

1 **Validation of models of the distribution of structure-forming invertebrates in**
2 **the eastern Bering Sea using an underwater stereo camera**

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6

7 **Abstract**

8 In summer 2014 we conducted a survey of the eastern Bering Sea slope and outer shelf using an
9 underwater stereo camera at 250 randomly selected transects. The objective of this survey was to
10 verify distribution models of coral, sponge, and sea whips that were based on bottom trawl
11 survey data that had been presented to the North Pacific Fishery Management Council in June
12 2013. Additionally, we collected data on invertebrate density, height, and fish associations and
13 documented the presence of fishing gear and damage to invertebrates. Presence or absence
14 models of coral, sponge and sea whips were also constructed from the camera survey data and
15 were compared to previous coral, sponge, and sea whip models constructed from bottom trawl
16 survey data. The model of coral presence or absence based on bottom trawl survey data was
17 generally accurate in predicting coral presence or absence in the camera survey. The bottom
18 trawl survey models were also accurate in predicting sponge and sea whip presence or absence,
19 but to a lesser degree than for coral. Corals were found at 32 of 250 transects, most of which
20 were located in Pribilof Canyon and the slope area to the northwest. Overall, the densities of
21 corals were low, averaging $0.005 \text{ individuals} \cdot \text{m}^{-2}$ and ranging from 0 to $0.28 \text{ individuals} \cdot \text{m}^{-2}$.
22 The low densities were consistent with the absence of hard substrates for coral attachment in
23 most areas of the eastern Bering Sea. Densities of corals were generally highest in Pribilof

24 Canyon and corals were largest in the slope area to the northwest of Pribilof Canyon. For
25 sponges, densities and heights were highest surrounding Pribilof Canyon, north of Bering
26 Canyon, and in some locations in Zhemchug Canyon. Sea whip densities and heights were
27 highest on the outer shelf between Pribilof and Zhemchug Canyon and in an area to the south of
28 Pribilof Canyon. There were significant positive relationships between fish density and the
29 presence of coral and sponge for some rockfish species and king crabs. There were significant
30 negative relationships for grenadiers and *Chionoecetes* crabs. Direct evidence of fishing gear
31 occurred at 12.8% of transects. Individual demosponges (0.3%), Isididae corals (2.9%) and sea
32 whips (9.0%) were observed to be damaged. Vulnerability of benthic invertebrates was estimated
33 from the field data on invertebrate density and height and was modeled for the entire eastern
34 Bering Sea outer shelf and slope. Based on height and density, the areas that appeared to be most
35 vulnerable for coral occurred in narrow areas of the two arms of Pribilof Canyon and in deeper
36 areas to the northwest along the slope. For sponge and sea whips, the most vulnerable areas were
37 centered around the shelf break and extended from Pribilof Canyon to the north for sponge and
38 from Bering Canyon to the north for sea whips. Although combining the bottom trawl survey
39 models and the camera survey models only exhibited some improvement over bottom trawl
40 survey data-based models alone, the combined models were able to integrate both bottom trawl
41 and camera data into a single map of the probability of invertebrate presence and from this a
42 prediction of density of invertebrates for the eastern Bering Sea slope and outer shelf.

43

44 **1. Introduction**

45 The fish and crab resources of the eastern Bering Sea slope and outer shelf are widely
46 utilized by commercial fisheries in Alaska. The eastern Bering Sea slope and outer shelf is a

47 region of enhanced primary and secondary productivity (the “Bering Sea Greenbelt”) that attracts
48 large numbers of fish, seabirds, and marine mammals; productivity is enhanced because of
49 physical processes at the shelf break including intensive tidal mixing and transverse circulation
50 and eddies in the Bering Slope Current which bring nutrients into the photic zone (Springer et al.
51 1996). About 40% of U.S. commercial fisheries catch originates from the eastern Bering Sea;
52 some of these fisheries concentrate on the slope and outer shelf. The eastern Bering Sea slope
53 contains 5 major canyons that incise the outer shelf (Figure 1). In 2012, the North Pacific Fishery
54 Management Council (NPFMC) received testimony from environmental organizations
55 suggesting management measures to provide Essential Fish Habitat (EFH) protection to coral,
56 sponge and other benthic habitat of fish and crab species for two of the five major eastern Bering
57 Sea canyons (Pribilof and Zhemchug).

58 Based on this testimony, the NPFMC requested that the Alaska Fisheries Science Center
59 (AFSC) conduct an analysis to determine whether Bering Sea canyons were unique habitats and
60 whether there were fish and invertebrate assemblages within the canyons vulnerable to the
61 effects of commercial fishing, such as coral and sponge communities. An analysis of existing
62 data was conducted and presented to the NPFMC in 2013 (Sigler et al. 2013, Sigler et al. 2015).
63 Their conclusions were that although there were some physical characteristics that distinguished
64 the canyons from the surrounding slope and shelf areas, there were no unique faunal features that
65 distinguished Pribilof or Zhemchug Canyons from the surrounding slope areas. The major
66 variables structuring the biological communities on the eastern Bering Sea slope and outer shelf
67 instead are depth and latitude (Sigler et al. 2015, Hoff in review).

68 As a part of the analysis by Sigler et al. (2013), models of the distribution of structure-
69 forming invertebrates (deep-sea corals, sponges, and sea whips) were developed based on bottom

70 trawl survey data. A key outcome of this distribution modeling was the finding that about 1/3 of
71 the predicted coral habitat for the eastern Bering Sea slope occurs in Pribilof Canyon, an area
72 that comprises only about 10% of the total slope area (Figure 2). Much of the remaining
73 predicted coral habitat was found in the inter-canyon slope area to the northwest of Pribilof
74 Canyon. This finding resulted in a request from the NPFMC for the AFSC to conduct further
75 field research in 2014 using a stereo drop camera to survey the eastern Bering Sea slope and
76 outer shelf.

77 The primary objective of this research was to validate the predictions of coral distribution
78 by testing the predictions of coral presence or absence using a randomized stereo camera survey.
79 The secondary objectives were to 1) validate the sponge and sea whip model predictions, 2)
80 measure heights and densities of structure-forming invertebrates where they occurred, 3)
81 examine any associations of structure-forming invertebrates and fish species, 4) document any
82 observations of fishing gear effects on the coral and sponge habitats, 5) collect data useful to
83 estimate an index of vulnerability of structure-forming invertebrates to commercial fishing, and
84 6) improve or refine the predictions of coral distribution if possible.

85

86 **2. Materials and Methods**

87

88 *Study area*

89 The eastern Bering Sea is dominated by a broad shallow continental shelf that stretches
90 east to west from the Alaska mainland to the shelf break roughly 700 km away (Figure 1). The
91 eastern Bering Sea shelf is commonly divided into three domains based on bathymetry and
92 oceanographic fronts, the inner shelf (0 to 50 m), the middle shelf (50 to 100 m) and the outer

93 shelf (100 to 180 m) (Coachman 1986). The shelf break is typically at 180 to 200 m depth,
94 except at the northern edge of Bering Canyon, where the shelf break is at 500 m (Sigler et al.
95 2015). The eastern Bering Sea slope is made up of 5 major canyons (Bering, Pribilof, Zhemchug,
96 Pervenets and Navarin canyons) with an inter-canyon area between each (Figure 1). There are
97 also multiple smaller canyons along the shelf break, but none incise the shelf to the degree of the
98 5 largest (Karl et al. 1996). The focus of this study is 10 regions, which includes the 9 regions
99 (canyon and intercanyon) along the continental slope as well as the outer region of the eastern
100 Bering Sea shelf.

101

102 *Survey design and field sampling*

103 A total of 300 station locations were randomly selected for sampling from August 8-
104 September 6, 2014. This sample size was chosen based on a simulation of the effect of sample
105 size on the performance of the coral presence/absence model as measured by the AUC-value, a
106 test statistic used for evaluating model performance (Hosmer and Lemeshow 2005). Based on the
107 bottom trawl survey model and data (Sigler et al. 2015), an AUC-value of 0.78 could be
108 achieved with sample size of 300, about 85% of the value achieved for sample sizes of 1,000-
109 2,000. Since AUC values of > 0.70 are considered acceptable and AUC values > 0.80 are
110 considered excellent (Hosmer and Lemeshow 2005); a sample size of approximately 300 stereo
111 camera drops was predicted to result in a model with acceptable to excellent predictive power.
112 Stations were chosen from a regular-spaced grid overlaid on the eastern Bering Sea outer shelf
113 and slope with each grid cell having 100 m by 100 m sides. Random stations were chosen in two
114 stages. For the first set of stations, 10 stations were chosen randomly from each of the 9
115 individual canyon and intercanyon areas ($n = 90$) to ensure that there was some spatial coverage

116 of each area. The large size of the eastern Bering Sea outer shelf area and potential for isolated
117 stations located far from other stations prevented us from choosing 10 at-random stations in this
118 area. For the second stage of sample site selection, we randomly chose 210 stations throughout
119 the nine slope areas and the outer shelf based on the probability of coral presence from the
120 bottom-trawl model of coral distribution (Sigler et al. 2015). Thus, areas with a higher
121 probability of coral presence (such as Pribilof Canyon, the adjacent intercanyon area to the
122 northwest and the outer shelf near Pribilof Canyon and to the north and south) received
123 proportionally more allocated stations (Figure 1). Due to poor weather and time constraints 250
124 of the 300 stations were occupied during field sampling (Table 1). The majority of the
125 unsampled stations were north of Zhemchug Canyon (Figure 1). The northernmost canyon,
126 Navarin Canyon, and the inter-canyon area between Navarin and Pervenets canyons, were not
127 sampled. As a result, a total of 8 of the 10 regions were sampled.

128 The primary sampling tools for this study were two stereo drop camera systems
129 (Williams et al. 2010). The camera systems were deployed from a chartered fishing vessel, the
130 FV *Vesteraalen*, during August 10 – September 5, 2014. Each stereo drop camera is designed to
131 be towed or drifted continuously along a linear transect at or near the seafloor, rather than a
132 camera that is lowered to the seafloor at one position and then brought immediately to the
133 surface or lowered to the seafloor and anchored during an observation period. The electronic
134 components of the drop cameras were protected from physical damage by a cage constructed
135 from aluminum tubing. Two machine-vision cameras spaced approximately 30 cm apart in
136 underwater housings were connected via ethernet cables to a computer also in an underwater
137 housing. On the first drop camera system, one of the paired cameras recorded monochromatic
138 still images sized at 1.45 megapixels (JAI, CM-140GE), while the other camera collected 1.73

139 megapixel color still images (JAI, AB-201GE). On the second drop camera system, one of the
140 paired cameras recorded monochromatic still images sized at 1.45 megapixels (JAI, CM-
141 140GE), while the other camera collected 2.82 megapixel color still images (Prosilica GX
142 1920C). Lighting was provided by four strobe lights constructed of four Bridgelux® BXRA LED
143 arrays capable of producing 1,300 lumens at 10.4 W. The computer, cameras, and lights were
144 powered by a 28 V NiMH battery pack. Synchronous images were collected from each of the
145 cameras at a frequency of one image per second and written to a computer hard drive.
146 Additionally, images from the monochrome camera were viewed in real time at a rate of four
147 images per second on a monitor at the surface aboard the vessel. This allowed the height of the
148 camera to be actively controlled to keep it just above the seafloor using a quick response electric
149 winch. A 1/4 inch diameter coaxial cable provided the connection from the drop camera system
150 to the winch at the surface and allowed image viewing in real time.

151 At each occupied station, the camera was deployed at the center of the grid cell and
152 lowered to the seafloor. Once seafloor contact was made, the drop camera was drifted along the
153 bottom for 15 minutes. During each deployment, the drop camera system was drifted or lightly
154 towed through the water column in the direction of the prevailing current at a speed of 0.48 to
155 3.34 km*hr⁻¹ (0.26 to 1.8 knots) approximately 1 to 2 m above the substrate with the cameras
156 pointed slightly downward at an angle of approximately 35° off parallel to the seafloor. The
157 research vessel GPS was used to determine the position of the camera throughout the
158 deployment. The deployment cable was held as near vertical as possible to improve positional
159 accuracy, given weather and wind conditions. The distances traveled during deployments ranged
160 from 27 m to 839 m (mean = 362 m, SE = 8.8). Only 4 tows were less than 100 m in total length

161 and these were the result of equipment failure (such as dying batteries) and over 85% of the
162 deployments had distances between 200 and 600 m

163

164 *Image analysis*

165 A post-cruise image analysis was conducted to determine substrate types, species
166 abundance, and composition and size. Image pairs collected during each deployment were
167 viewed using stereo image processing software developed in the Python programming language
168 (Kresimir Williams, AFSC-RACE Division, unpublished software). To compute range and size
169 information for simultaneously captured image pairs, the cameras were calibrated following
170 methods described in Williams et al. (2010). The calibration procedure corrects for image
171 distortion due to the lens and viewport optics, and solves for the epipolar geometry between the
172 two cameras. The image analysis software incorporates the camera calibrations and determines
173 the three-dimensional coordinates for any corresponding point that is identified in the stereo-
174 image pair using a stereo-triangulation function.

175 The substrate observed in the underwater video transects was classified by a commonly
176 used seafloor substratum classification scheme (Stein et al. 1992, Yoklavich et al. 2000). The
177 classification consists of a two-letter coding of substratum type denoting a primary substratum
178 with > 50% coverage of the seafloor bottom and a secondary substratum with 20% - 49%
179 coverage of the seafloor. There were eight identified substratum types: mud (M), sand (S),
180 gravel-pebble (G, diameter < 6.5 cm), mixed coarse material (MC), cobble (C, 6.5 < diameter <
181 25.5 cm), boulder (B, diameter > 25.5 cm), exposed low relief bedrock (R), and exposed high
182 relief bedrock and rock ridges (K). By this classification, a section of seafloor covered primarily
183 in cobble, but with boulders over more than 20% of the surface, would receive the substratum

184 code cobble-boulder (Cb) with the secondary substratum indicated by the lower-case letter. The
185 primary substratum code was only changed if a substratum encompassed more than 10 images.
186 The size of each substrate was estimated from the viewing path width or by direct measurement.

187 All fishes and commercially important crabs were identified to the lowest taxonomic
188 level possible and counted for each image pair. Structure-forming invertebrates (corals, sponges
189 and sea whips) were also identified to the lowest possible taxonomic level (typically genus for
190 corals and sea whips and order for sponges) and counted for each image pair. Careful
191 examination and accounting of individual targets in adjacent frames was used to ensure that
192 objects were counted only once. Species identifications for sponges and corals were based on
193 Stone et al. (2011), Stone (2014) and Stone (personal communication). Demosponges on four
194 transects were too numerous to individually count. In this case 135 image pairs were randomly
195 subsampled and all of the individual sponges in these frames counted. The counts from this
196 subsample of frames were then expanded to the un-sampled frames. Sponges less than 10 cm in
197 height were difficult to discern from other small white- or yellow-colored items on the seafloor,
198 so these were not included in the counts or analyses.

199 Densities of individual taxa were calculated by dividing counts by the area swept
200 (distance observed*path width observed). The image analysis software provided a range (in cm)
201 from the camera to each individual target that was identified in an image pair. The path width
202 was estimated from the median of this range for each transect. The median range of all objects
203 counted on a transect was assumed to be the distance from the camera where 100% of fishes and
204 invertebrates were detected for that transect. The viewing angle for each camera is known (and
205 fixed by the camera lens). Using the median range and the known viewing angle, a horizontal
206 line in front of the camera can be calculated using formulae for sizing triangle components. Since

207 we have an angle (viewing angle) and the adjacent side of a triangle (range) for each camera, the
208 length of the opposite side can be calculated. This opposite side is the viewing path width at the
209 median range for each transect. This width was calculated for each transect and used as the path
210 width in density estimation. The mean path width across all transects was 3.08 m (SE = 0.05),
211 with a minimum of 1.55 m and a maximum of 5.51 m for any individual transect.

212 Fish lengths and invertebrate heights were obtained by identifying the pixel coordinates
213 of corresponding points (such as a fish snout or tail) seen in the left and right camera frames.
214 These points were used to calculate three-dimensional coordinates in the images by triangulation
215 using the calibration-derived parameters. All fish where the snout and tail were visible in both
216 cameras were measured for length using stereo techniques, with the exception of fish whose
217 body position was too curved to obtain an accurate length. Heights of all corals where the base
218 and tip could be observed were also measured. Heights were measured for all sea whips for
219 transects with less than ~500 individual sea whips. For transects with more than ~500 individual
220 sea whips or sponges, a random subsample of 135 paired images were selected to obtain ~200
221 individual heights for each taxonomic grouping. Curved sea whips were measured to their
222 highest point above the seafloor. Except where noted, the height and length data from each
223 transect presented here were weighted by the density of the taxa for that transect.

224 The data resulting from image analysis include densities of fishes, crabs, and structure-
225 forming invertebrates (no.*m⁻²); fish lengths for each species; heights of structure-forming
226 invertebrates; and the proportions of each type of substrate for the 250 transects.

227

228 **2.1 Validation of presence/absence models based on bottom trawl data**

229

230 In the time between the original presentation of the coral, sponge and sea whip models
231 (June 2013) and the camera survey (August 2014), some improvements were made to the
232 distribution models based on bottom trawl survey data. The grid size of the original bottom trawl
233 survey models (Sigler et al. 2015) was reduced from 1 km² to 1 hectare (100 m by 100 m grid
234 size). Improved bathymetry layers became available in early 2014 (M. Zimmermann and M.
235 Prescott, AFSC-RACE Division, unpublished data) and were incorporated into the new model.
236 An additional environmental variable, tidal current speed, was also incorporated into the new
237 model and the position of the net behind the trawl survey vessel was corrected for using the
238 depth and wire out measured at the time of the trawl. The revised models fit slightly better and
239 had higher resolution, but did not change the overall picture of the distribution of corals,
240 sponges, and sea whips (Figure 2), as most areas of predicted presence remained in Pribilof
241 Canyon and to the northwest of Pribilof Canyon, similar to the June 2013 model. Hereafter, the
242 models used for validation are the improved versions of the Sigler et al. (2015) distribution
243 models.

244 Model validation was conducted by comparing the predictions of probability of structure-
245 forming invertebrate presence or absence from the models based on bottom trawl survey data to
246 the observations of structure-forming invertebrate presence or absence from the camera survey.
247 Since model predictions were made on a map, the camera survey transects were overlaid on each
248 of the prediction maps and the underlying predictions were extracted. Because each camera
249 transect may have viewed multiple grid cells on the prediction map, the maximum probability
250 value underlying each camera survey drop was extracted and then compared to the observation
251 of presence or absence from image analysis at that site.

252 The area under the receiver operating curve (AUC) was used to evaluate the fit of the
253 trawl survey model to the camera drop observations. The AUC is a measure of rank-correlation
254 and can range from zero to one. It compares the probability associated with randomly selected
255 presence sites to randomly selected absence sites and determines if the probability is higher at
256 random sites with observed presence than random sites with observed absence. A value of 0.5
257 indicates model predictions are only as good as a random guess. A high AUC value indicates the
258 model better fits the observations. The correlation between the observations and predictions was
259 also calculated.

260 As a secondary test of the model fit, a threshold probability was calculated where the rate
261 of false positives (prediction of presence where absence was observed) was equal to the rate of
262 false negatives (prediction of absence where presence was observed). This threshold probability
263 was applied to all the camera survey sites to produce a matrix indicating the percent correctly
264 predicted. A Cohen's Kappa was also computed using the threshold value, which is another
265 statistic used to measure goodness-of-fit for presence-absence models.

266 Various plots of model accuracy are also included for reference. All of the model
267 evaluations were carried out on the three taxonomic groups of structure-forming invertebrates
268 (corals, sponges and sea whips). All the analyses, modeling and mapping were carried out using
269 R software (R Core Development Team 2013).

270

271 **2.2 Model improvements and model averaging**

272

273 Using only the camera survey data, a new model was developed for presence or absence
274 of structure-forming invertebrates. A generalized additive modeling framework (GAM; Wood

275 2006) was used with some of the same explanatory variables (latitude, depth, bottom
276 temperature, slope, mean current speed, mean tidal current speed, ocean color, grain size and
277 sediment sorting) as the bottom trawl survey model, to predict presence or absence of the camera
278 survey data. Longitude was not included in the camera survey model, as based on previous
279 results (Sigler et al. 2015, Hoff in review), latitude and depth were expected to be the most
280 important variables driving community patterns on the eastern Bering Sea slope. Removing
281 longitude also minimized the number of model parameters that had to be used in the smaller
282 camera survey data set.

283 The camera survey model was evaluated using the same methods as were used for
284 evaluating the bottom trawl survey model. AUC and correlation were calculated, a threshold
285 probability was estimated that balanced the false positive and false negative error rates, the
286 percent classified correctly and the Cohen's Kappa were also computed. These same diagnostics
287 were computed comparing the bottom trawl survey observations to the camera survey model.
288 These camera survey models were developed independently for coral, sponges, and sea whips.

289 The camera model predictions were combined with the bottom trawl model predictions
290 using model prediction averaging. The predictions of the two models were averaged for each
291 grid cell on the raster maps and weighted by the inverse of the standard error of the prediction for
292 each grid cell of each model. This resulted in a map of predictions where values for each
293 particular grid cell reflected the average predicted probability for the two models, as well as the
294 confidence of each models prediction (i.e. grid cells where the bottom trawl based model had a
295 high prediction error were down-weighted relative to the camera based model if its prediction
296 error was low). Since the camera survey extended only to a depth of 808 m depth, whereas the
297 trawl survey extended to 1200 m in depth, the average model was only extended to a depth of

298 825 m where both models were supported by observations. The resulting average model was
299 tested against the observations from the two surveys (bottom trawl and camera) using the
300 standard set of diagnostics (AUC, correlation, percent correct and Cohen's Kappa).

301

302 **2.3 Density and height distribution of structure-forming invertebrates**

303

304 The densities of structure-forming invertebrates (corals, sponges, and sea whips) were
305 compared among the eight eastern Bering Sea slope and outer shelf regions sampled during the
306 camera survey. Height frequencies were also compared among the regions using frequency plots
307 and mean values. These heights were weighted by the density of the structure-forming
308 invertebrates to account for differences in abundance among transects. Densities and mean
309 heights were compared among regions using analysis of variance (ANOVA) to test for
310 significant differences at $p = 0.05$. When significant differences were found, Tukey's post-hoc
311 tests for multiple comparisons were conducted to determine pairwise significant differences.

