bedrock/Shell	5	2	29.7	53–365
Sand/Siltstone/Bedrock	1	1	2.0	1095
Sand/Siltstone/Hexactinellid	11	1	14.5	583–999
Sand/Siltstone/Cobble	7	2	8.4	777–1686
Sand/Siltstone/Pebble	11	3	13.5	249–1686
Sand/Siltstone/Silt	11	3	15.0	894–1250
Sand/Hexactinellid /Bedrock	3	1	3.9	837–935
Sand/Hexactinellid /Siltstone	1	1	1.2	946
Sand/Hexactinellid /Boulder	8	1	10.3	476–791
Sand/Hexactinellid /Cobble	68	1	96.2	248–1004
Sand/Hexactinellid /Pebble	232	2	310.5	245–988
Sand/Hexactinellid /Silt	36	1	45.6	981–1038
Sand/Boulder/Bedrock	34	5	51.5	491–2348
Sand/Boulder/Hexactinellid	9	1	12.1	247–488
Sand/Boulder/Cobble	216	9	507.2	99–2438
Sand/Boulder/Pebble	56	10	102.9	109–2431
Sand/Boulder/Silt	6	3	8.5	1079–2434
Sand/Boulder/Shell	2	2	6.3	109–125
Sand/Cobble/Bedrock	57	6	101.1	63–2344

Appendix IV (cont.)

Substrate type	Number of frames	Number of transects	Area (m²)	Depth range (m)
Sand/Cobble/Siltstone	1	1	2.1	1177
Sand/Cobble/Hexactinellid	52	1	68.7	240–734
Sand/Cobble/Boulder	101	9	273.8	106–2385
Sand/Cobble/Pebble	226	19	353.9	96–2414
Sand/Cobble/Silt	10	4	14.2	234–1559
Sand/Cobble/Shell	22	5	42.8	80–516
Sand/Pebble/Bedrock	84	8	131.2	109–2299
Sand/Pebble/Siltstone	2	2	2.5	249–1676
Sand/Pebble/Hexactinellid	276	2	337.9	235–1027
Sand/Pebble/Boulder	67	10	117.4	63–2365
Sand/Pebble/Cobble	865	22	1232.0	63–2415
Sand/Pebble/Silt	35	6	46.3	152–2434
Sand/Pebble/Shell	294	12	471.7	68–601
Sand/Silt/Bedrock	141	6	204.8	194–1895
Sand/Silt/Siltstone	68	3	88.0	894–1359
Sand/Silt/Hexactinellid	186	1	238.1	265–1260
Sand/Silt/Boulder	85	5	215.3	152–2521
Sand/Silt/Cobble	361	11	537.9	153–2515
Sand/Silt/Pebble	751	10	1003.1	133–2467
Sand/Silt/Shell	9	1	15.0	295–306
Sand/Shell/Bedrock	1	1	5.6	89
Sand/Shell/Boulder	1	1	1.5	102
Sand/Shell/Cobble	8	3	14.1	79–315
Sand/Shell/Pebble	97	5	170.2	66–600
Sand/xxxx/xxxx/xxxx	241	14	492.8	85–2514
Total (Sand)	20,236	27	29,302.4	53–2583
Silt	7907	4	11,510.7	119–2947
Silt/Bedrock	34	3	50.7	148–1582
Silt/Siltstone	72	2	117.5	1518–2892
Silt/Boulder	19	2	35.4	130–1567
Silt/Cobble	16	3	29.5	99–1634
Silt/Pebble	3	1	5.2	1197–1198
Silt/Sand	1816	5	1487.2	102–1843
Silt/Shell	4	1	5.0	1537–1807
Silt/Bedrock/Cobble	7	3	13.0	149–1595
Silt/Bedrock/Pebble	1	1	1.4	1220
Silt/Bedrock/Sand	37	3	52.4	786–1652
Silt/Bedrock/Shell	1	1	2.2	128
Silt/Siltstone/Pebble	1	1	1.6	1198
Silt/Siltstone/Sand	1	1	1.8	1196
Silt/Boulder/Cobble	10	1	20.8	129–150
Silt/Boulder/Sand	4	1	4.4	115–117
Silt/Boulder/Shell	1	1	2.3	126
Silt/Cobble/Bedrock	1	1	1.8	150
Silt/Cobble/Boulder	8	2	13.4	105–149
Silt/Cobble/Sand	5	2	7.0	106–884
Silt/Pebble/Sand	2	1	2.4	1543
Silt/Sand/Bedrock	58	3	77.1	820–1675
Silt/Sand/Siltstone	3	1	2.3	1284–1285
Silt/Sand/Boulder	10	3	15.1	114–1663
Silt/Sand/Cobble	19	5	26.7	105–1681
Silt/Sand/Pebble	3	1	2.6	1194–1643
Silt/Sand/Shell	20	1	13.7	102–103
Silt/Shell/Bedrock	1	1	1.5	1673
Silt/xxxx/xxxx/xxxx	4	3	5.2	1212–1593
Total (Silt)	10,068	12	13,509.9	99–2947

Appendix IV (cont.)

Substrate type	Number of frames	Number of transects	Area (m^2)	Depth range (m)
Shell/Sand	1	1	1.4	91
Shell/Silt	1	1	1.0	1746
Shell/Pebble/Sand	4	2	4.7	90–386
Shell/Sand/Boulder	1	1	.8	87
Shell/Sand/Pebble	6	1	14.3	91–98
Shell/xxxx/xxxx/xxxx	1	1	1.5	489
Total (Shell)	14	5	23.7	90–1746
Grand total	33,718	29	48,985.3	52–2947