312 Finally, hurdle models (Cragg 1971, Potts and Elith 2006) predicting spatial distribution
313 of density and height using the camera survey data were produced for each structure-forming
314 invertebrate taxonomic grouping. Hurdle models predict the spatial distribution of abundance (or
315 in this case abundance and height) in three stages: 1) probability of presence is predicted from
316 presence-absence data; 2) a threshold presence probability is determined; 3) a separate model is
317 constructed that predicts abundance (or height). In the first step, we used the average models for
318 each taxonomic group developed in Section 2.2. In the second step, we used the optimum
319 thresholds determined by the camera data from Table 4 (since the density and height data were
320 derived from the camera survey). In the third step, we modeled the density and height data from

321 the camera survey. In this third step, the density models and height models used only data from
322 the camera survey because density and height information were not available from the bottom
323 trawl survey data. For each taxonomic grouping, the density or height of the species was
324 predicted by a GAM model utilizing latitude, depth, bottom temperature, ocean color, current
325 speed, sediment size and tidal current speed. In the GAM model estimation, only transects where
326 non-zero values were included. Density data was fourth-root transformed to meet the assumption
327 of normality, height was untransformed. Models of density and height were evaluated against
328 observations using the deviance explained and correlations between observations and
329 predictions.

330

331 **2.4 Fish and structure-forming invertebrate associations**

332

333 Associations between fish and structure-forming invertebrates were examined through
334 analysis of covariance (ANCOVA) to test whether the presence of structure-forming
335 invertebrates at a transect had a significant positive or negative effect on fish densities for that
336 transect. For these analyses, fish and crabs were placed into one of the following groupings:
337 rockfishes (all *Sebastes* sp.), sculpins, grenadiers, flatfishes, *Chionoecetes* crabs, king crabs, and
338 skates and analyzed separately. In addition, the individual species of Pacific ocean perch,
339 shortraker rockfish, shortspine thornyhead, Pacific cod, pollock, northern rockfish, sablefish, and
340 rougheye/blackspotted rockfish were also analyzed independently. Fish density was fourth root
341 transformed and used as the dependent variable. The independent variables were presence or
342 absence of corals, presence or absence of sponges, or presence or absence of sea whips and

343 depth. All covariate-invertebrate group interactions were included and stations were used as
344 replicates. Statistical significance was judged at $p = 0.05$.

345

346 **2.5 Observations of fishing gear and damage to structure-forming invertebrates**

347

348 Direct evidence of fishing (e.g., lost gear) was documented during the underwater camera
349 survey. Fishing evidence was classified as lost longline or crab gear, lost trawl net, or trawl
350 tracks. We computed the proportion of affected transects and mapped their locations.

351 Damage to structure-forming invertebrates also was documented during the underwater
352 camera survey. Damage may be due to natural causes (e.g., nudibranch predation of sea whip
353 soft tissue) or fishing (e.g., moving fishing gear that knocks down sea whips). While we were
354 able to identify damaged structure-forming invertebrates, we were unable to identify the cause of
355 this damage (i.e., the proportion damaged by fishing is unknown). During image analysis, we
356 recorded individual sponges and corals that were observed to be broken or broken off and lying
357 on the seafloor. For sea whips, damage was difficult to discern, but individuals with tissue
358 damage (abrasions or exposed axial rods) or individual sea whips that were lying horizontal on
359 the seafloor either dead (axial rod exposed) or possibly alive (apparently fleshy and otherwise
360 undamaged) were recorded as dead or damaged. We computed the proportion of transects with
361 damaged taxa and mapped their locations. We also computed the overall proportion of damaged
362 coral, sponge, and sea whips relative to their total numbers and compared their locations and
363 depths to all coral, sponge, and sea whips.

364

365 **2.6 Framework for estimating vulnerability of structure-forming invertebrates**

366

367 In its simplest form, vulnerability of structure-forming invertebrates to fishing gear and
368 other anthropogenic activities should reflect 1) the abundance of the organism, 2) the size of the
369 organism, 3) the rate of the impact and 4) the amount of time it will take the population to
370 recover to the existing state post-impact. The data collected during the camera survey can be
371 used to address the first two items. We did not examine vulnerability of structure-forming
372 invertebrates directly, but instead we examined the areas with the highest densities and largest
373 sizes of each taxonomic group of structure-forming invertebrates based on the model results
374 from section 2.3 above. Quantiles of density were computed for the grid cells of the best-fitting
375 density models. The two upper quartiles of density were then plotted for each taxonomic group.
376 This was repeated for the height models and the two resulting upper quartile plots were
377 combined; grid cells where either the density or height was in the upper quartile and the other
378 measure (density or height) was in the upper two quartiles were plotted for each taxa. It is
379 important to note that the thresholds (in our case quantile divisions) are rather arbitrary and could
380 be set to alternative values.

381

382 **3. Results**

383

384 The 250 successfully occupied stations sampled much of the area of the eastern Bering
385 Sea outer shelf and slope (Figure 1). Stations were occupied from Bering Canyon in the south to
386 Pervenets Canyon in the north (Table 1). The depths sampled ranged from 91 m to 808 m, with a
387 median depth of 276 m. The area viewed on each transect averaged 1,131 m² (SE = 34) and
388 ranged from 84 m² to 3,441 m². Sand was the dominant substrate observed (Figure 3). Over 97%

389 of the images of the seafloor were classified as containing only unconsolidated substrates (mud,
390 sand, gravel, pebble or mixed coarse material). The remaining 2.8% of images contained some
391 type of rocky substrate (cobble, boulder or exposed bedrock), however, only 0.8% of the images
392 had rocky substrates as the primary substrate type (Figure 3). Some amount of rocky substrate
393 occurred at 45 transects (18%), while the remaining transects lacked rocky substrates.

394 Over 7,000 fishes and crabs were counted from roughly 52 different species or taxonomic
395 groupings (Table 2). Eelpouts and *Chionoecetes* crabs dominated (~57% of the total
396 observations). However, grenadiers and rockfishes (especially Pacific ocean perch) were also
397 common. The abundant species mostly were small benthic dwelling fishes such as eelpouts,
398 snailfishes, sculpins, and poachers. Over 70,000 structure-forming invertebrates were observed
399 (Table 3). Most were demosponges (55%), predominantly from two individual transects, and sea
400 whips (40%). Few were corals (2%, < 1500 individuals).

401 Corals occurred on 32 of the 250 survey transects (Table 1). They were classified into 5
402 taxonomic groups including three families (Primnoidae, Plexauridae, and Isididae) and two
403 genera (*Plumarella* sp. and *Swiftia* sp.). The most common corals were *Plumarella* sp., which are
404 members of the Primnoidae family, and *Swiftia* sp., which are members of the Plexauridae
405 family. The median depth at which coral occurred was 451 m (range = 201 – 770 m), much
406 deeper than the median depth of all transects (276 m). Coral did not occur in Bering Canyon,
407 Pervenets Canyon, or the regions between Bering and Pribilof canyons or between Zhemchug
408 and Pervenets canyons. Coral occurred at 50% of transects in Pribilof Canyon and about 18% of
409 transects in the inter-canyon area between Pribilof and Zhemchug Canyons. Coral was present at
410 one station on the outer shelf and one station in Zhemchug Canyon (Figure 4).

411 Sponges occurred on 113 of the 250 survey transects (Table 1). They were classified into
412 three orders; hexactinellids, demosponges, and calcareous sponges. The vast majority of sponges
413 were hexactinellids. The median depth at which sponges occurred was 311 m, and they covered
414 almost the entire depth range of sampling from 111 m to 781 m. Sponges were widely distributed
415 and occurred in all of the sampled regions (Figure 4), ranging from a low of 17% of the stations
416 in Pervenets Canyon to a high of 73% of stations in the inter-canyon region between Zhemchug
417 and Pervenets canyons.

418 Sea whips were also widely distributed both in terms of depth and region. They occurred
419 at depths from 91 m to 760 m (median = 266 m) at 105 of the 250 stations surveyed (Table 1). At
420 least two different species of sea whip were observed, *Halipteris willemoesi* and an unidentified
421 *Halipteris* species. Sea whips occurred in all regions, occurring at a low of 25% of the stations
422 in Pribilof Canyon to a high of 53% of stations in the inter-canyon region between Bering and
423 Pribilof Canyons (Figure 4).

424

425 **3.1 Validation of presence/absence models based on bottom trawl data**

426

427 The model based on bottom trawl survey data predicted the distribution of presence or
428 absence of coral in the camera survey data very well. The AUC was 0.73 (standard deviation =
429 0.05) and the correlation was highly significant ($r = 0.28$, $p < 0.0001$) indicating model
430 predictions were well correlated to observations (Table 4). The observations of coral presence (n
431 = 32) occurred mostly in Pribilof Canyon and the area to the northwest of Pribilof Canyon,
432 which corresponded well with the predictions from the bottom trawl survey model (Figure 4).
433 The AUC diagnostics indicated that through most of the data, as the probability of occurrence

434 was predicted to increase, the observations of occurrence also increased (Figure 5). At the higher
435 probabilities of occurrence (> 0.60), there appeared to be a drop off in model performance at 11
436 stations where coral didn't occur but was predicted to be present. The prediction error for these
437 11 stations was about twice (0.19) the overall average (0.09). Six of these stations were located
438 in Pervenets Canyon, and the remaining five were scattered in the region between Pribilof
439 Canyon and Zhemchug Canyon. A threshold probability of 0.19 best balanced the false positive
440 and false negative error rates for coral prediction. Applying this threshold resulted in a Cohen's
441 Kappa of 0.26 (standard deviation = 0.06) and a percentage of stations with presence predicted
442 correctly of 72% (standard deviation = 0.03).

443 The model based on bottom trawl survey data predicted the distribution of presence or
444 absence of sponge in the camera survey data less well. The AUC was 0.63 (standard deviation =
445 0.04), although the correlation was highly significant ($r = 0.21$, $p = 0.0006$) indicating model
446 predictions were well correlated to observations (Table 4). The observations of sponge presence
447 ($n = 113$) occurred throughout all areas and depths (Figure 4). The AUC diagnostics indicated
448 that through most of the data, as the probability of occurrence was predicted to increase, the
449 observations of occurrence also increased (Figure 5). A threshold probability of 0.70 best
450 balanced the false positive and false negative error rates for sponge prediction. Applying this
451 threshold resulted in a Cohen's Kappa of 0.17 (standard deviation = 0.06) and a 59% of stations
452 with presence predicted correctly (standard deviation = 0.03).

453 The bottom trawl survey model predicted the distribution of sea whips in the camera
454 survey data fairly well. The AUC was 0.69 (standard deviation = 0.03), although the correlation
455 was highly significant ($r = 0.30$, $p < 0.0001$) indicating model predictions were well correlated to
456 observations (Table 4). The observations of sea whip presence ($n = 105$) occurred throughout all

457 areas and depths (Figure 4). The AUC diagnostics indicated that through most of the data, as the
458 probability of occurrence was predicted to increase, the observations of occurrence also
459 increased (Figure 5). In contrast to the coral model, the sea whip model was almost always
460 correct in predicting presence at high probabilities. A threshold probability of 0.06 best balanced
461 the false positive and false negative error rates for sponge prediction. Applying this threshold
462 resulted in a Cohen's Kappa of 0.29 (standard deviation = 0.06) and a percentage of stations with
463 presence predicted correctly of 65% (standard deviation = 0.03).

464

465 **3.2 Model improvements and model averaging**

466

467 The best-fitting model of coral presence or absence based on the camera survey data
468 contained four significant terms, with depth and latitude being the most important (Table 5).
469 Probability of coral presence increased sharply with increasing depth to about 300 m and then
470 leveled off with further increase in probability of presence below 600 m (Figure 6).
471 Unsurprisingly, the model predicted higher probabilities of presence in the middle latitudes of
472 the eastern Bering Sea slope. Probability of presence of coral increased slightly with increasing
473 tidal currents and increased sediment sorting (Figure 6). The model explained about 51% of the
474 deviance in the camera observations, the AUC of the camera survey model was 0.95 (SD = 0.01)
475 and the correlation was 0.67. A threshold probability of 0.21 best balanced error rates resulting in
476 a Cohen's Kappa of 0.57. The model predicted 87% of the stations correctly. The predictions
477 from the camera-based model (Figure 7) were similar to the predictions of the trawl survey-based
478 model (Figure 2).

479 When the camera survey model was used to predict the observations of coral presence or
480 absence in the bottom trawl survey data, the results were very good (Table 4). The AUC was
481 0.73 (SD = 0.04) and the correlation was 0.27. Using a threshold of 0.01, the Cohen's Kappa was
482 0.19 (SD = 0.03) and 78% of the bottom trawl survey observations were predicted correctly by
483 the camera survey model. Most of the mismatches were in the northern portion of the eastern
484 Bering Sea slope and outer shelf, where no camera stations were occupied, but there was bottom
485 trawl survey data.

486 The average model (combining both the predictions from the bottom trawl survey model
487 and the camera survey model) exhibited a similar pattern to the individual models, with most
488 areas of high probability of coral occurrence found in Pribilof Canyon and the area to the
489 northwest (Figure 8). This model also performed well at predicting the observations from both
490 the bottom trawl survey (AUC = 0.85, SD = 0.03) and the camera survey (AUC = 0.90, SD =
491 0.02) (Table 4). Using a combined threshold of 0.02, resulted in correctly predicting 81% of the
492 100 observations of coral (n = 68 for the bottom trawl survey and n = 32 for the camera survey)
493 correctly.

494 The best-fitting model of sponge presence or absence based on the camera survey data
495 contained seven significant terms (Table 5). Probability of sponge presence increased to a peak
496 at a depth of ~300 m and then decreased at deeper depths (Figure 10). Probability of sponge
497 presence decreased with increasing long-term average temperature and was highest at the large
498 and small extremes of sediment sorting. There were increases in sponge probability of presence
499 related to slope and sediment size and there was a dome-shaped relationship between sponge
500 presence and ocean productivity (Figure 10). The model explained only about 16% of the
501 deviance in the camera observations of sponge presence or absence. The AUC of the camera

502 survey model was 0.80 (SD = 0.03) and the correlation was 0.52 (Table 4). A threshold
503 probability of 0.44 best balanced error rates resulting in a Cohen's Kappa of 0.45 (SD = 0.06).
504 The model predicted 73% of the stations correctly. The predictions from the camera-based model
505 (Figure 7) were similar to the predictions of the trawl survey-based model (Figure 2), although
506 the bottom trawl survey model predicted a wider range of high probability sponge areas along
507 the outer shelf, and the camera based model predicted a higher probability of presence in the
508 northeastern outer shelf. The camera based predictions on the northeastern outer shelf were
509 undoubtedly spurious, as no camera sampling was conducted here. The camera and trawl survey
510 models did agree that sponge occurs in most areas of the outer shelf and slope.

511 When the camera survey model was used to predict the observations of presence or
512 absence of sponge in the bottom trawl survey data, the results were not very good (Table 4). The
513 AUC was 0.54 and the correlation was negative. Using a threshold of 0.56, only 50% (i.e., only
514 equal to chance) of the bottom trawl survey observations were predicted correctly by the camera
515 survey model. Most of the mismatches were in the northern and northeastern portion of the
516 eastern Bering Sea slope and outer shelf, where no camera stations were occupied and the
517 camera model predicted a high probability of sponge presence, but sponge catches in the bottom
518 trawl survey were generally minimal.

519 The average sponge model (combining both the predictions from the bottom trawl survey
520 model and the camera survey model) combined the best features of the individual models, with
521 most areas of high probability of sponge occurrence found in Bering Canyon, Pribilof Canyon
522 and the area to the northwest, Zhemchug Canyon and in areas of the outer shelf (Figure 8). This
523 model performed well at predicting the observations from both the bottom trawl survey (AUC =
524 0.71, SD = 0.01) and the camera survey (AUC = 0.76, SD = 0.03) (Table 4). Using a combined

525 threshold of 0.59 resulted in correctly predicting 70% of the 724 observations of sponge presence
526 (n = 611 for the bottom trawl survey and n = 113 for the camera survey) correctly.

527 The best-fitting model of sea whip presence or absence based on the camera survey data
528 contained seven significant terms, with sediment grain size being the most important (Table 5).
529 Probability of sea whip presence increased sharply with increasing grain size to a value of ~4
530 (which corresponds to very fine sand) and then decreased (Figure 11). The model predicted
531 higher probabilities of presence in the middle latitudes of the eastern Bering Sea slope.
532 Probability of presence of sea whips had a dome-shaped relationship with depth, peaking at
533 about 450 m. There was generally a nonlinear increase in sea whip probability of presence with
534 increasing temperature, slope and tidal currents and a linear increase in probability of presence
535 with current speed. The model explained only about 26% of the deviance in the camera
536 observations; the AUC of the camera survey model was 0.83 (SD = 0.03) and the correlation was
537 0.56 (Table 4). A threshold probability of 0.44 best balanced error rates resulting in a Cohen's
538 Kappa of 0.51 (SD = 0.05). The model predicted 76% of the stations correctly. The predictions
539 from the camera-based model (Figure 7) were different from the predictions of the trawl survey-
540 based model (Figure 2), in that the camera model predicted a much wider depth range for sea
541 whips and a much broader distribution on the outer shelf. Similar to the case for the sponges, the
542 high probability of presence in the northeastern outer shelf and also in the southeastern outer
543 shelf were outside the area of sampling for the camera survey and should be viewed with some
544 caution.

545 When the camera survey model was used to predict the observations of presence or
546 absence of sea whips in the bottom trawl survey data, the results were mixed (Table 4). The
547 AUC was relatively low at 0.57 (SD = 0.02) and the correlation between predictions and

548 observations was 0.12. Using a threshold of 0.72, only 55% of the bottom trawl survey
549 observations were explained by the camera survey model (only slightly better than chance). Most
550 of the mismatches were at deeper depths where bottom trawl survey catches of sea whips were
551 not common and in the previously mentioned northern areas and northeastern outer shelf where
552 there were no camera observations.

553 The average model (combining both the predictions from the bottom trawl survey model
554 and the camera survey model) performed better with extensive predictions of presence of sea
555 whips along the outer shelf and some in deeper waters (Figure 8). This model also performed
556 well at predicting the observations from both the bottom trawl survey (AUC = 0.82, SD = 0.02)
557 and the camera survey (AUC = 0.74, SD = 0.03). Using a combined threshold of 0.31 resulted in
558 correctly predicting 67% of the 250 observations of sea whip presence (n = 145 for the bottom
559 trawl survey and n = 105 for the camera survey) correctly (Table 4).

560

561 **3.3 Density and height distribution of structure-forming invertebrates**

562

563 The densities of coral found at transects were very low (mean = 0.005, SE = 0.002) and
564 ranged from 0 to 0.28 individuals/m². Of the 32 transects with coral, 11 had less than 5
565 individuals occurring on them. The highest densities of corals were observed in Pribilof Canyon
566 and the area to the northwest (Figure 12). The best-fitting GAM model predicting coral density
567 included only bottom depth and slope as significant factors (Table 5). The model explained 70%
568 of the variability in the coral density data and generally, density increased with increasing depth
569 and decreased with increasing slope (Figure 13). Density of coral predicted by the GAM model

570 was highest in Pribilof Canyon and to the northwest of Pribilof Canyon in deeper waters (Figure
571 14).

572 The densities of sponge found at transects averaged 0.11 individuals/m² (SE = 0.06) and
573 ranged from 0 to a high of 13.1 individuals/m². The density of hexactinellid sponges was 0.006
574 (SE = 0.002) and the density of demosponges was 0.11 (SE = 0.06). Four of the transects had
575 densities of sponges in excess of 0.5 individuals/m² (one in Pribilof Canyon, one in Zhemchug
576 Canyon, one in the intercanyon area near Zhemchug Canyon, and one on the outer shelf
577 northwest of Pribilof Canyon; Figure 12). The best-fitting GAM model predicting sponge density
578 included latitude, current speed, and grain size as significant factors. The GAM model explained
579 only 20% of the variability in the sponge densities, which were highest at the middle latitudes of
580 the eastern Bering Sea outer shelf and slope (Table 5). Density decreased with decreasing
581 current speed, and sponge density was highest at the smallest grain sizes and at phi of ~4.5.
582 However, this relationship may have reflected low sample sizes at some of the middle values of
583 phi (Figure 15). Density of sponge predicted by the GAM model was highest in Pribilof Canyon
584 and on the surrounding outer shelf, to the northwest of Pribilof Canyon in deeper waters, and in
585 Zhemchug Canyon and to the north (Figure 14). Two large areas of predicted high density of
586 sponge on the outer shelf northeast of Zhemchug Canyon and southeast of Pervenets Canyon
587 were not sampled during the camera survey and may be spurious.

588 The densities of sea whips found at transects averaged 0.11 individuals/m² (SE = 0.04)
589 and ranged from 0 to a high of 8.4 individuals/m². Ten of the transects had densities of sea whips
590 in excess of 0.5 individuals/m² (one in Bering Canyon, one in the area between Bering Canyon
591 and Pribilof Canyon, three in the intercanyon area between Pribilof Canyon and Zhemchug
592 Canyon, and five on the outer shelf; Figure 12). The best-fitting GAM model predicting sea whip

593 density included only bottom depth and slope as significant factors. The same as for the coral
594 GAM model (Table 5). The sea whip GAM model explained 33% of the variability in the sea
595 whip density data. Unlike the model of coral density, sea whip density decreased with increasing
596 depth, except for an uptick in density at the deepest depths below 600 m (Figure 16). Density
597 decreased with increasing slope. Density of sea whips predicted by the GAM model was
598 relatively uniform (and high) throughout the outer shelf and slope (Figure 14).

599 The size of corals varied by taxonomic group (Table 6). On average, individuals from the
600 family Isididae were the largest, ranging from 10 cm to 116 cm tall. The *Swiftia* sp. were the
601 smallest corals observed ranging from 2 cm to 24 cm, but most of the other taxonomic groups of
602 coral averaged less than 20 cm in height (Figure 17). Observed average coral heights were
603 highest on the slope northwest of Pribilof Canyon (Figure 18). Sponges from all groups averaged
604 about 17 cm in height, similar to the height distribution of corals (Figure 17). However, sponges
605 less than 10 cm in height were not measured or counted. Of the sponge groups, hexactinellid
606 sponges tended to be the largest, with one specimen having a height of greater than 2 m (Table
607 6). Sponges were tallest at or near the shelf break around Bering Canyon, Pribilof Canyon, and to
608 the northwest of Pribilof Canyon (Figure 18). Sea whips exhibited a bimodal height frequency
609 (Figure 17) with many individuals smaller than 40 cm tall, but also with another peak in height at
610 about 110 cm. This is reflected in the overall average height of sea whips of 62 cm (Table 6). On
611 a few occasions sea whip heights were estimated at > 2 m as well. The largest sea whips were
612 observed between Pribilof Canyon and Zhemchug Canyon at or near the shelf break (Figure 20).

613 The best-fitting GAM model predicting coral height included latitude, tidal current speed,
614 slope, sediment grain size, temperature, and average current speed as significant factors (Table
615 5). The model explained 93% of the variability in observed coral heights data and generally,

616 heights increased with increasing slope and were highest at the latitudes around Pribilof Canyon
617 and to the northwest (Figure 19). Interestingly, heights of coral increased with increasing average
618 current speed, but decreased strongly with increasing tidal current speed. Corals were predicted
619 by the GAM model to be tallest in the deeper waters between Pribilof Canyon and Zhemchug
620 Canyon (Figure 20).

621 The best-fitting GAM model predicting sponge height included temperature, slope, and
622 sediment grain size as significant factors (Table 5). The model explained 41% of the variability
623 in observed sponge heights data and generally, heights increased with increasing slope and
624 temperature and peaked at a phi of about 3.5 (corresponding to fine sand to very fine sand)
625 (Figure 21). Sponges were predicted to be tallest in Bering Canyon and on the outer shelf area to
626 the north and around Pribilof Canyon and deeper waters to the northwest (Figure 20).

627 The best-fitting GAM model predicting sea whip height included depth, temperature,
628 latitude, average current speed, and sediment grain size as significant factors (Table 5). The
629 model explained 60% of the variability in observed sea whip height. Sea whip height decreased
630 with increasing depth, temperature, and sediment size (Figure 22). Sea whip height also
631 decreased from south to north. Current speed was the only factor that had a positive effect on sea
632 whip height as it increased. Sea whips were tallest in the outer shelf region between Pribilof and
633 Zhemchug Canyons (Figure 20).

634

635 **3.4 Fish and structure-forming invertebrate associations**

636

637 Most of the fish and crab species and taxa groupings examined from the camera survey
638 had strong associations with depth (Table 7). Of the 15 groups examined, the presence of coral

639 had a positive effect on the density of shortraker rockfish, combined king crabs, and rougheye-
640 blackspotted rockfish. Sponge presence had a significantly positive effect on density of
641 combined rockfishes, Pacific ocean perch, and combined king crabs. Sea whip presence had a
642 positive effect on flatfish species and a negative effect on shortspine thornyhead, Pacific cod, and
643 grenadier. Grenadier was interesting in that they were the only group where the presence of
644 either corals, sponges, or sea whips negatively affected their densities. The density of
645 *Chionoecetes* crabs was lower where sponge or coral were present; but the presence of sea whips
646 had no effect. The density of combined rockfishes was higher where sponges were present and
647 lower where corals were present. The densities of pollock, sculpins, skates, northern rockfish,
648 and sablefish were not related to the presence of structure-forming invertebrates (Table 7).

649

650 **3.5 Observations of fishing gear and damage to structure-forming invertebrates**

651

652 At least one damaged coral, sponge, or sea whip was identified on 0-24% of transects,
653 depending on taxa (Table 8). Only the taxa Isididae (0.8% of transects), demosponge (2.8%), and
654 *Halipteris* sp. (24%) were identified as damaged. The other observed taxa were Gorgonacea,
655 *Plumarella aleutiana*, *Plumarella* sp., Primnoidae, Porifera, Calcarea, and Hexactinellid, but
656 none were identified as damaged. Damaged taxa were found on 27.2% of transects, with only
657 one transect with two taxa damaged (both Demosponge and *Halipteris* sp. were found damaged
658 on one transect). Damaged *Halipteris* sp. were widespread, whereas damaged Isididae were
659 limited to Pribilof Canyon and westward and damaged demosponge were limited to Pribilof
660 Canyon and westward as well as Pervenets Canyon (Figure 23).

661 Of the three taxa identified as damaged, demosponge was the most common (present on
662 42.4% of transects), followed by *Halipteris* sp. (42.0%) and Isididae (2.8%) (Table 9). On
663 transects where they occurred, damage of *Halipteris* sp. was most common (one or more
664 damaged *Halipteris* sp. was identified on 57.1% of transects where *Halipteris* sp. was observed),
665 followed by Isididae (28.6%) and demosponge (6.6%). The remaining coral and sponge taxa
666 were found on 0.4% (Gorgonacea) to 22.4% (Hexactinellid) of transects, but none were
667 identified as damaged. Undamaged and damaged *Halipteris* sp. were widely distributed. Isididae
668 were limited to Pribilof Canyon and westward as were damaged Isididae. In contrast,
669 demosponges were widespread but damaged demosponges were limited to Pribilof Canyon and
670 westward as well as Pervenets Canyon. While transects with damaged *Halipteris* sp. were
671 common (present on 24% of transects), the proportion of damaged individuals was much smaller
672 (9% of *Halipteris* sp. were damaged) (Table 10). Similarly, only 2.9% of individual Isididae and
673 0.3% of individual demosponges were identified as damaged. *Halipteris* sp. were found over a
674 wide depth range (91-760 m) and were concentrated at 100-150 m; damaged *Halipteris* sp. also
675 were found over a wide range (91-719 m) and were concentrated at 100-150 m (Figure 24).
676 Demosponges also were found over a wide depth range (110-770 m), but damaged demosponges
677 were found within a narrower depth range (206-412 m). Isididae were found from 349-760 m
678 and damaged Isididae were found over a narrower depth range (455-760 m).

679 Evidence of fishing was found on 0.8-7.6% of transects, depending on the type of
680 evidence (Table 8). Evidence of fishing included trawl net (0.8% of transects), longline or crab
681 gear (4.4%), and trawl tracks (7.6%). Evidence of fishing was found on 12.8% of transects, each
682 with only one type of fishing evidence. Evidence of longline or crab gear occurred from Pribilof
683 Canyon northward to Pervenets Canyon, whereas evidence of trawl gear (either gear itself or

684 trawl tracks) occurred primarily from Pribilof Canyon southward to Bering Canyon, except for
685 trawl tracks at the north edge of Zhemchug Canyon and at Pervenets Canyon (Figure 25).

686 Evidence of longline or crab fishing was found over a depth range of 241-748 m. Evidence of
687 trawl fishing was found from 111-394 m and was somewhat concentrated at 100-150 m.

688 Damaged taxa and/or evidence of fishing were found on 36.8% of transects (Table 8).

689 Both damaged taxa and evidence of fishing occurred on 3.2% of transects (8 of 250). Of these 8
690 transects, 7 had damaged *Halipteris* sp. and 1 had damaged demosponge. Damaged *Halipteris*
691 sp. were observed on 5 transects with trawl tracks, one transect with trawl net, and one transect
692 with either longline or crab gear. The damaged demosponge was observed on a transect with
693 derelict longline or crab gear. Damaged taxa and/or evidence of fishing was most common from
694 Pribilof Canyon and northward to Pervenets Canyon (Figure 26).

695 The depth distributions of undamaged and damaged taxa nearly completely overlapped,
696 except for *Halipteris* sp., which was the only taxa found at <100 m (minimum depth of 91 m).

697 The depth distributions of the undamaged taxa were 695 m (Gorgonacea), 455-759 m
698 (Plexauridae), 349-761 m (*Plumarella aleutiana*), 201-761 m (*Plumarella* sp.), 212-760 m
699 (Primnoidae), 264-770 m (*Swiftia* sp.), 150-761 m (Porifera), 215-532 m (Calcarea), and 110-
700 770 m (Hexactinellid). The depth distributions of the damaged taxa were 349-760 m (Isididae),
701 91-760 m (*Halipteris* sp.), and 110-770 m (demosponge). The two most commonly observed
702 sponge taxa (Hexactinellid and demosponge) were observed within the same depth range (110-
703 770 m). However, only demosponges were identified as damaged.

704

705 **3.6 Vulnerability of structure-forming invertebrates**

706

707 The upper quartiles of coral density occurred in the two arms of Pribilof Canyon, to the
708 northwest of Pribilof Canyon and in spots along the eastern Bering Sea slope in deeper waters
709 from Pribilof Canyon to Zhemchug Canyon (Figure 27). For sponge, the upper quartiles of
710 density occurred on the northern edge of Pribilof Canyon and to the northwest of Pribilof
711 Canyon along the slope (Figure 27). There were also significant areas of sponge abundance in
712 Zhemchug Canyon and north of Zhemchug Canyon. Two large areas on the outer shelf were
713 unsampled by the camera survey, so they should be viewed with caution. The upper quartiles of
714 sea whip density were scattered all along the outer shelf between Bering Canyon and Pervenets
715 Canyon in a fairly distinct band along the shelf break with some gaps above Pribilof Canyon and
716 Zhemchug Canyon (Figure 27).

717 The upper quartiles of coral height occurred predominantly in deeper waters off to the
718 north of Pribilof Canyon and in a small area in the southeastern arms of Pribilof Canyon and
719 Zhemchug Canyon (Figure 28). The upper quartiles of sponge height occurred predominantly in
720 deeper waters from Bering Canyon through Pribilof Canyon and to the northwest of Pribilof
721 Canyon and then in Zhemchug Canyon and to the north (Figure 28). Sea whip heights were
722 predicted to be highest on the inner portion of the outer shelf to the north and east of Zhemchug
723 canyon; however these areas were not sampled using the camera so are likely spurious. The more
724 likely areas for tall sea whips are in a band along the outer shelf between Pribilof Canyon and
725 Zhemchug Canyon (Figure 28).

726 The combined density-height quartiles indicated only very small areas where high density
727 and greater heights both occurred for corals, such as in the two arms of Pribilof Canyon and in
728 deeper waters scattered along the slope (Figure 29). There was also a patch in the southern
729 portion of Zhemchug Canyon. The intersection of the upper quartiles of height and density for

730 sponge occurred for the northern section of Pribilof Canyon and to the northwest along the slope
731 and sections of Zhemchug Canyon. Taller and more dense sea whips were found mostly at the
732 shelf break in a fairly narrow band (Figure 29) and in unsampled sections of the outer shelf
733 where the potential for spurious results mean these should be viewed with caution. .

734

735 **4. Discussion**

736

737 The 2014 camera survey indicated that coral is mostly limited to Pribilof Canyon and
738 northwest of Pribilof Canyon, whereas sponge and sea whips are more widespread. The depth
739 distributions of the different types of coral overlapped to a large degree, but all were located
740 below 200 m in depth. *Plumarella* sp. and *Swiftia* sp. were the most commonly observed corals,
741 and they generally occurred in highest densities at depths between 200 and 525 m (8 of the top
742 10 highest coral densities) and in Pribilof Canyon (8 of the top 10 coral densities). *Isididae*
743 species were somewhat deeper, with all but a single occurrence below 435 m and less than half
744 (3 of 7) of the transects with *Isididae* sp. were found in Pribilof Canyon. Because of the relative
745 size differences among these groups (with *Isididae* being the tallest corals observed), the tallest
746 corals tended to be observed in deep water on the slope between Pribilof and Zhemchug canyons.

747 This area was also where the largest sponges were observed, with some of the largest
748 hexactinellid species observed in the deeper waters. However, the most dense aggregations of
749 sponge tended to occur in shallower waters on the outer shelf and shelf break. These shallow
750 sponges were a mixture of predominantly demosponges with some hexactinellids and calcareous
751 sponges mixed in at lower densities.

752 The most dense areas of sea whips occurred in both shallow areas (at the shelf break) and
753 on a couple of deep transects. These two distributions probably represented two different species
754 of sea whips (*Halipteris willoemesi* and *Halipteris* sp.; Robert Stone, AFSC-ABL, personal
755 communication), especially as the shallow species tended to be much larger than the deeper
756 group. The size distribution of sea whips within a transect was sometimes variable and
757 sometimes uniform, i.e., the sizes could be a mixture of very small and very large individuals in
758 some places or either uniformly tall or uniformly short in others, with no obvious cause for these
759 differences.

760

761 **4.1 Validation of presence/absence models based on bottom trawl data**

762

763 The results of the camera survey supported the presence-absence coral model that was
764 developed from bottom trawl survey data. Both the model diagnostics and the observed coral
765 presence overlaid on maps of predictions of probability of coral presence indicated that the
766 bottom trawl survey model was accurate in predicting coral distribution. The bottom trawl survey
767 model for sponge did less well at predicting the camera observations for sponge, although the
768 results were still better than chance. The bottom trawl survey model for sea whips also predicted
769 the sea whip data from the camera observations fairly well. The most likely reason for the
770 different accuracy in model predictions from the three invertebrate groupings was that the
771 allocation of stations was designed to test the predictions of coral presence or absence based on
772 the bottom trawl survey model. Since the bottom trawl survey model predicted a higher
773 probability of coral in and around Pribilof Canyon, more stations were allocated to these areas.
774 If, for example, we had allocated stations to validate the bottom trawl survey sponge model, the

775 distribution of stations would have been different, probably with more stations on the outer shelf
776 around Pribilof Canyon and fewer stations within Pribilof Canyon. This may have resulted in the
777 data better resolving the full distribution of sponge on the outer shelf. However, allocating
778 stations in this way would have resulted in a correspondingly worse dataset for evaluating the
779 coral model since Pribilof Canyon would have received fewer stations. Model estimates likely
780 were degraded by the sometimes poor bathymetry near the shelf break, which was observed
781 during the camera survey.

782 Independent surveys to validate distribution models are rarely undertaken. In most cases,
783 model validation is performed by re-substitution (Kumar and Stohlgren 2009, Krigsman et al.
784 2012) or splitting the data set at random into training and testing data sets (Bryan and Metaxis
785 2007, Franklin et al. 2013, Sagarese et al. 2014). Using newly collected data that is independent
786 of the original data set is less common, but usually utilizes data collected in additional years or
787 additional areas (Eskildsen et al. 2013, Rooper et al. 2014). Using an independent data set
788 collected with an entirely different survey design and data collection method is very rare, but it
789 can provide the most insight into model performance (Elith et al. 2006).

790 The type of validation technique utilized can influence the perception of the model's
791 predictive ability. In general, the more independent the cross-validation, the higher the chances
792 that the cross-validation can indicate problems in the original model. Because the GAM
793 methodology used here can represent very complex relationships between organisms and their
794 environment, the GAMs are prone to over-fitting the data. We limited the number of inflection
795 points ("knots") in the functional relationships in the GAMs, but this alone cannot entirely
796 prevent model overfitting. The support of the independent camera survey observations for the

797 bottom trawl survey coral model provides confidence in the model predictions and an additional
798 measure of the uncertainty around those predictions (Guisan et al. 2013).

799

800 **4.2 Model improvements and model averaging**

801

802 The coral model that blended both the bottom trawl survey model and the camera survey
803 model best matched both data sets. Each individual data set best fit to its individual model, as
804 expected. For example, the AUC for the bottom trawl model predicting bottom trawl catches of
805 coral was 0.92 and the AUC for the camera model predicting the camera data was 0.95, whereas
806 the cross-predictions yielded AUCs of 0.73 in both cases (bottom trawl model predicted camera
807 observations and vice versa). The combined model fit resulted in AUCs of 0.85 and 0.90 for the
808 bottom trawl data, and camera data respectively, which is better than the cross-predictions for the
809 individual models. For coral, the combined model best matched both data sets, with a little better
810 fit to the camera data than the bottom trawl data. The favorable matching of both data sets likely
811 occurred because both individual coral models (bottom trawl and underwater camera) showed
812 almost exactly the same spatial pattern of coral distribution.

813 This is in contrast to the sponge model, where the two independent models and data
814 sources did not agree very well (e.g., the bottom trawl model for sponge was negatively
815 correlated with the camera data observations). In this case, the combined model fit both the
816 camera and trawl survey observations reasonably well (AUCs of 0.76 and 0.71), but not as well
817 as for the coral model. This lack of coherence for the sponge models may have been due to the
818 fact that the camera observations did not cover shallow areas of the outer shelf where there was
819 trawl survey data. This implies that the sponge model is inadequate for extrapolating outside the

820 camera survey area. Much of the disagreement between the camera and bottom trawl models was
821 on the northeast outer shelf where the camera model predicted a high probability of sponge
822 occurrence. Because the probability of sponge presence increased with latitude (Figure 10) and
823 camera sampling in the high latitude shallow areas was lacking, these predictions represent
824 extrapolation outside the camera survey area and thus are probably inaccurate. The same
825 phenomenon was also apparent with the sea whip predictions in the same area (northeastern
826 outer shelf). These predictions should be viewed with caution.

827 Catchability for sponges may be higher in the bottom trawl survey compared to the
828 camera survey. Only sponges that exceeded 10 cm height were counted in the image analysis,
829 since smaller specimens could not be identified from other white- or yellow-colored items
830 on the seafloor., However, some fraction of these smaller sponges are caught by the trawl survey,
831 thus contributing to the mismatch between the bottom trawl and camera based models. The
832 opposite effect likely occurs for sea whips. All sea whips were easily observed and counted in
833 the camera survey, but their trawl catchability likely is lower because of their flexibility and low
834 profile, thus contributing to the mismatch between the camera and bottom trawl sea whip
835 models.

836

837 **4.3 Density and height distribution of structure-forming invertebrates**

838

839 The densities of corals and sponges observed on the eastern Bering Sea slope and outer
840 shelf in this study were low (mean = 0.005 individuals*m⁻², SE = 0.002) compared with other
841 areas of Alaska where similar studies have been conducted. In 2012 a randomized stereo camera
842 survey was conducted in the eastern and central Aleutian Islands (n = 93 transects) and Bowers

843 Bank (n = 19 transects) using the same methodology and covering a similar depth range (C.
844 Rooper, AFSC-RACE Division, unpublished data) as the eastern Bering Sea study. The Aleutian
845 Islands study found that coral densities (predominantly gorgonian species) averaged 0.11
846 individuals*m⁻² (SE = 0.03) and ranged as high as 1.3 individuals *m⁻² (Figure 30). On Bowers
847 Bank, coral densities ranged as high as 1.67 individuals*m⁻² and averaged 0.21 individuals*m⁻²
848 (SE = 0.11), although the Bowers Bank corals were predominantly small hydrocorals
849 (Stylasteridae) from two very dense transects. Hydrocorals were not observed in the Bering Sea.
850 A randomized survey conducted in 2010 at two areas closed to fishing (to protect coral) in the
851 Gulf of Alaska estimated average density of corals at 0.10 individuals*m⁻² (SE = 0.04) and a
852 maximum density of 1.2 individuals*m⁻² (C. Rooper, AFSC-RACE Division, unpublished data).
853 The survey design differed somewhat from the eastern Bering Sea and Aleutian Islands surveys
854 in that the transects were shorter and the depths examined ranged only from 78-359 m.
855 Additionally, this study was conducted in an area that had been closed to protect presumed coral
856 habitat, so the densities probably do not reflect the overall Gulf of Alaska average.

857 Other published density estimates for coral are available for Pribilof and Zhemchug
858 canyons from a study conducted in 2007. The densities of gorgonian corals found in Pribilof
859 Canyon was 0.73 individuals*m⁻² (SE = 0.4) and Zhemchug Canyon densities were 0.13
860 individuals*m⁻² (SE = 0.1), while maximum densities were 2.41 individuals*m⁻² (Miller et al.
861 2012). These density estimates are higher than the densities we found, likely due to differences
862 in sampling design. In the Miller et al. (2012) study, the transects were placed systematically
863 rather than randomly as in our study, and their sample size was low (16 transects). Transects
864 sometimes were clustered so that fewer distinct geographic locations were sampled; 5 distinct
865 geographic locations were sampled within or near Zhemchug Canyon and 4 distinct geographic

866 locations were sampled within or near Pribilof Canyon (Miller et al., 2012). In contrast, we
867 sampled 25 locations within Zhemchug Canyon and 36 locations within Pribilof Canyon. In
868 addition, the Miller et al. (2012) densities were calculated treating each frame as an independent
869 sample rather than each transect (adjacent frames are correlated). In other areas of Alaska, a
870 study in the central Aleutian Islands yielded an average coral density of 1.23 individuals*m⁻² and
871 a maximum density of 3.85 individuals*m⁻² (Stone 2006). For the Gulf of Alaska, a study of
872 *Primnoa* thickets yielded densities of red tree coral of 0.52 individuals*m⁻² (Stone 2014).

873 Coral densities differ among the three regions of Alaska because of differences in the
874 amount of appropriate substrates available for colonization. In the studies above that performed
875 random camera surveys in the Aleutian Islands, Bowers Bank, and Gulf of Alaska (C. Rooper,
876 AFSC-RACE Division, unpublished data), the percentage of transects with rocky habitat
877 somewhere present on the transect was 63%, 42% and 58%, respectively, compared to 18% for
878 the current study. A linear relationship of the percentage of transects with some rocky habitats
879 and the overall density of coral in the four regions (0.106, 0.015, 0.100 and 0.005 individuals*m⁻²)
880 explains most (~82%) of the variability in average density among the areas. In addition, the
881 percentage of individual frames that were dominated by rocky substrates was 23% in the
882 Aleutian Islands, 8% at Bowers Bank and only 0.8% in the eastern Bering Sea. These substrate
883 differences also heavily influenced the overall distribution of corals as well. Since corals require
884 hard substrate for attachment, most were found in areas with more exposed substrate, such as the
885 areas in Pribilof Canyon and to the northwest along the slope. These tended to be the only areas
886 where rocky substrate occurred deep enough to support coral attachment. One shallow rocky
887 outcrop was sampled in the middle of the outer shelf. Although this area supported the densest

888 observed aggregation of sponges, coral was absent. According to the coral model, this location
889 was too shallow but otherwise was suitable coral habitat.

890 Sponge densities were highly variable in the eastern Bering Sea, ranging from 0 to 13
891 individuals*m⁻², averaging 0.11 individuals*m⁻². In the Aleutian Islands camera survey, sponge
892 densities averaged 0.50 individuals*m⁻² (SE = 0.18). In the Bowers Bank area, the density of
893 sponge was 0.22 individuals*m⁻² (SE = 0.09) and in the Gulf of Alaska closed areas, sponge
894 density averaged 0.07 individuals*m⁻² (SE = 0.02). Bowers Bank and the Aleutian Islands both
895 had substantially higher densities of sponge than the eastern Bering Sea, while the densities in
896 the Gulf of Alaska closed areas were slightly lower. Another study in Alaska conducted by
897 Stone et al. (2014) found densities of 2.51 individuals*m⁻². The study of Pribilof and Zhemchug
898 canyons by Miller et al. (2012) reported densities of hexactinellid sponges of 0.40 and 0.02,
899 respectively, and for other sponges (likely demosponges) 0.24 and 0.001 individuals*m⁻². The
900 overall density of sponges, as well as the individual groups reported by Miller et al. (2012) was
901 higher than we found, although as mentioned previously, this is probably a factor of sampling
902 design differences.

903 Sea whip densities were higher on average in the eastern Bering Sea than in the Aleutian
904 Islands, Gulf of Alaska, or Bowers Bank. In the eastern Bering Sea, sea whip densities were
905 more than twice as high (0.11 individuals*m⁻²) than in the Aleutian Islands (0.04 individuals*m⁻²)
906 and were orders of magnitude higher than at Bowers Bank (0.004 individuals*m⁻²). No sea
907 whips were observed in the closed areas in the Gulf of Alaska. The differences between the
908 regions are probably also related to the amount of sandy habitat available near the shelf break.
909 Overall sea whip densities reported in Miller et al. (2012) were generally higher than we found in
910 Pribilof Canyon (0.24 individuals*m⁻²), and lower in Zhemchug Canyon (0.05 individuals*m⁻²).

911 Brodeur (2001) reported densities in a grove of sea whips near Pribilof Canyon of 0.25
912 individuals*m⁻². In other studies in Alaska, especially in the Gulf of Alaska some areas of dense
913 sea whips have also been observed, such as the sea whip grove in southeastern Alaska studied by
914 Malecha and Stone (2009), which had densities of ~0.5 individuals*m⁻², and the maximum
915 densities of *Protoptilum* sp. and *H. willemoesi* near Kodiak found by Stone et al. (2005) of 16
916 and 6 individuals*m⁻².

917 Coral heights averaged 20 cm or less for most taxonomic groups. The exception was the
918 bamboo corals, Isididae. These corals occurred in deeper water on the slope to the north of
919 Pribilof Canyon. Primnoa corals, such as the red tree corals (*Primnoa resedaeformis*) can grow
920 to very large sizes, exceeding 1 m tall in areas of southeast Alaska (Andrews et al. 2002). In the
921 Aleutian Islands survey mentioned above, the average gorgonian coral size was 33 cm (SE =
922 0.45). The species composition was much richer in the Aleutian Islands than was found for the
923 eastern Bering Sea, but when only the common groups were compared, *Plumarella* sp. (mean =
924 0.36, SE = 0.92), *Swiftia* sp. (mean = 26, SE = 2.07) and Plexauridae (mean = 25.6, SE = 1.43)
925 were all about twice as tall in the Aleutian Islands as in the eastern Bering Sea. The only
926 exception was for Isididae, which were about 48 cm tall (SE = 5.1) in the eastern Bering Sea on
927 average and were about 44 cm tall in the Aleutian Islands (SE = 9.8). Growth rates for Isididae
928 indicate that large specimens of these species (>70 cm) are likely in excess of 50 years old
929 (Andrews et al. 2009). A single specimen from the Gulf of Alaska with a height of 120 cm
930 (similar to the maximum height found during this study) was estimated to be 116 years of age.
931 There have been no aging studies for the other species of corals observed during this study, but
932 the large red tree corals (~2 m) found in southeastern Alaska have been aged to be over 100
933 years old (Andrews et al. 2002).

934 In the eastern Bering Sea, sponge height differed by group, as the hexactinellid sponges
935 tended to be taller than the demosponges. In the Aleutian Islands, demosponges were on average
936 about 10 cm taller than in the eastern Bering Sea. However in the Aleutian Islands, demosponges
937 < 20 cm were not measured (as opposed to the Bering Sea where sponges < 10 cm were not
938 measured). This implies that sponge sizes between the two regions were roughly the same. This
939 is supported by the average height for hexactinellid sponges, which averaged 24 cm (SE = 1.59)
940 in the Aleutian Islands and 25 cm (SE = 0.78) in the eastern Bering Sea.

941 Sea whips were also found to be very similar in size between the Aleutian Islands and the
942 eastern Bering Sea. In the Aleutian Islands survey, sea whip heights averaged 68 cm, although
943 they were also highly variable (SE = 21.69) as very few were measured. In the eastern Bering
944 Sea, the average sea whip height was 62 cm (SE = 0.92). In an ageing study of sea whips,
945 Wilson et al. (2002) estimated a linear growth rate of $7.42 \text{ cm} \cdot \text{yr}^{-1}$ for the interval between small
946 (~27 cm) and medium (~100 cm) sea whips. Based on these growth rates, the average sea whip
947 from the eastern Bering Sea or Aleutian Islands (62-68 cm tall) would be between ~ 12-14 years
948 of age.

949

950 **4.4 Fish and structure-forming invertebrate associations**

951

952 Fish associations were similar to findings from other studies in Alaska. Rockfish species
953 tended to be associated with corals and sponges, in particular, Pacific ocean perch, shorttraker
954 rockfish and rougheye-blackspotted rockfishes. Similar associations were found by Miller et al.
955 (2012) in their study of Pribilof and Zhemchug canyons. Similar patterns were found in analyses
956 of trawl survey catches (Malecha et al. 2005, Heifetz 2002, Rooper and Boldt 2005, Laman et al.

957 2015). Pacific ocean perch were strongly associated with sea whip forests near Pribilof Canyon
958 during the night-time when these fish were resting (Brodeur 2001) and a similar relationship
959 between sponge and northern rockfish was observed near Zhemchug Canyon (Rooper et al.
960 2010). We did not perform nighttime camera survey operations, so our data would not have
961 detected these types of associations. The association of king crabs with corals and sponges has
962 also been observed in previous studies. Most of the king crabs that we observed during the
963 camera survey were juvenile king crabs. In previous laboratory and field studies, juvenile king
964 crab were found to seek out complex structure (Sundberg and Clausen 1977, Loher and
965 Armstrong 2000, Stoner 2009, Pirtle and Stoner 2010). Two taxonomic groups that have
966 negative associations with coral and sponge were *Chionoecetes* crabs and grenadiers, which
967 likely reflects differences in habitat preferences.

968

969 **4.5 Observations of fishing gear and damage to structure-forming invertebrates**

970

971 Quantifying anthropogenic damage to deepwater benthic organisms, such as sponge and
972 coral, is challenging. Many species have irregular and sometimes amorphous body shapes that
973 make simple identifications difficult. In fact, determining sponge species often requires
974 examining spicules under magnification because the same species may exist in various shapes
975 and sizes. These growth form variations make distinguishing damage problematic because
976 damage may not be obvious within the spectrum of body shapes for some species. Additionally,
977 the variability of response to damage of the individual taxa may bias observations because it may
978 be easier to identify damage among some species. For instance, sea whips and bamboo corals
979 have bright white internal skeletons that, when exposed (i.e., denuded of their overlying soft

980 tissues) are very conspicuous especially when lying on the seafloor. Depending on sedimentation
981 rates, the skeletons of these species may remain conspicuous for long periods of time since they
982 are made of durable materials. Conversely, other species such as *Fanellia* sp. and *Calciorgia* sp.
983 have dark internal skeletons that are less conspicuous when exposed and damage is more
984 difficult to detect among these species whether they are upright or prone.

985 Direct evidence of fishing (mostly trawl tracks, but also some lost trawl net, crab pot and
986 longline gear) occurred at 32 (12.8%) transects. The proportion of observed damage for coral
987 (2.9%) and sponge (0.3%) was low. About 9% of individual sea whips observed were classified
988 as either being somehow damaged, dead, or lying horizontal on the seafloor. In most cases, it
989 was difficult to determine if the damage was human-induced (e.g., fishing or other activity) or
990 natural (e.g., brittle star or nudibranch predation, ocean currents). Few transects showed both
991 clear evidence of fishing activity (e.g., trawl tracks or fishing gear) and damaged coral, sponges,
992 or sea whips. This occurred in just 3.2% of our transects (8 of 250). We observed effects of
993 fishing slightly less frequently than a previous study of Pribilof and Zhemchug canyons, which
994 observed effects on 3 of 16 transects (Miller et al. 2012); this difference may simply be due to
995 chance and their much smaller sample size. This difference also may be due to sampled depths;
996 ours covered a wider depth range and differences in fishing effort with depth is a confounding
997 factor in comparing the two studies.

998 *Halipteris* sp. were the most common taxa observed and the largest taxa observed, as well
999 as the most common taxa damaged. *Halipteris* sp. differ from the remaining coral taxa and the
1000 sponge taxa by largely occurring on the continental shelf, where softer sediments occur, and not
1001 on the continental slope. Damaged *Halipteris* sp. occurred on 24% of transects, but a relatively
1002 low proportion of damaged individuals (9%) was observed. *Halipteris* sp. were concentrated at

1003 depths 100-150 m, as was evidence of damaged *Halipteris* sp. (Figure 5). Damaged *Halipteris*
1004 sp. on an individual basis were more frequent at depths 100-150 m (12.9%) than for all depths
1005 (9%). Effects of fishing on *Halipteris* sp. also were observed in previous studies at Pribilof
1006 Canyon (Brodeur et al. 2001, Miller et al. 2012), but the proportions affected were not stated.
1007 Two sponge taxa occurred over the same depth ranges (Figure 9) yet only one taxa was identified
1008 as damaged (demosponge, 6.6% of transects) and the other taxa was not (Hexactinellid, 0% of
1009 transects). Both taxa were found over a wide depth range (110-770 m) and frequently co-
1010 occurred (19.6% of transects). The lack of identified co-occurrent damage of Hexactinellid and
1011 demosponge may simply be due to chance; damaged demosponge was infrequent (only 7 of 250
1012 transects) and Hexactinellid only co-occurred on three of these transects.

1013

1014 **4.6 Vulnerability of structure-forming invertebrates**

1015

1016 Vulnerability of invertebrates to fishing impacts is a function of several processes. Data
1017 was collected during this research that addresses two aspects of vulnerability, density, and
1018 height. We provided an example based on the modeled distribution of height and density of areas
1019 where each taxa may be most vulnerable. However, the thresholds in terms of density and height
1020 that we set (the upper quartiles) may not be equally appropriate for all groups. The sensitivity
1021 and vulnerability of deepwater coral and sponge varies greatly between taxa. For this reason, an
1022 equal level of disturbance may present a wide range of observed damage responses. Factors that
1023 influence vulnerability include flexibility and height above the seafloor. Flexible species are less
1024 vulnerable than rigid ones, as they are able to bend and rebound from impact. Likewise, low
1025 lying and encrusting species are less vulnerable than upright species that extend into the water

1026 column since their exposure to passing fishing gear is reduced. Some species, such as *Farrea*
1027 *occa*, are fragile and may break apart with light disturbance. Evidence of damage to a species
1028 such as this may be ephemeral, as fragments of the damaged individuals are quickly dispersed.
1029 Lacking lasting evidence, their damage rate appears low.

1030

1031 **5. Conclusions**

1032

1033 We attempted to address six objectives during the 2014 eastern Bering Sea slope and
1034 outer shelf survey. Based on the data collected on the survey we conclude that:

- 1035 ● The model of coral presence or absence based on bottom trawl survey data only was
1036 generally accurate in predicting presence or absence in the camera survey. The bottom
1037 trawl survey models were also accurate in predicting sponge and sea whip presence or
1038 absence, but to a lesser degree than for coral.
- 1039 ● The combined distribution models based on the bottom trawl survey models and models
1040 derived from the camera survey data also performed well. These combined models
1041 predicted the distribution of corals, sponges, and sea whips with better accuracy than the
1042 individual models did during cross-validation. For example, the combined sponge model
1043 performed better at predicting the camera observations of sponge than the bottom trawl
1044 survey sponge model data did at predicting the camera survey observations.
- 1045 ● Densities and heights of corals were generally highest in Pribilof Canyon and to the
1046 northwest of Pribilof Canyon along the slope. For sponges, densities and heights were
1047 highest surrounding Pribilof Canyon, north of Bering Canyon and in some locations in

- 1048 Zhemchug Canyon. Sea whip densities and heights were highest on the outer shelf
1049 between Pribilof and Zhemchug Canyon and in an area to the south of Pribilof Canyon.
- 1050 ● There were significant positive relationships between fish density and the presence of
1051 coral and sponge for some rockfish species and king crabs. There were significant
1052 negative relationships for grenadiers and *Chionoecetes* crabs.
 - 1053 ● Evidence of fishing gear or damage to benthic invertebrates occurred at 37% of transects.
1054 Individual demosponges (0.3%), Isididae corals (2.9%) and sea whips (9.0%) were
1055 observed to be damaged.
 - 1056 ● Two pieces of data important for estimating vulnerability of benthic invertebrates
1057 (density and height) were estimated from the field research and modeled for the entire
1058 eastern Bering Sea outer shelf and slope.
 - 1059 ● Combining the bottom trawl survey models and models based on the camera survey
1060 showed improvement over bottom trawl survey-based models alone.

1061

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1063

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1073

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8. Tables

Table 1. Summary of stations occupied in each area of the eastern Bering Sea slope and outer slope. The total number of station with each taxonomic group of structure-forming invertebrates is also given for each area.

Area	Stations sampled	Stations with coral present	Stations with sponge present	Stations with sea whips present
Bering Canyon	10	0	5	3
Bering -Pribilof Canyon	17	0	4	9
Pribilof Canyon	36	18	24	9
Pribilof -Zhemchug Canyon	68	12	29	31
Zhemchug Canyon	25	1	12	11
Zhemchug -Pervenets Canyon	15	0	11	7
Pervenets Canyon	12	0	2	4
Outer Shelf	67	1	26	31

Table 2. Summary of fishes observed during the eastern Bering Sea slope and outer shelf camera survey.

Species or group	Number observed
Eelpout (<i>Bothracara</i> sp., <i>Lycodes</i> sp., unid.)	2155
<i>Chionocetes</i> sp.	2068
Popeye grenadier (<i>Coryphaenoides cinereus</i>)	1481
Pacific ocean perch (<i>Sebastes alutus</i>)	1225
Sculpin unid. (Cottidae)	924
Golden king crab (<i>Lithodes aequispina</i>)	746
Snailfish unid. (Liparidinae)	613
Other decapods (<i>Hyas</i> sp., <i>Oregonia</i> sp., Paguridae, etc.)	601
Poacher unid. (Agonidae)	600
Flatfish unid. (Pleuronectidae)	505
Roundfish unid.	404
Giant grenadier (<i>Albatrossia pectoralis</i>)	370
Shortspine thornyhead (<i>Sebastolobus alascanus</i>)	281
Northern rockfish (<i>Sebastes polyspinis</i>)	226
Grenadier sp. (Macrouridae)	217
<i>Sebastes</i> sp.	213
Searcher unid. (Bathymasteridae)	154
Skate unid. (Rajidae)	148
<i>Atheresthes</i> sp.	123
Deep sea sole (<i>Embassichthys bathybius</i>)	76
Walleye pollock (<i>Gadus chalcogramma</i>)	72
Rex sole (<i>Glyptocephalus zachirus</i>)	69
Prickleback unid. (Stichaeidae)	67
Shortraker rockfish (<i>Sebastes borealis</i>)	61
Octopus unid. (Octopodidae)	56
Flathead sole (<i>Hippoglossoides elassodon</i>)	48
Halibut (<i>Hippoglossoides stenolepis</i>)	33
Harlequin rockfish (<i>Sebastes variegatus</i>)	31
King crab unid. (Lithodidae)	30
Pacific cod (<i>Gadus macrocephalus</i>)	27
<i>Gadus</i> sp.	15
Blackspotted rockfish (<i>Sebastes melanostictus</i>)	13
Bigmouth sculpin (<i>Hemitripteris bolini</i>)	12
Darkfin sculpin (<i>Malacocottus zonerus</i>)	11
Greenland turbot (<i>Reinhardtius hippoglossoides</i>)	10
Sablefish (<i>Anoplopoma fimbria</i>)	8
Alaska skate (<i>Bathyraja parmifera</i>)	5
Whiteblotched skate (<i>Bathyraja maculata</i>)	5
Whitebrow skate (<i>Bathyraja minispinosa</i>)	5
Aleutian skate (<i>Bathyraja aleutica</i>)	4
Rougheye rockfish (<i>Sebastes aleutianus</i>)	4
Scarlet king crab (<i>Lithodes couesi</i>)	4
Starry flounder (<i>Platichthys stellatus</i>)	2
Atka mackerel (<i>Pleurogrammus monopterygius</i>)	2
Dusky rockfish (<i>Sebastes variabilis</i>)	2
Herring (Clupeidae)	1
Prowfish (<i>Zaprora silenus</i>)	1
Dover sole (<i>Microstomus pacificus</i>)	1
Greenling sp. (<i>Hexagrammos</i> sp.)	1
Spinyhead sculpin (<i>Dasycottus setiger</i>)	1
Commander skate (<i>Bathyraja lindbergi</i>)	1
Tubeshoulder unid. (Platytroutidae)	1

Table 3. Summary of structure-forming invertebrate taxonomic groupings that were observed during the 2014 camera survey on the eastern Bering Sea outer shelf and slope. Also given are the mean, minimum, and maximum depths at which each taxa was observed.

Taxonomic grouping	Number observed	Mean depth (m)	Minimum depth (m)	Maximum depth (m)
Demosponges	37682	352	110	770
<i>Halipteris</i> sp.	29435	304	91	760
Hexactinellid sponges	1952	395	110	770
<i>Plumerella</i> sp.	775	555	349	761
<i>Swiftia</i> sp.	537	546	264	770
Isididae	69	562	349	760
Primnoidae	38	492	212	760
<i>Plumerella aleutiana</i>	36	555	349	761
Calcareous sponges	31	428	215	532
Unidentified sponges	27	553	150	761
Plexauridae	8	631	455	759
Unidentified corals	2	695	--	--

Table 4. Summary of model fits and AUC for model validation (trawl model vs. camera observations and camera model vs. trawl observations).

Taxonomic group	Observations	Bottom trawl survey model					Camera survey model					Average model				
		AUC	Correlation	Percent correct	Threshold	Kappa	AUC	Correlation	Percent correct	Threshold	Kappa	AUC	Correlation	Percent correct	Threshold	Kappa
Corals	Bottom trawl data	0.92 (0.01)	0.53	0.8	0.08	0.27 (0.03)	0.73 (0.04)	0.27	0.78	0.01	0.19 (0.03)	0.85 (0.03)	0.48	0.8	0.01	0.22 (.03)
	Camera data	0.73 (0.05)	0.28	0.72	0.19	0.26 (0.06)	0.95 (0.01)	0.67	0.87	0.21	0.57 (0.07)	0.90 (0.02)	0.54	0.82	0.11	0.43 (0.07)
Sponges	Bottom trawl data	0.83 (0.01)	0.56	0.74	0.53	0.48 (0.02)	0.54 (0.02)	-0.07	0.5	0.56	-0.01 (0.03)	0.71 (0.01)	0.46	0.7	0.59	0.41 (0.01)
	Camera data	0.63 (0.04)	0.21	0.59	0.7	0.17 (0.06)	0.80 (0.03)	0.52	0.73	0.44	0.45 (0.06)	0.76 (0.03)	0.44	0.71	0.6	0.41 (0.06)
Sea whips	Bottom trawl data	0.89 (0.01)	0.58	0.8	0.13	0.37 (0.03)	0.57 (0.02)	0.12	0.55	0.72	0.04 (0.02)	0.82 (0.02)	0.37	0.72	0.4	0.24 (0.03)
	Camera data	0.69 (0.03)	0.3	0.65	0.06	0.29 (0.06)	0.83 (0.03)	0.56	0.76	0.44	0.51 (0.05)	0.74 (0.03)	0.41	0.7	0.155	0.40 (0.06)

Table 5. Best-fitting models predicting presence or absence, density and height of corals, sponges and sea whips using data from the 2014 camera survey of the eastern Bering Sea slope and outer shelf. Model terms are listed in order of importance in the models, estimated degrees of freedom (edf) for each of the variables are also given.

Response variable	Model	Deviance explained	edf	R ²
Coral presence or absence	s(depth)+s(latitude)+s(tidal current)+s(sediment sorting)	51%	2.9; 2.3; 2.3; 1.9	0.43
Sponge presence or absence	s(slope)+s(sediment sorting)+s(depth)+s(latitude)+s(grain size)+s(temperature)+s(ocean color)	16%	2.9; 1.0; 2.8; 2.9; 2.0; 2.8; 2.2	0.22
Sea whip presence or absence	s(grain size)+s(temperature)+s(depth)+s(tidal current)+s(current speed)+s(latitude)+s(slope)	26%	2.5; 2.6; 2.7; 2.8; 1.0; 2.3; 2.2	0.26
Coral density	s(slope)+s(depth)	70%	2.3; 2.7	0.62
Sponge density	s(latitude)+s(grain size)+s(current speed)	20%	2.3; 2.9; 1.0	0.13
Sea whip density	s(depth)+s(slope)	33%	2.9; 2.6	0.28
Coral height	s(latitude)+s(tidal current)+s(slope)+s(grain size)+s(temperature)+s(current speed)	93%	3.0; 1.0; 1.2; 1.8; 2.1; 2.6	0.86
Sponge height	s(temperature)+s(slope)+s(grain size)	41%	2.0; 2.0; 2.6	0.36
Sea whip height	s(depth)+s(temperature)+s(latitude)+s(current speed)+s(grain size)	60%	2.4; 2.7; 1.9; 1.0; 1.0	0.55

Table 6. Average heights for invertebrate taxa measured during the eastern Bering Sea slope and outer shelf camera survey. The number measured (n), mean, standard deviation (SD), minimum (Min) and maximum (Max) heights are given in centimeters.

Species	n	Mean	SD	Min	Max
Gorgonacea	2	21	9.2	15	28
Isididae	31	48	28.4	10	116
Plexauridae	1	16		16	16
<i>Plumerella aleutiana</i>	4	12	7.2	6	22
<i>Plumerella</i> sp.	265	16	9.4	4	53
Primnoidae	19	11	8.3	4	33
<i>Swiftia</i> sp.	41	10	4.2	2	24
Porifera	3	17	4.4	13	22
Upright calcarea	12	13	2.0	10	18
Upright demosponge	1972	18	8.3	10	135
Upright hexactinellid	569	25	18.5	10	204
<i>Halipterus</i> sp.	3496	62	54.2	2	266

Table 7. Summary table of analyses of covariance of fish density and structure-forming invertebrates (and depth). The table presents where there was a significant effect (meaning fish density was significantly higher or lower) of the presence of invertebrates by taxa. The interaction terms refer to the interaction between the factors (invertebrate presence or absence) and depth. “ns” indicates the relationship was non-significant, “sig” indicates a significant depth relationship, “sig +” indicates a positive effect of presence on density and “sig –“ indicates a negative effect of presence on density.

Species/group	Main				Interaction		
	Sponge	Coral	Whips	Depth	Sponge	Coral	Whips
Rockfish (all <i>Sebastes</i>)	sig +	sig -	ns	sig	sig	sig	ns
POP	sig +	ns	ns	sig	sig	sig	ns
Shortraker	ns	sig +	ns	ns	ns	ns	ns
SST	ns	ns	sig -	sig	ns	ns	sig
Cod	ns	ns	sig -	sig	ns	ns	ns
Sculpins	ns	ns	ns	sig	ns	ns	ns
Grenadier	sig -	sig -	sig -	sig	ns	ns	sig
Flatfish	ns	ns	sig +	sig	ns	ns	sig
Pollock	ns	ns	ns	sig	ns	ns	ns
Chionoecetes	sig -	sig -	ns	sig	ns	sig	ns
King crabs	sig +	sig +	ns	sig	ns	ns	ns
Skates	ns	ns	ns	sig	ns	ns	ns
Northern rockfish	ns	ns	ns	ns	sig	ns	ns
Rougheye/blackspotted	ns	sig +	ns	ns	ns	sig	ns
Sablefish	ns	ns	ns	ns	ns	ns	ns

Table 8. The number and proportion of transects with damaged coral, sponge, or sea whip or evidence of fishing (e.g., lost gear). Only the 3 taxa listed were found damaged. The other observed taxa were Gorgonacea, *Plumarella aleutiana*, *Plumarella* sp., Primnoidae, *Swiftia* sp., Porifera, Calcarea, and Hexactinellid, but none were found damaged. The total sample size was 250 transects.

Classification	Number of transects	Proportion of transects
Damaged Isididae	2	0.008
Damaged Demosponge	7	0.028
Damaged Halipteris	60	0.240
Damaged taxa subtotal	68	0.272
Longline or crab gear	11	0.044
Trawl net	2	0.008
Trawl tracks	19	0.076
Evidence of fishing subtotal	32	0.128
Damaged taxa or evidence of fishing total	92	0.368
Damaged taxa and evidence of fishing total	8	0.032

Table 9. The number and proportion of transects with damaged coral, sponge, or sea whip. Only the 3 taxa listed were found damaged. The other observed taxa were Gorgonacea, *Plumarella aleutiana*, *Plumarella* sp., Primnoidae, *Swiftia* sp., Porifera, Calcarea, and Hexactinellid, but none were found damaged. The total sample size was 250 transects.

Taxa	Damaged		Total		Proportion of transects with damage
	Number of transects	Proportion of transects	Number of transects	Proportion of transects	
Isididae	2	0.008	7	0.028	0.286
Gorgonacea	0	0	1	0.004	0.000
Plexauridae	0	0	5	0.020	0.000
<i>Plumarella aleutiana</i>	0	0	2	0.008	0.000
<i>Plumarella</i> sp.	0	0	22	0.088	0.000
Primnoidae	0	0	6	0.024	0.000
<i>Swiftia</i> sp.	0	0	19	0.076	0.000
<i>Halopteris</i> sp.	60	0.240	105	0.420	0.571
Demosponge	7	0.028	106	0.424	0.066
Porifera	0	0	9	0.036	0.000
Calcarea	0	0	4	0.016	0.000
Hexactinellid	0	0	56	0.224	0.000

Table 10. The number and proportion of individual coral, sponge, or sea whip that were damaged. Only the 3 taxa listed were found damaged. The other observed taxa were Gorgonacea, *Plumarella aleutiana*, *Plumarella* sp., Primnoidae, *Swiftia* sp., Porifera, Calcarea, and Hexactinellid, but none were found damaged.

Taxa	Damaged	Undamaged	Total	Proportion damaged
Isididae	2	67	69	0.029
Gorgonacea	-	2	2	0.000
Plexauridae	-	8	8	0.000
<i>Plumarella aleutiana</i>	-	36	36	0.000
<i>Plumarella</i> sp.	-	775	775	0.000
Primnoidae	-	38	38	0.000
<i>Swiftia</i> sp.	-	537	537	0.000
<i>Halipteris</i> sp.	2,653	26,782	29,435	0.090
Demosponge	115	37,567	37,682	0.003
Porifera	-	27	27	0.000
Calcarea	-	31	31	0.000
Hexactinellid	-	1,952	1,952	0.000

9. Figures

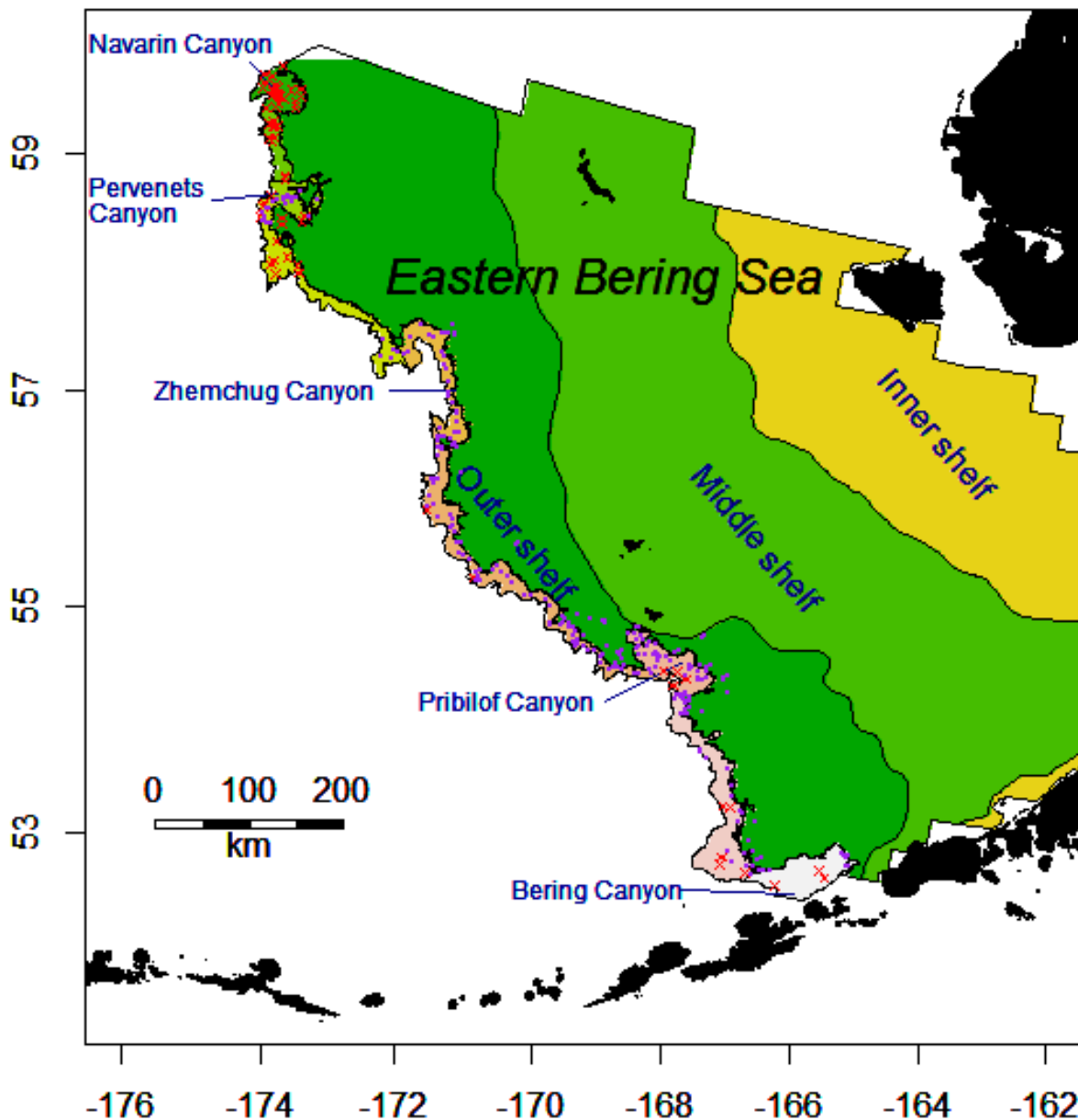


Figure 1. Eastern Bering Sea shelf and slope divided into the three major shelf domains. The map includes locations of the five major canyons and the intercanyon areas. Randomly selected sample sites are indicated by purple dots (occupied sites) and red crosses (sites that were not sampled due to time or depth constraints).

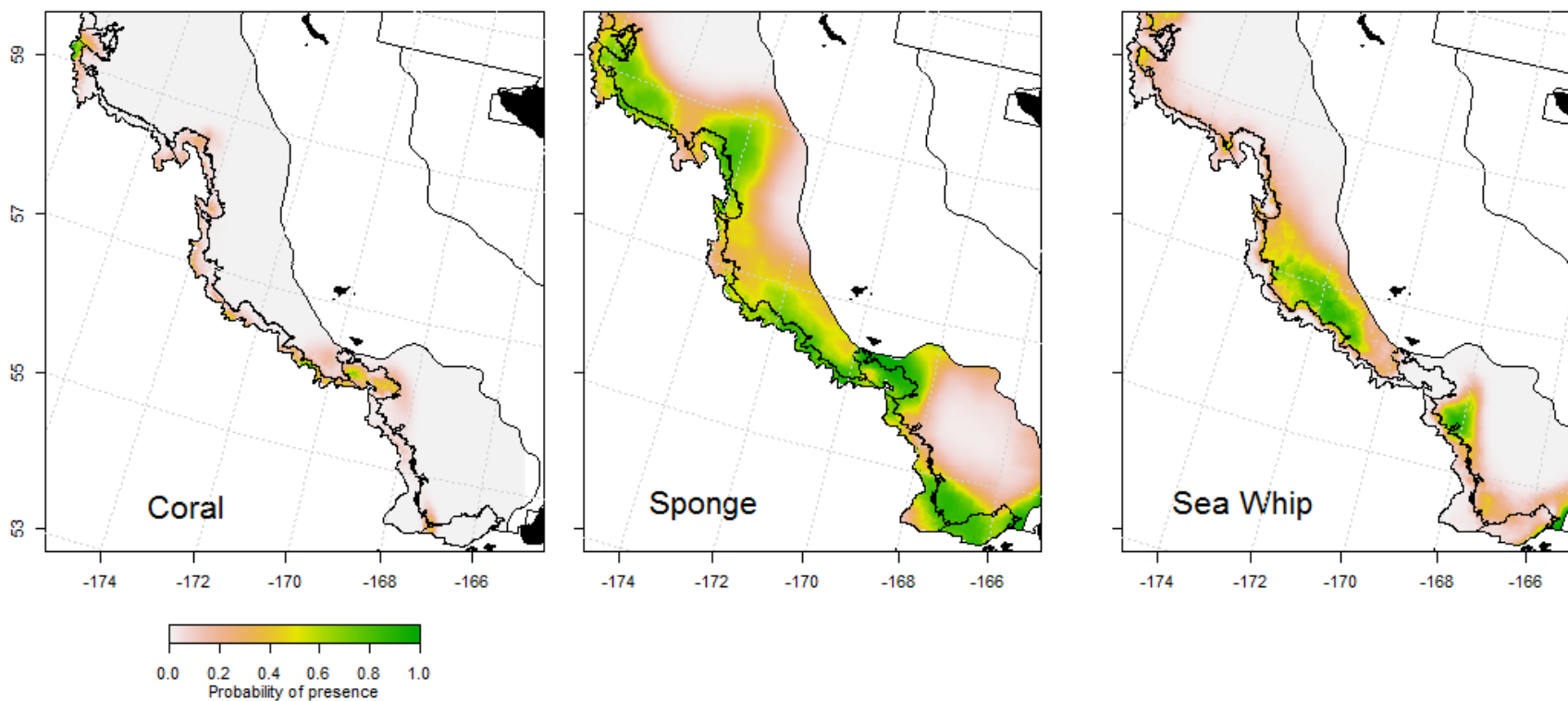


Figure 2. Predicted probability of structure-forming invertebrate presence predicted from the best fitting GAM model of presence or absence in the bottom trawl survey data.

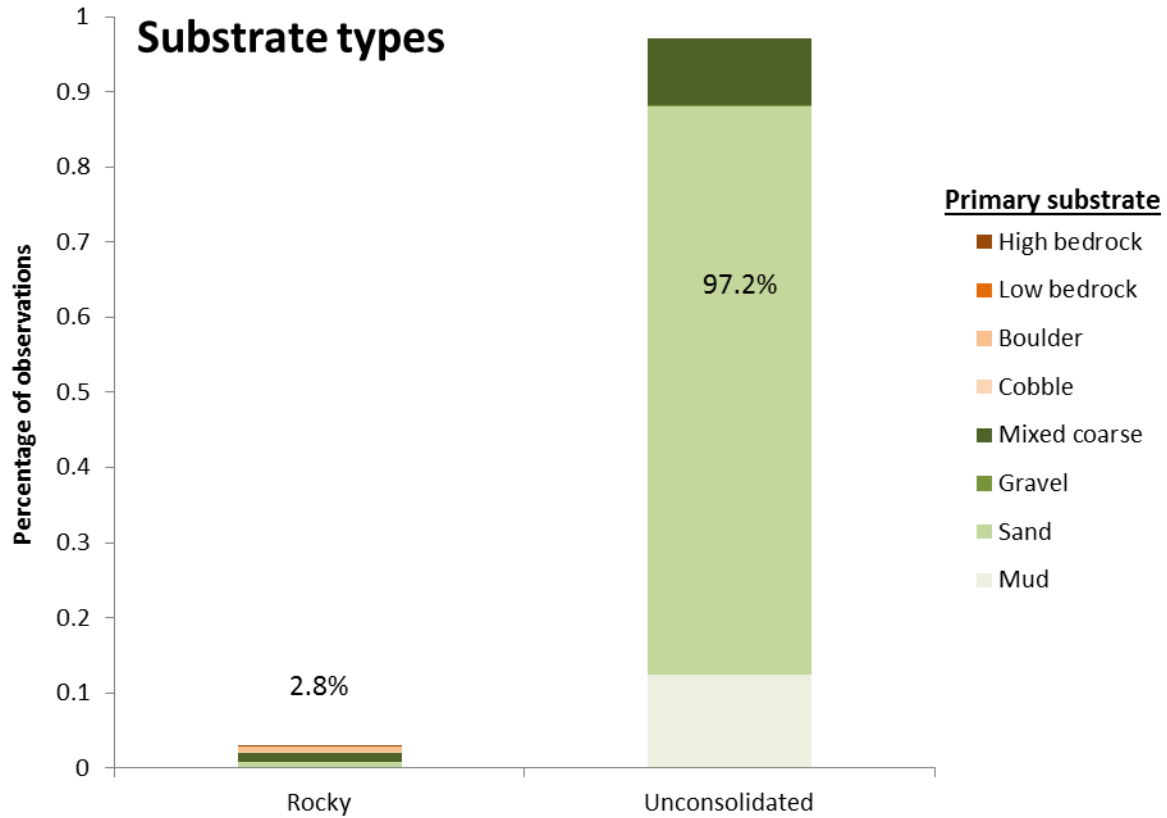


Figure 3. The proportions of seafloor substrates observed during the 2014 camera survey. Substrates were divided into purely unconsolidated (containing only mud, sand, gravel or mixed coarse substrates) and rocky substrates (those containing any type of cobble, boulder, or exposed bedrock). Colors indicate the primary substrate that was observed.

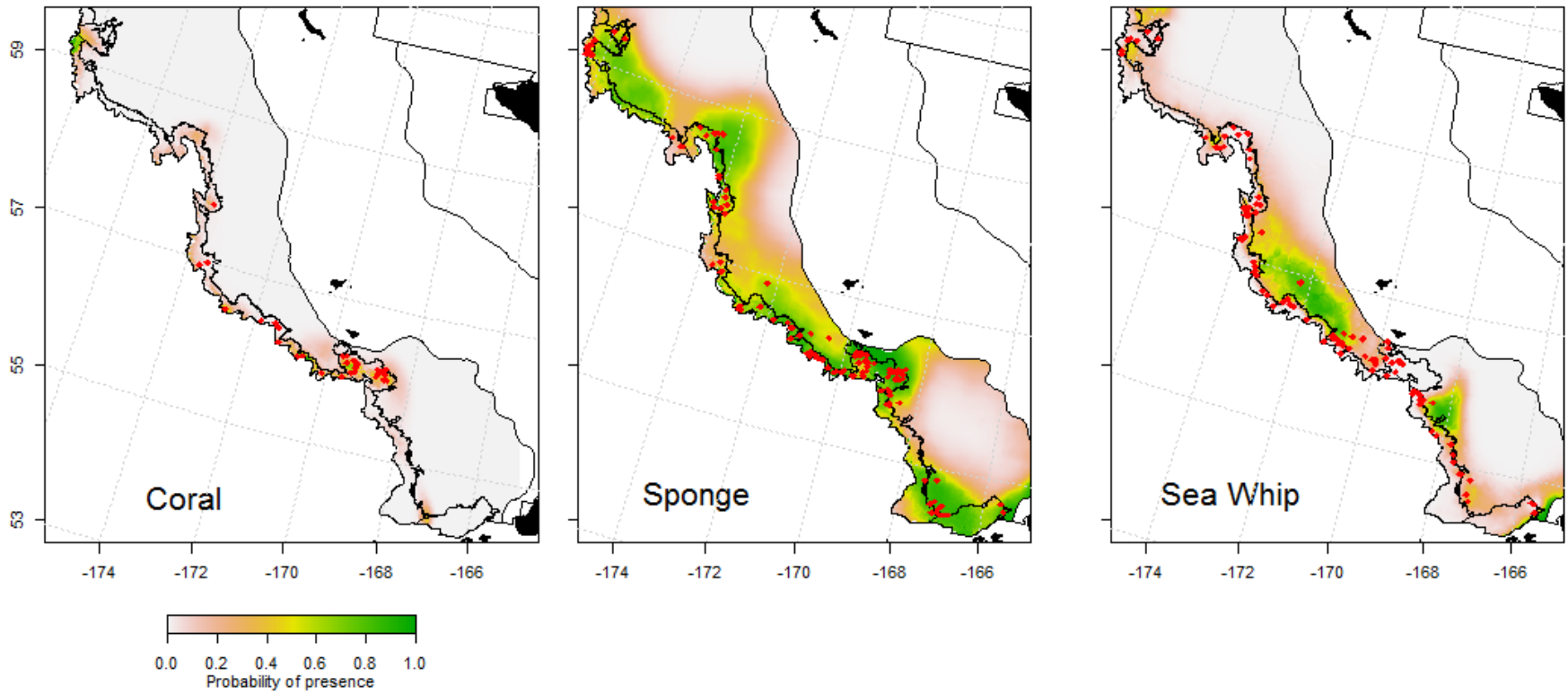


Figure 4. Predicted probability of presence for each taxa of structure-forming invertebrates with the points where each taxonomic group was observed during the 2014 stereo camera survey indicated in red.

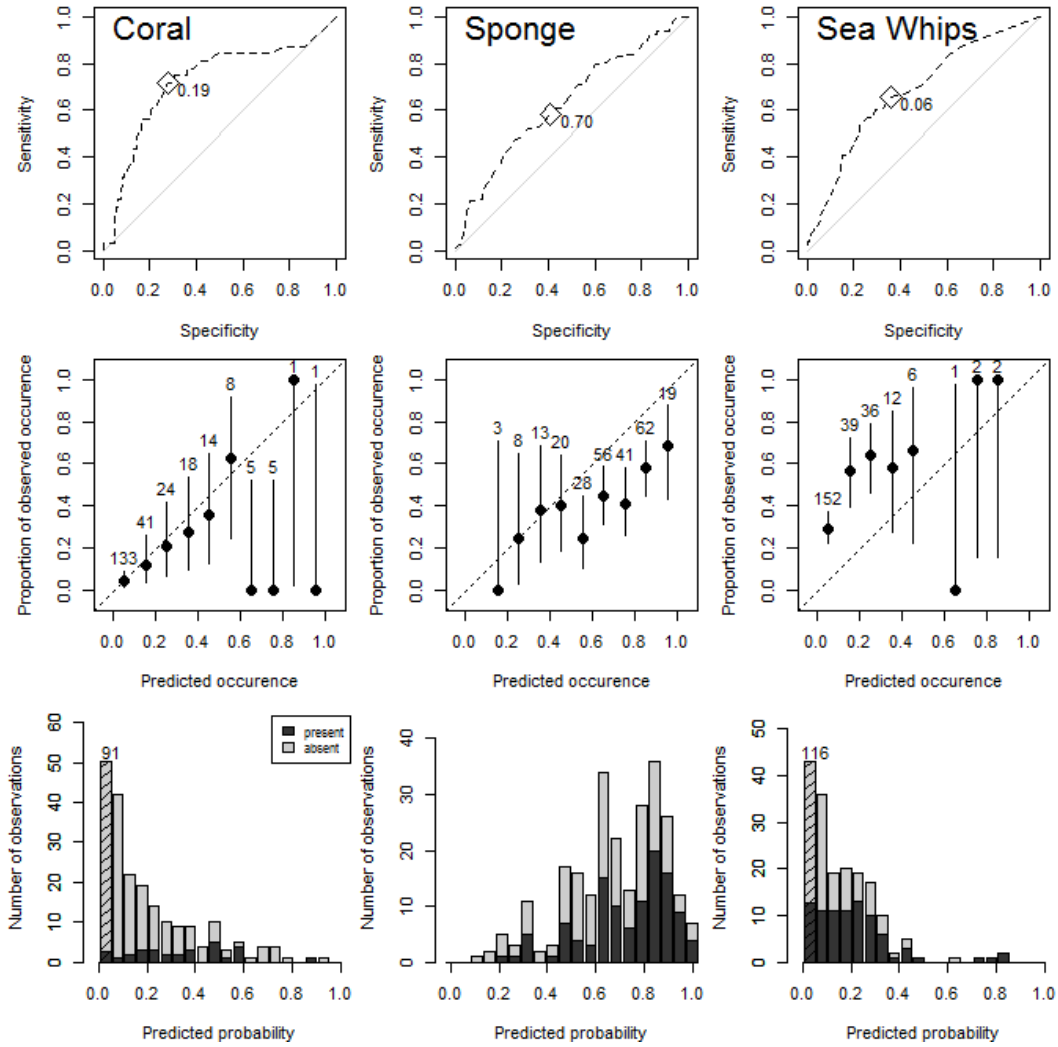


Figure 5. Diagnostic plots for the coral, sponge, and sea whip presence or absence observations from the camera survey tested against the models based on the bottom trawl survey data. The top row shows the area under the receiver operating curve (AUC) plot with a point indicating the threshold probability where sensitivity (true positive rate) is plotted against specificity (the false positive rate). The middle row of plots shows the goodness-of-fit plots of observed versus predicted values within probability bins (i.e. based on the threshold probability from the figure above, what proportion of observations were predicted present in each bin). The bottom row of plots shows the histogram of observed presence or absence plotted against the predicted probability.

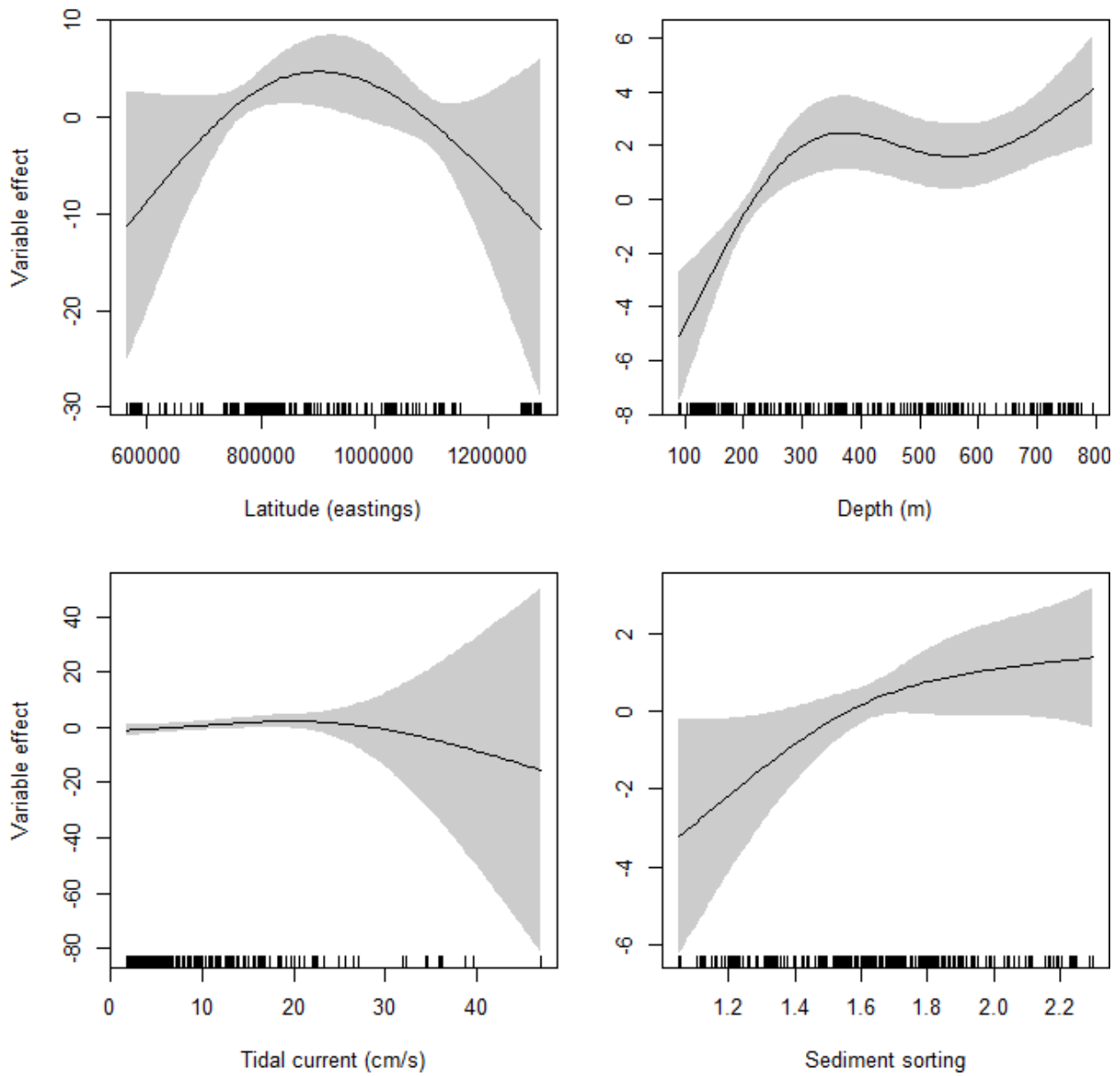


Figure 6. Smoothed relationships from the best-fitting GAM model between explanatory variables and the presence or absence of corals observed in the camera survey. Only significant variables are shown.

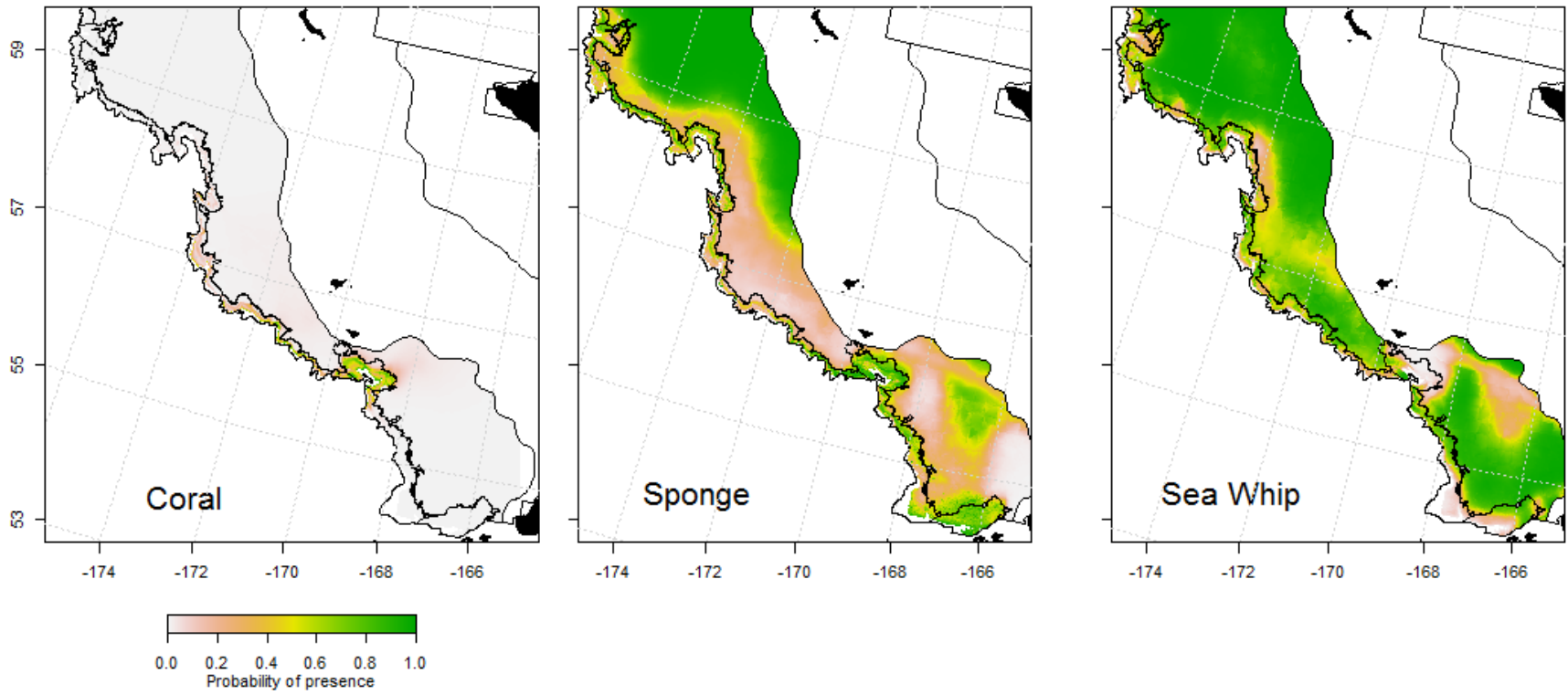


Figure 7. Predicted probability of structure-forming invertebrate presence predicted from the best fitting GAM model of presence or absence in the camera survey data. Panels represent coral, sponge and sea whips, predictions are made on a 100 m by 100 m grid.

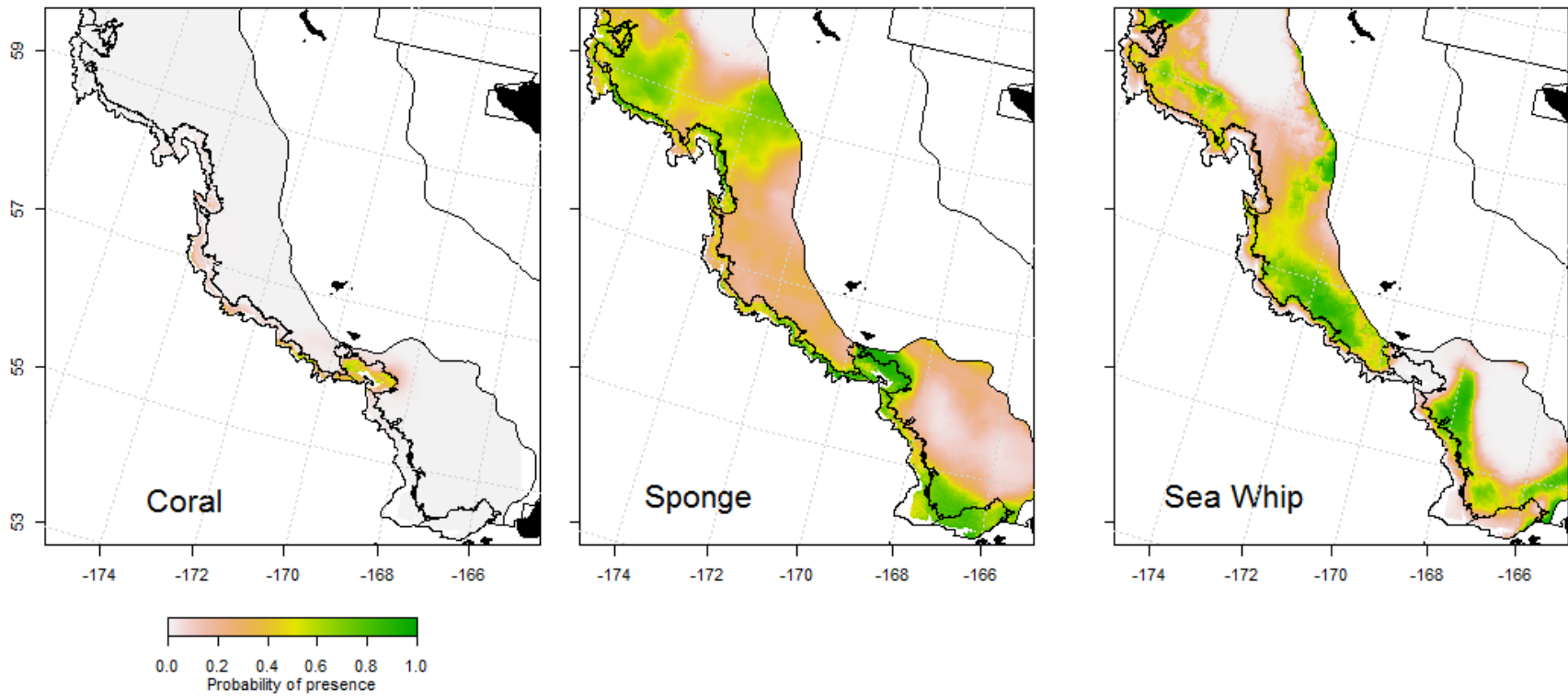


Figure 8. Predicted probability of structure-forming invertebrate presence predicted from the average of the best-fitting GAM models of presence or absence from the trawl survey data and camera survey data. The predictions were averaged by weighting with the inverse of the prediction error. Panels represent coral, sponge, and sea whip predictions on a 100 m by 100 m grid.

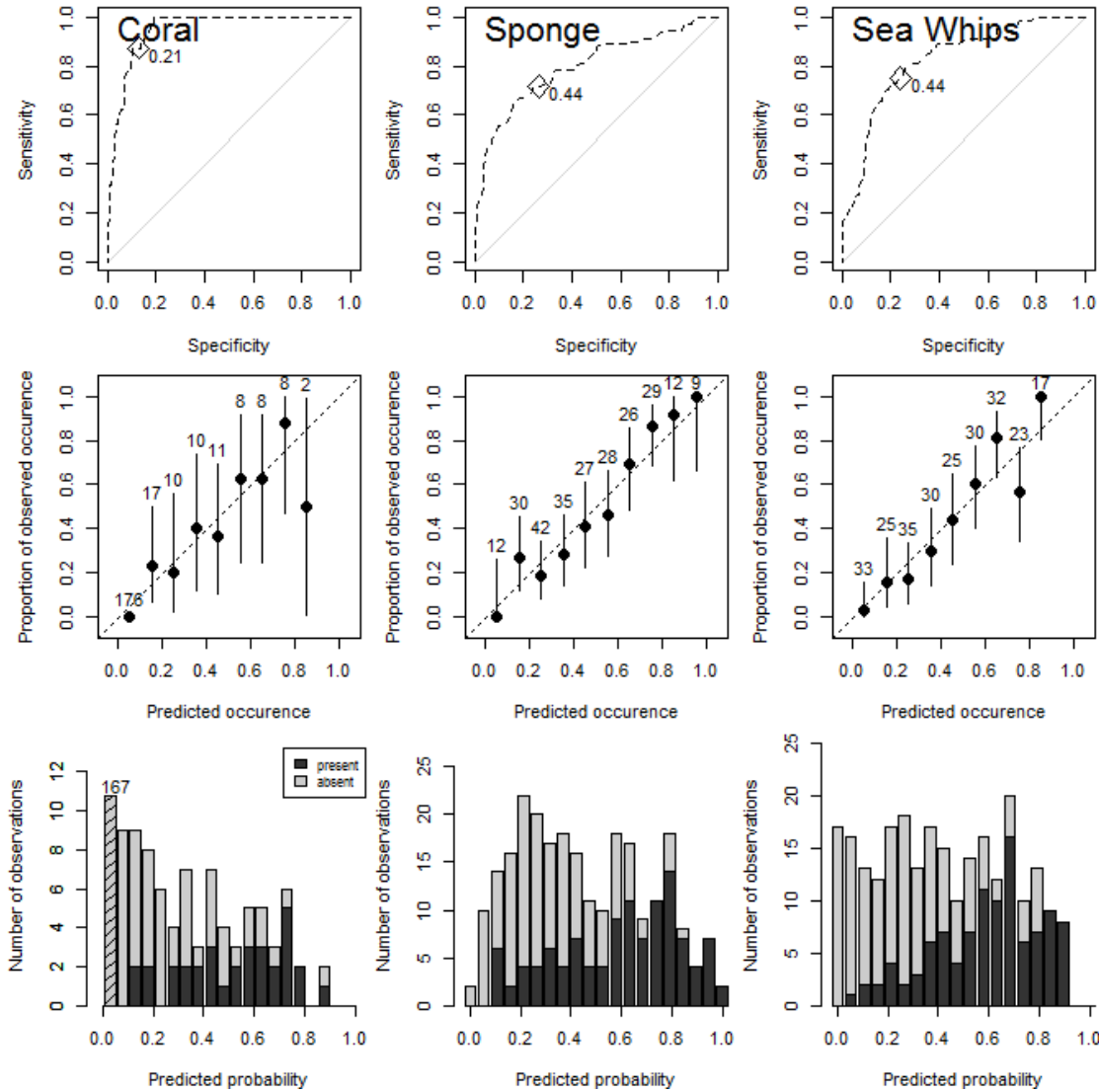


Figure 9. Diagnostic plots for the coral, sponge, and sea whip presence or absence observations from the camera survey tested against the model based on the camera survey data. The top row shows the area under the receiver operating curve (AUC) where sensitivity (true positive rate) is plotted against specificity (the false positive rate). The points indicate the threshold probability for presence. The middle plots show the goodness-of-fit of observed versus predicted values within probability bins (i.e. based on the threshold probability from the figure above, what proportion of observations were predicted present in each bin). The bottom row of plots shows the histogram of observed presence or absence plotted against the predicted probability.

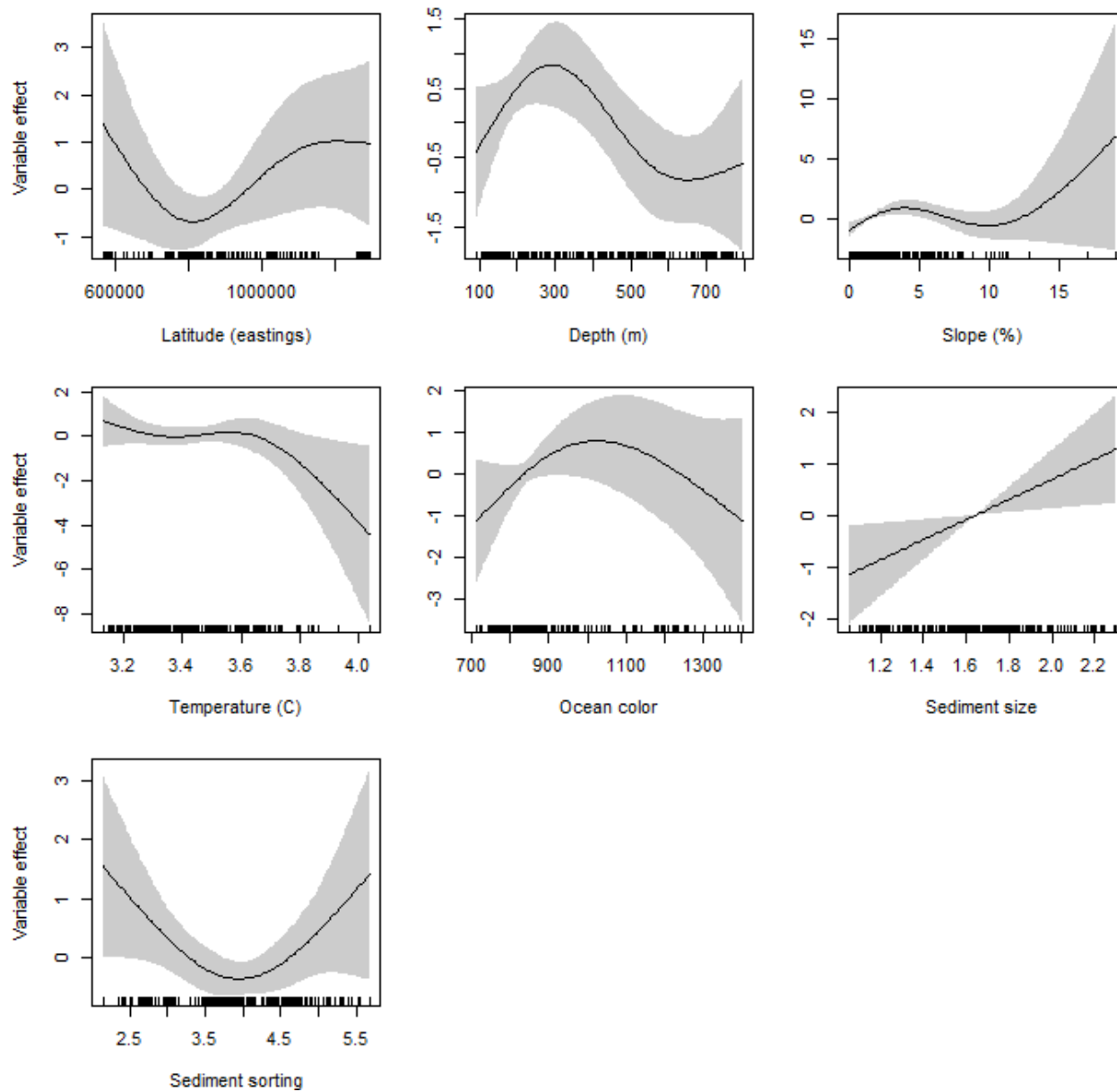


Figure 10. Smoothed relationships from the best-fitting GAM model between explanatory variables and the presence or absence of sponges observed in the camera survey. Only significant variables are shown.

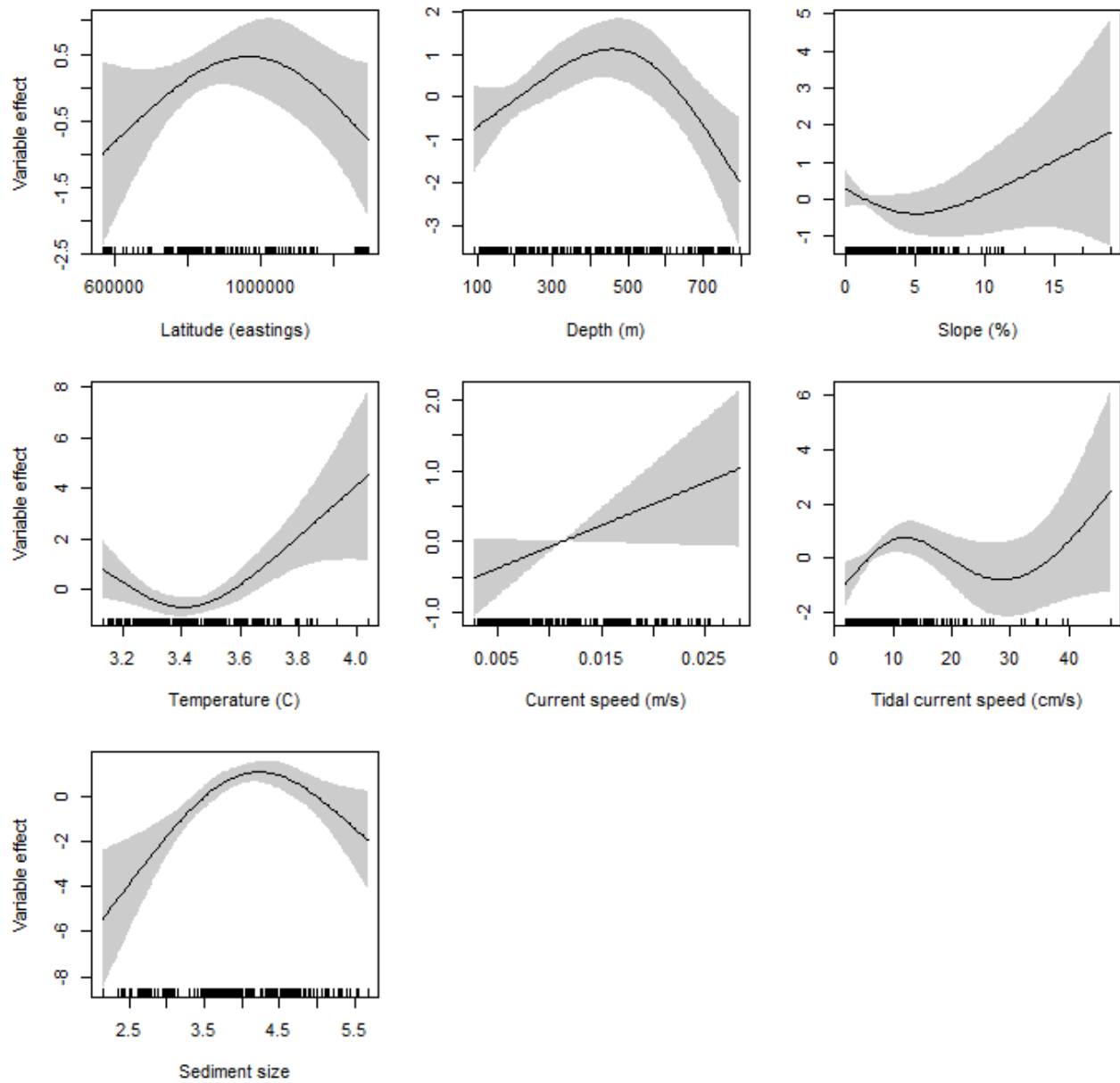


Figure 11. Smoothed relationships from the best-fitting GAM model between explanatory variables and the presence or absence of sea whips observed in the camera survey. Only significant variables are shown.

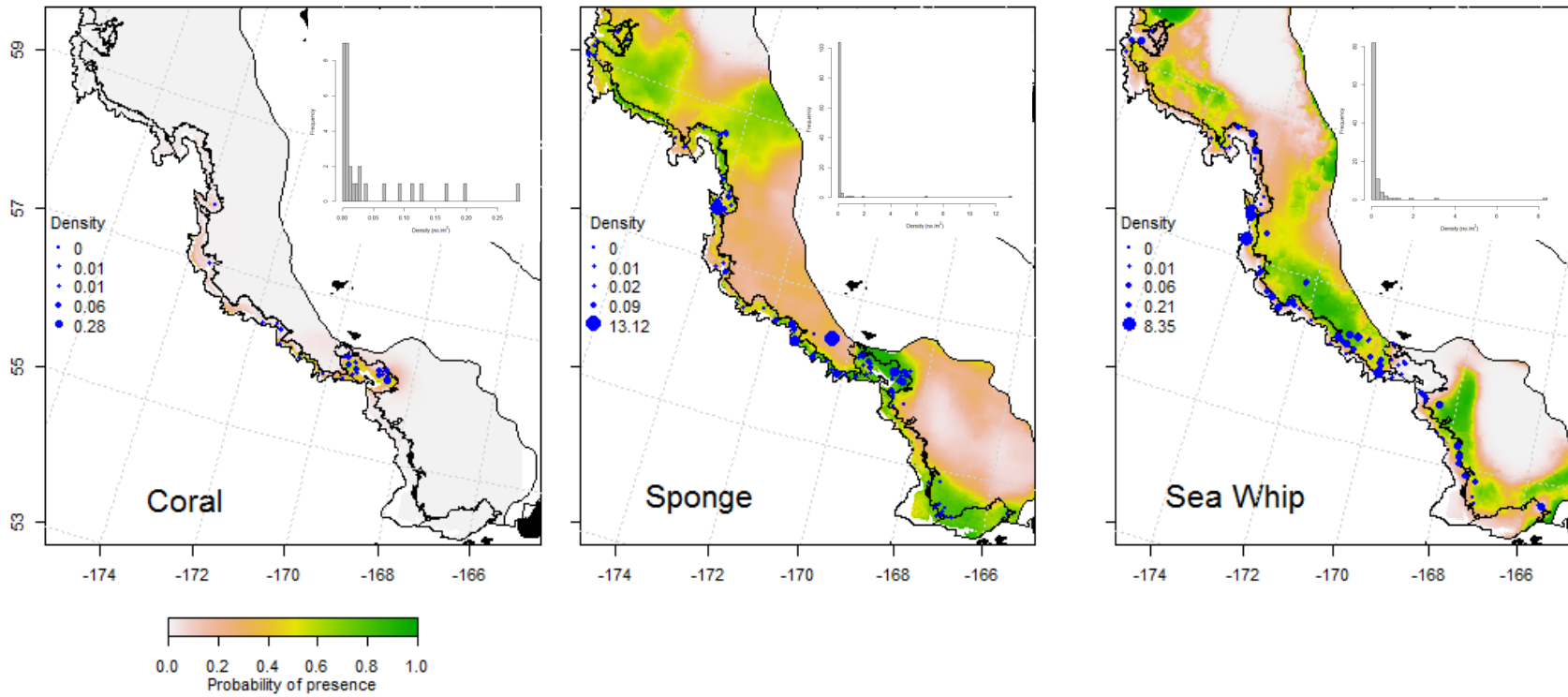


Figure 12. Observed structure-forming invertebrate densities (separated into quantiles) from the camera survey. The background shows the average presence absence model from Figure 8. The inset bar charts show the frequency histogram of observed density for stations where the invertebrate taxon was observed.

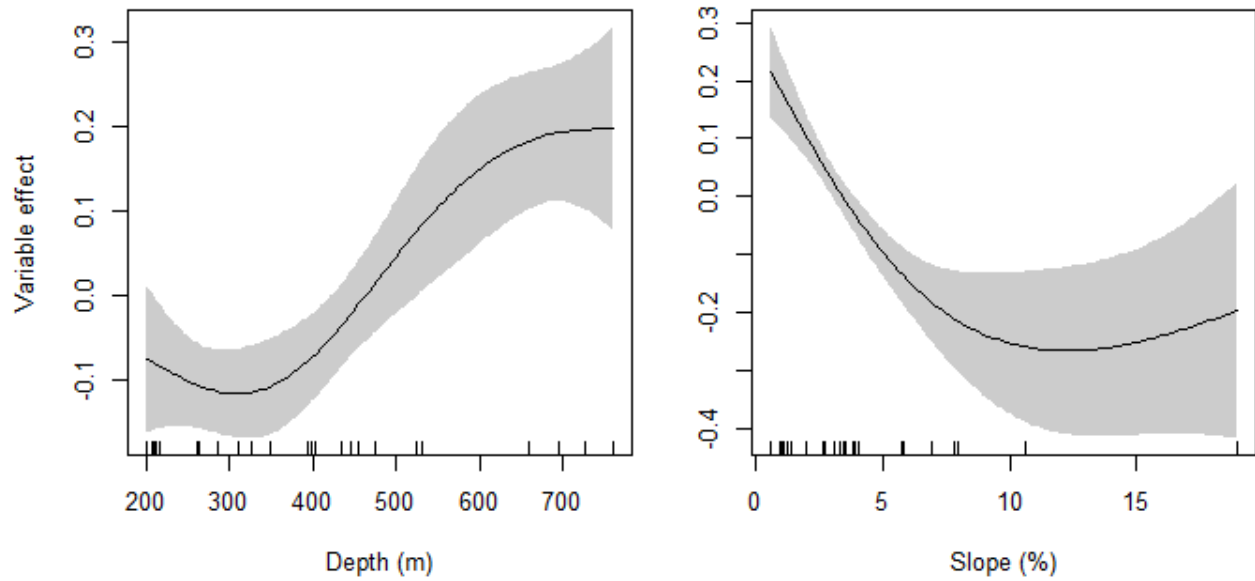


Figure 13. Smoothed relationships from the best-fitting GAM model between explanatory variables and density of corals ($\text{no.} \cdot \text{m}^{-2}$) observed in the camera survey. Only significant variables are shown.

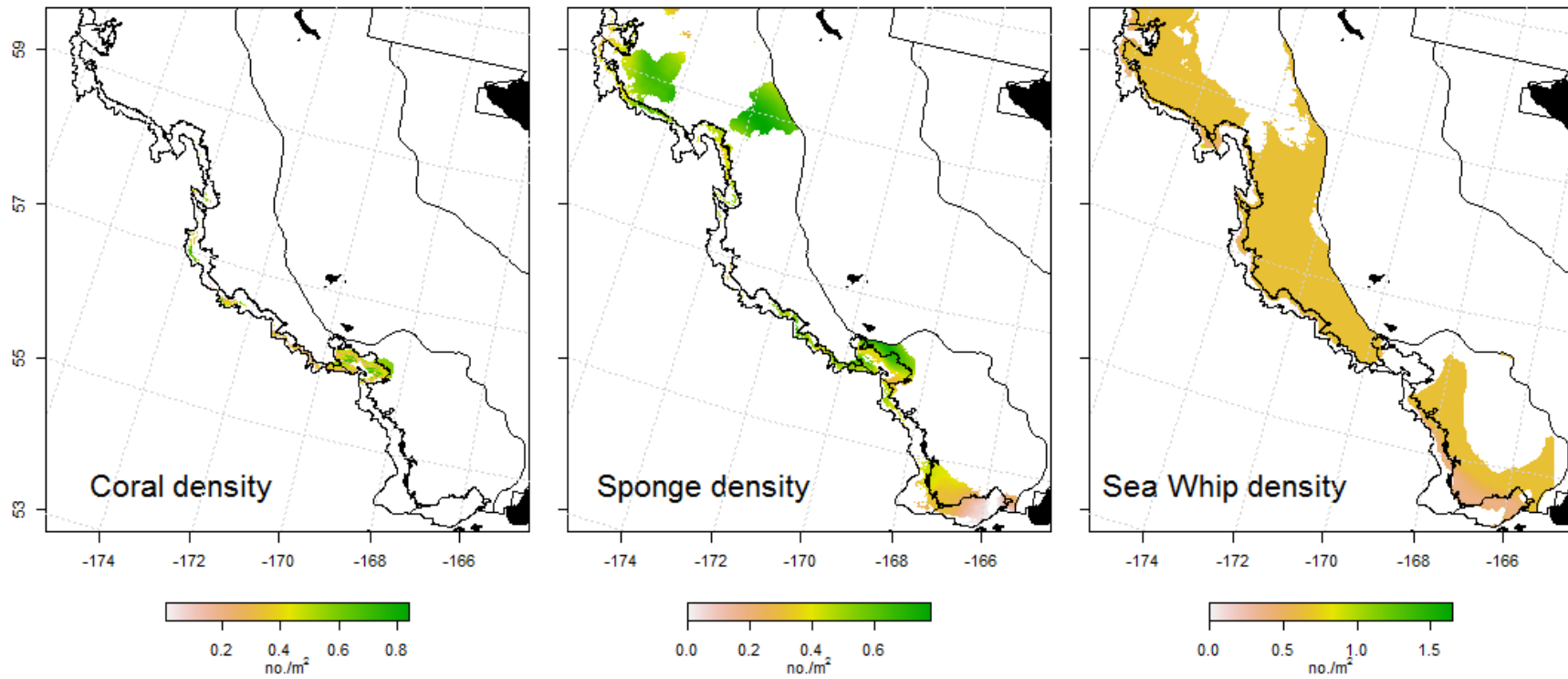


Figure 14. Predicted fourth-root transformed density ($\text{no.} \cdot \text{m}^{-2}$) of corals, sponges, and sea whips based on GAM models of camera survey density data. Predictions are shown for only those grid cells where the average presence-absence model indicated that the invertebrate taxa would be present.

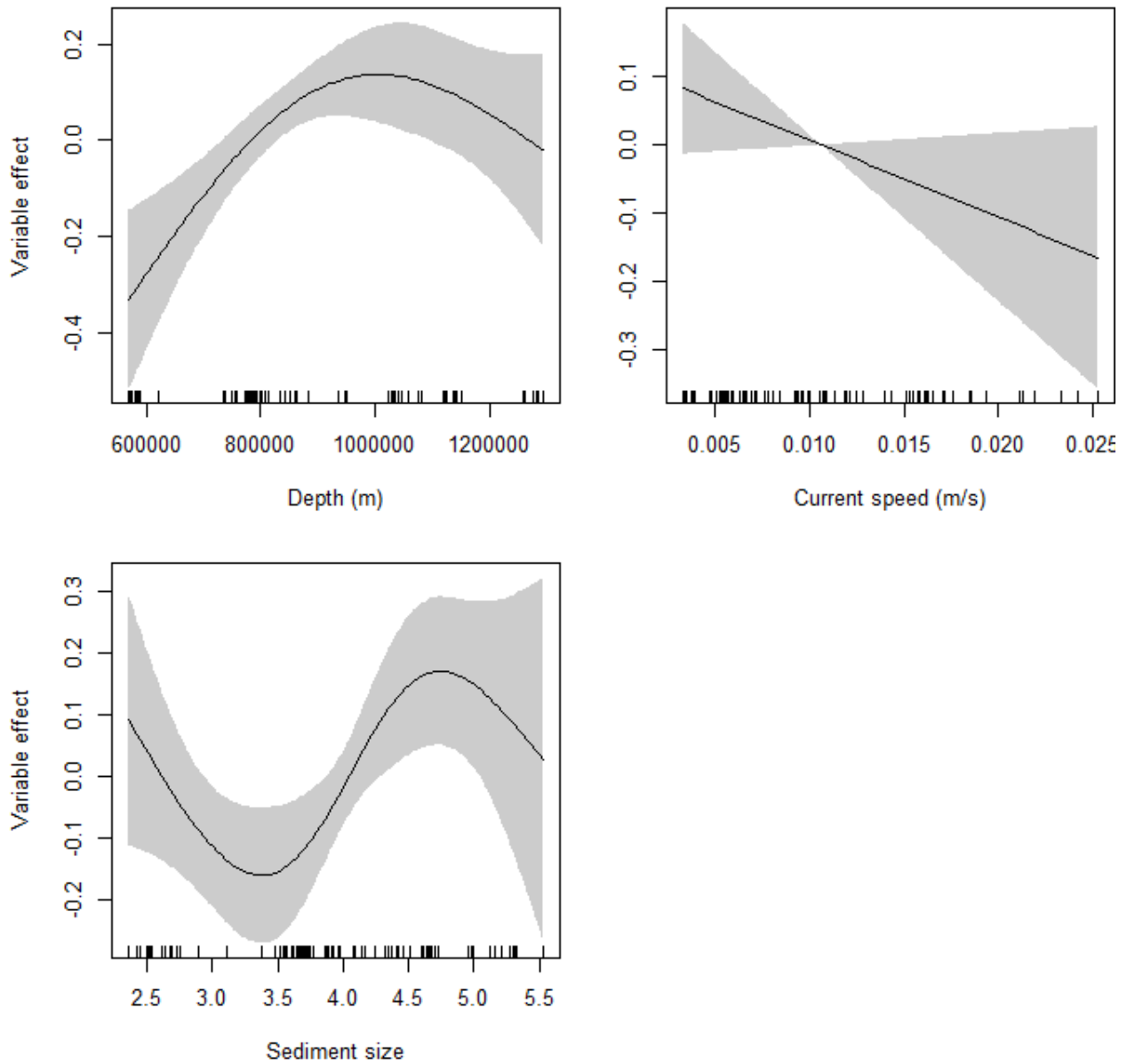


Figure 15. Smoothed relationships from the best-fitting GAM model between explanatory variables and density of sponges (no.*m⁻²) observed in the camera survey. Only significant variables are shown.

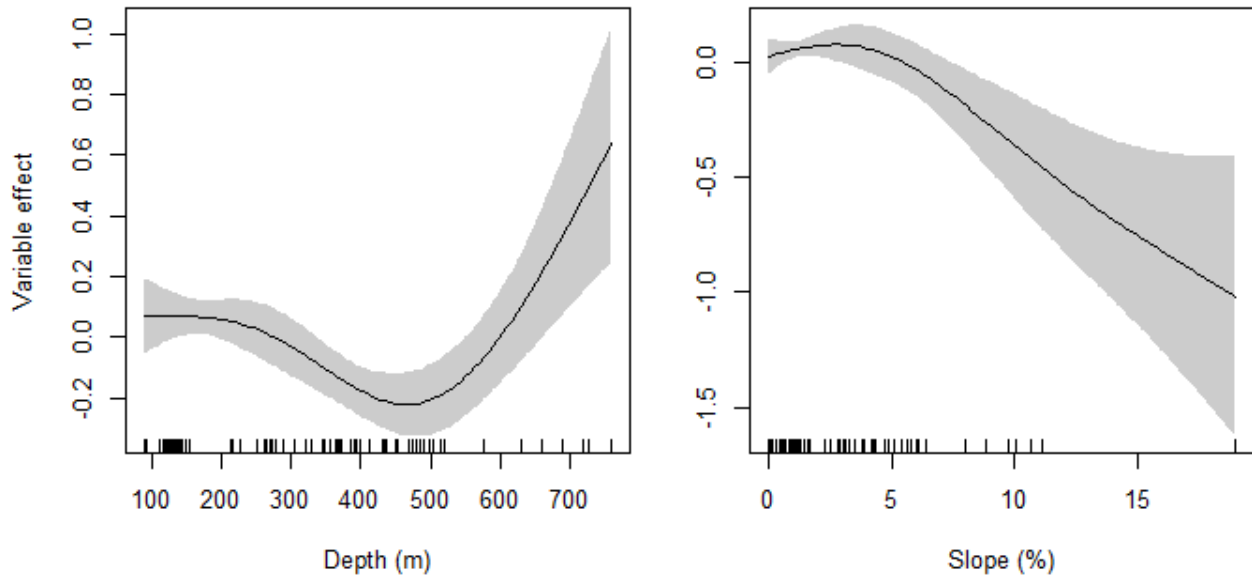


Figure 16. . Smoothed relationships from the best-fitting GAM model between explanatory variables and density of sea whips (no.*m⁻²) observed in the camera survey. Only significant variables are shown.

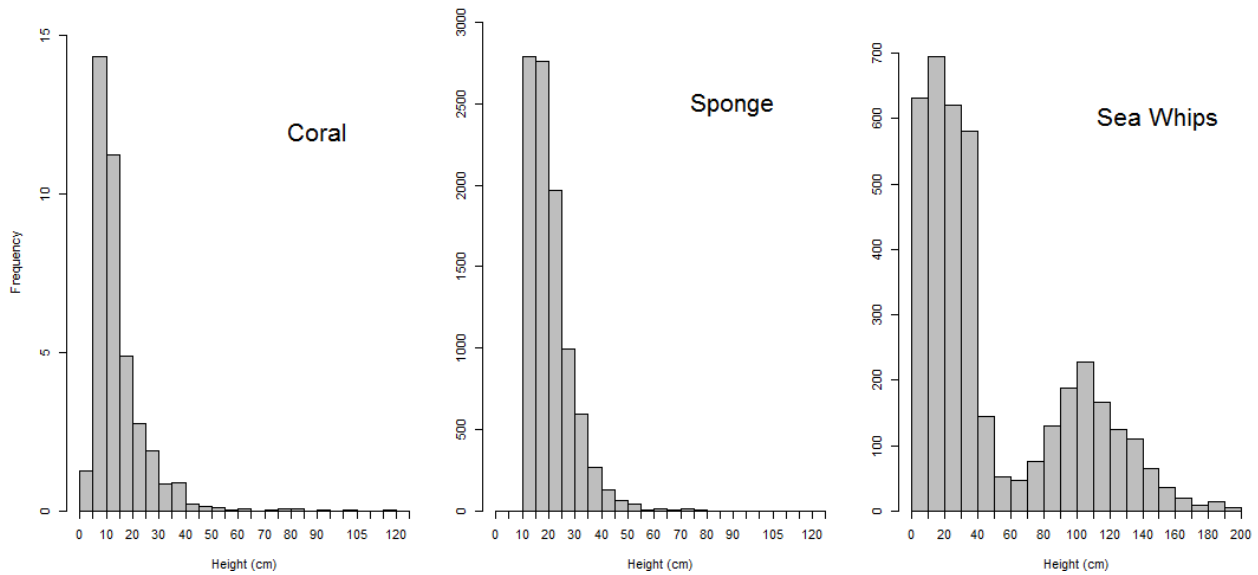


Figure 17. Height frequencies measured by the stereo camera for invertebrate taxa; corals, sponges and sea whips.

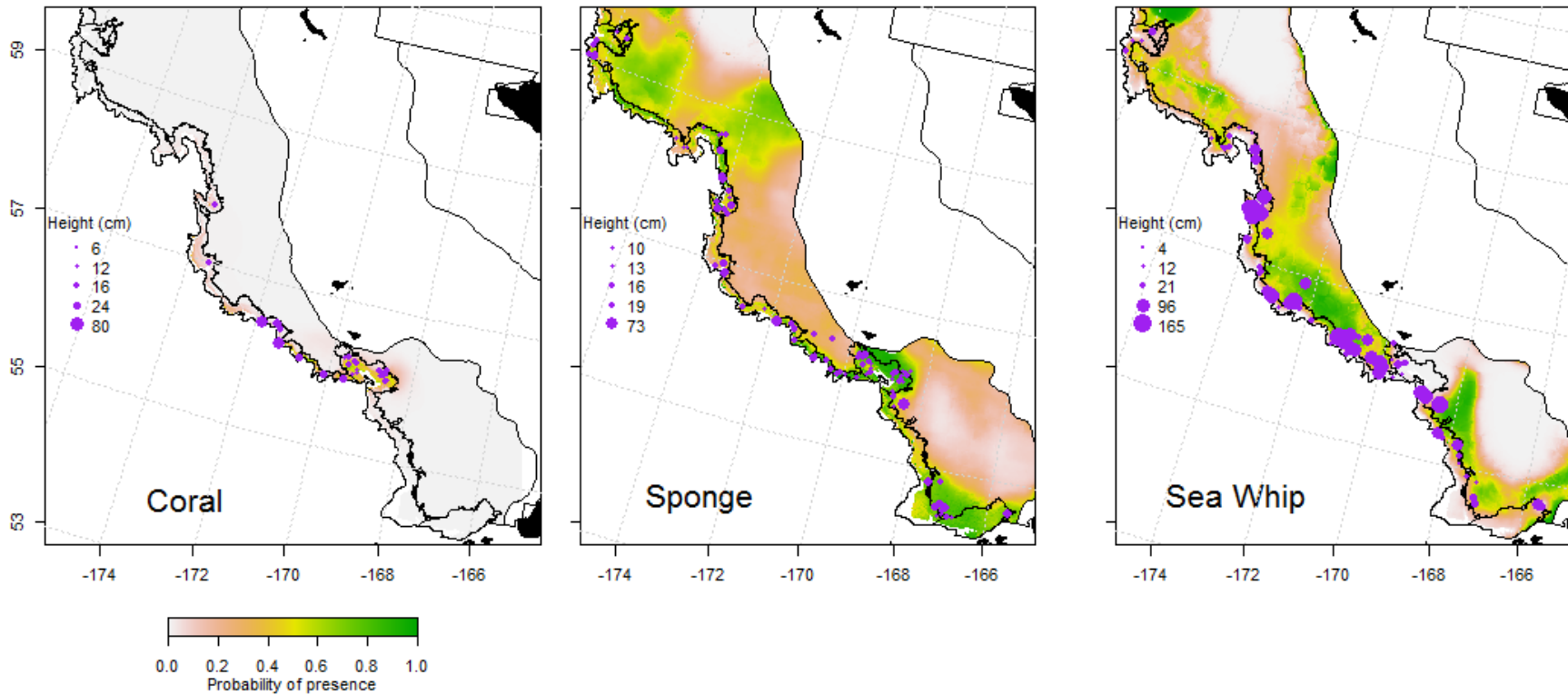


Figure 18. Observed structure-forming invertebrate average heights (separated into quantiles) from the camera survey. The background shows the average presence absence model from Figure 8.

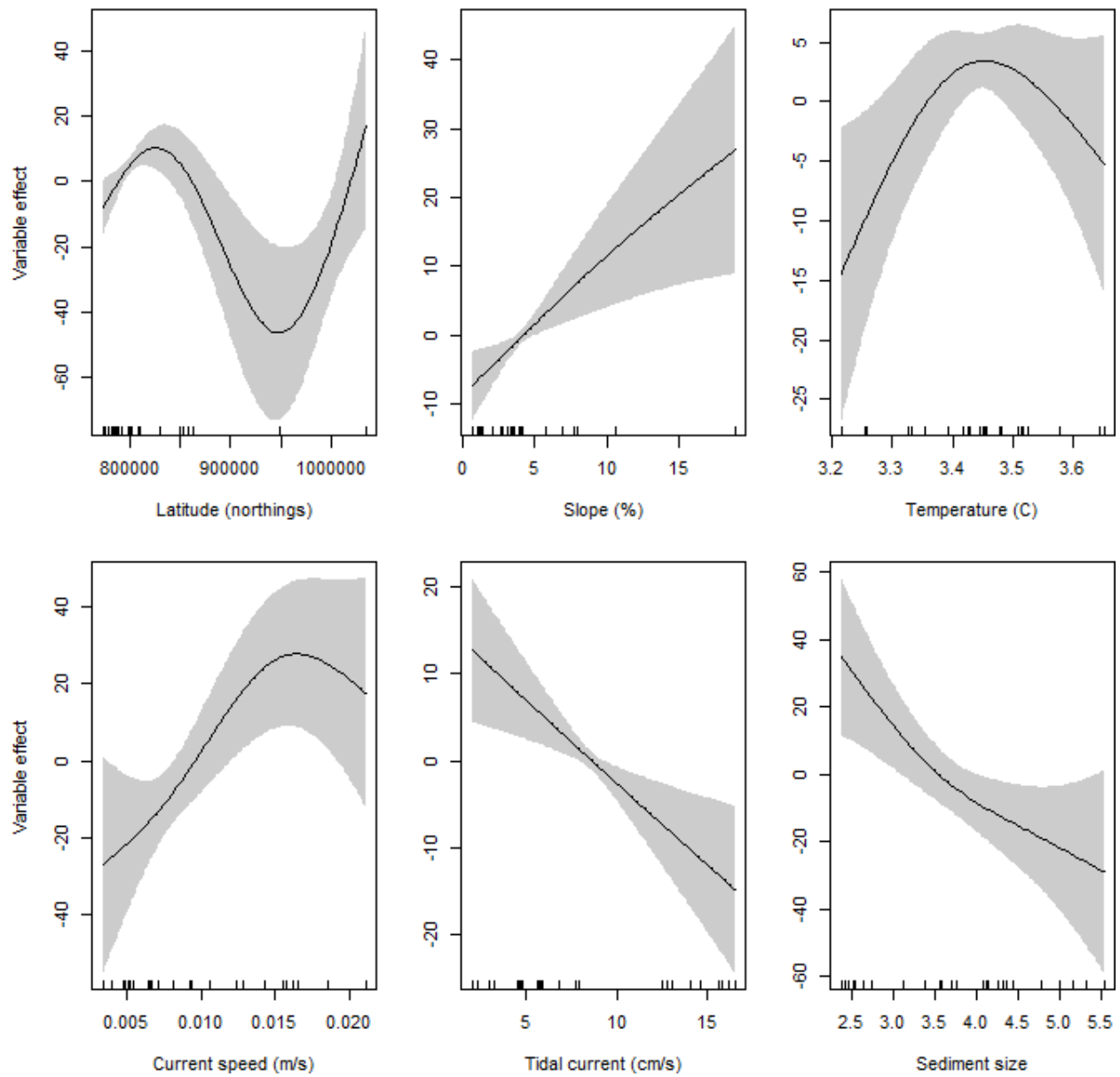


Figure 19. Smoothed relationships from the best-fitting GAM model between explanatory variables and height of coral (cm) observed in the camera survey. Only significant variables are shown.

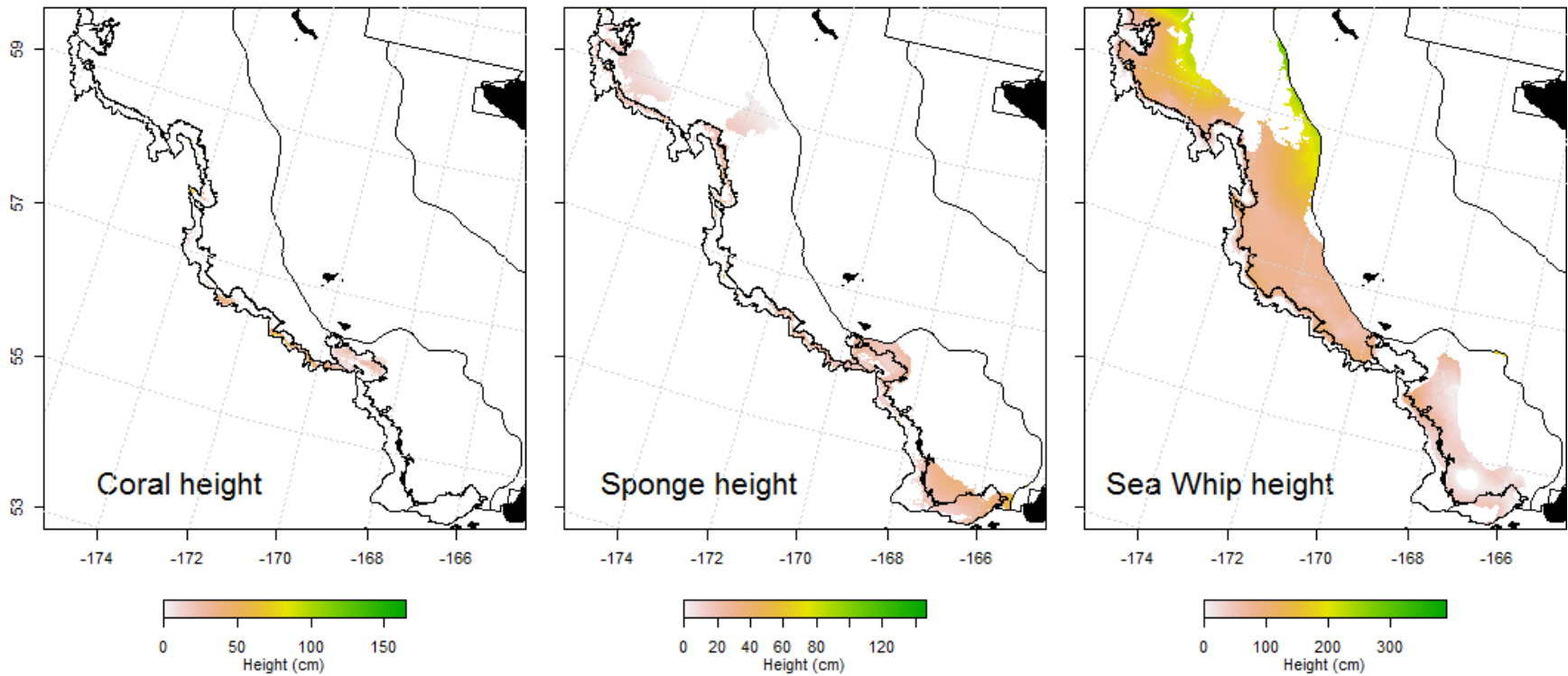


Figure 20. Predicted heights of corals, sponges, and sea whips based on GAM models of camera survey density data. Predictions are shown for only those grid cells where the average presence-absence model indicated that the invertebrate taxa would be present.

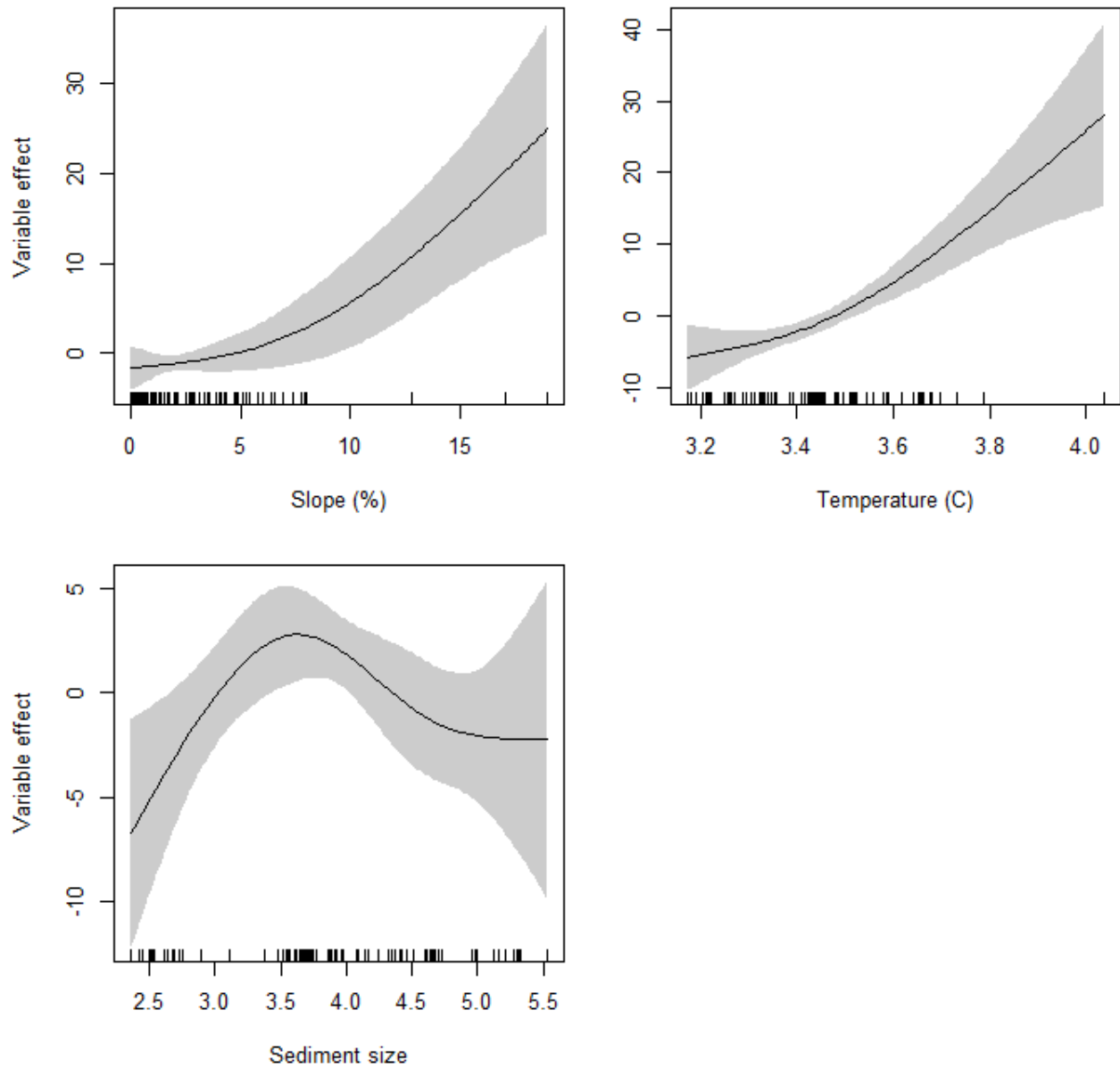


Figure 21. Smoothed relationships from the best-fitting GAM model between explanatory variables and height of sponges (cm) observed in the camera survey. Only significant variables are shown.

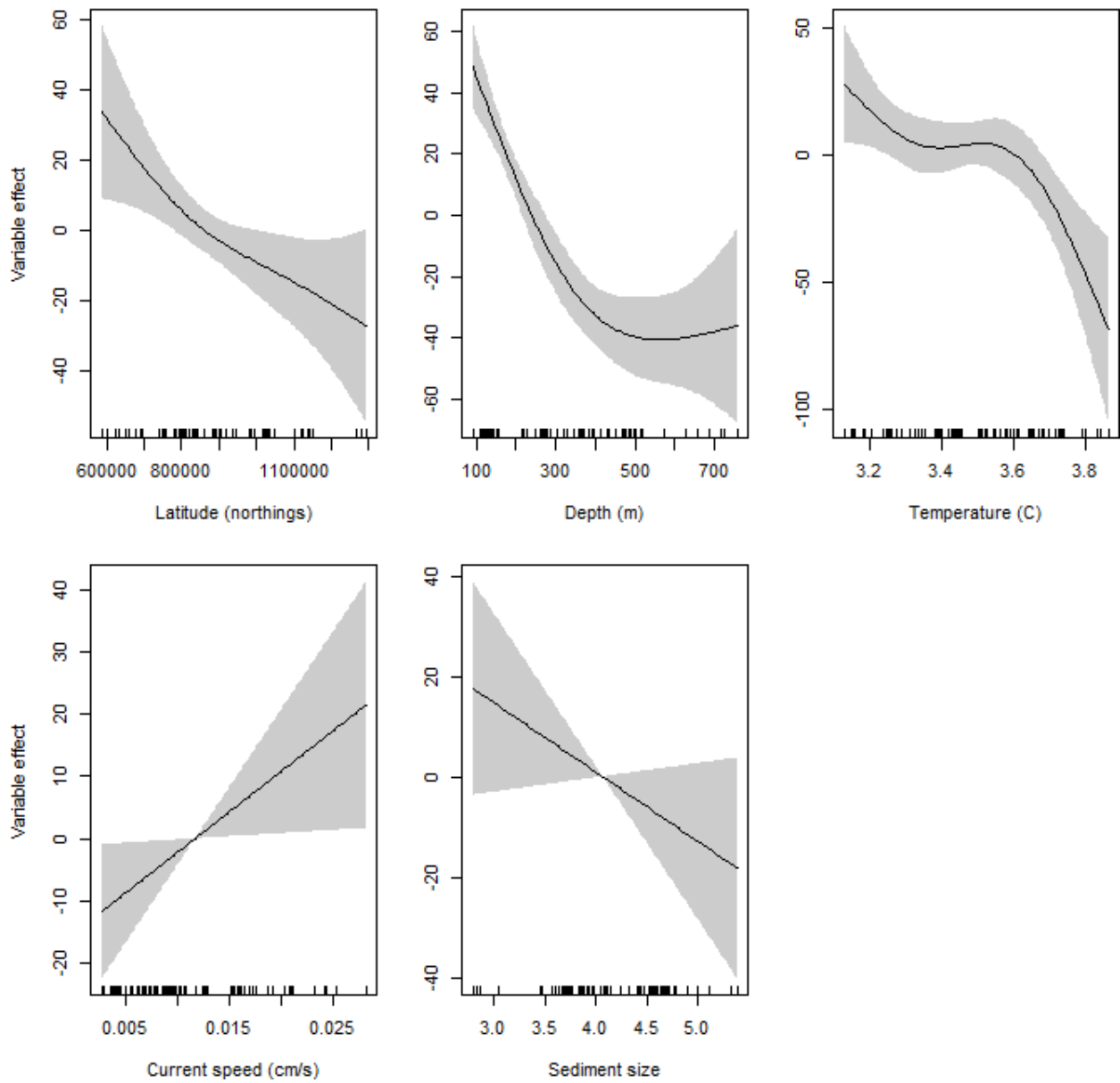


Figure 22. Smoothed relationships from the best-fitting GAM model between explanatory variables and height of sea whips (cm) observed in the camera survey. Only significant variables are shown.

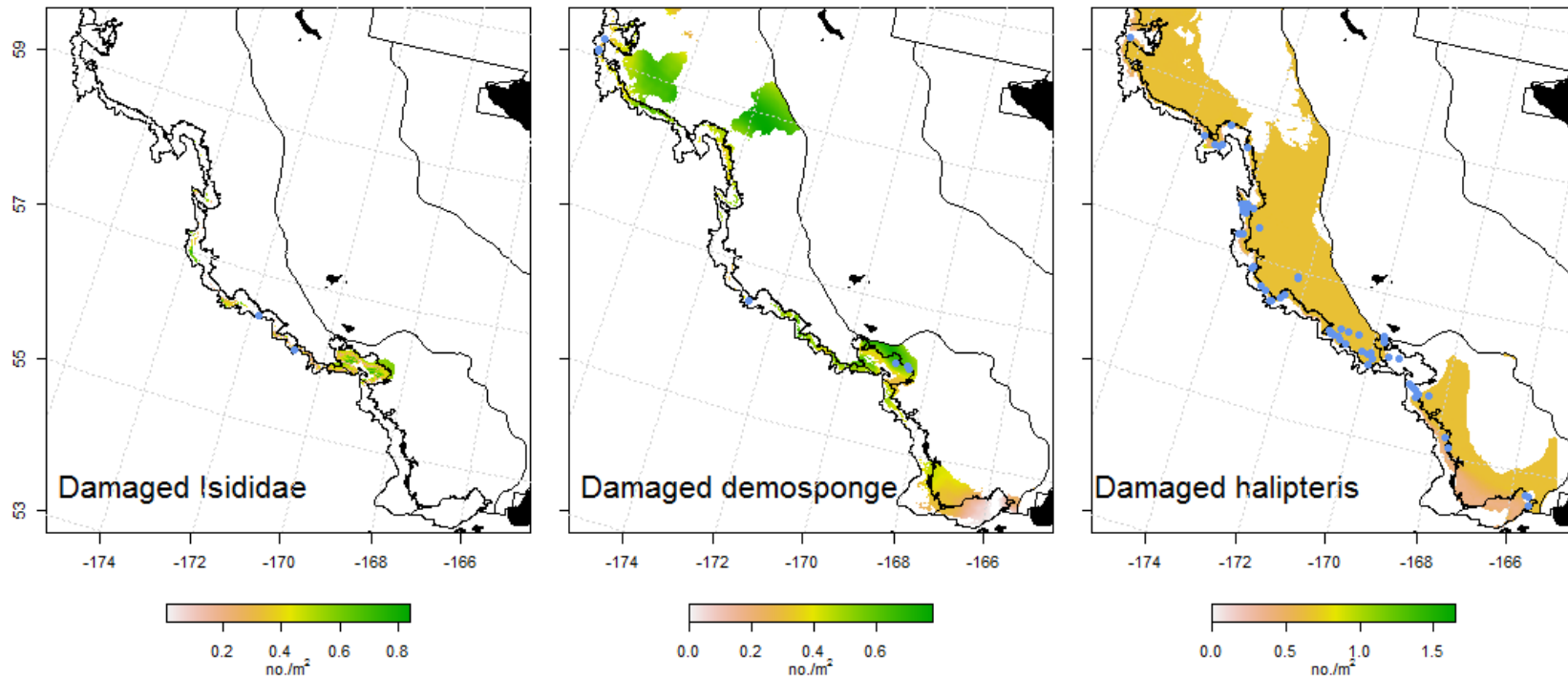


Figure 23. The location of transects with damaged coral, sponge, or sea whip indicated by blue dots. The dots are overlaid on predicted density for the coral, sponge, and sea whip models.

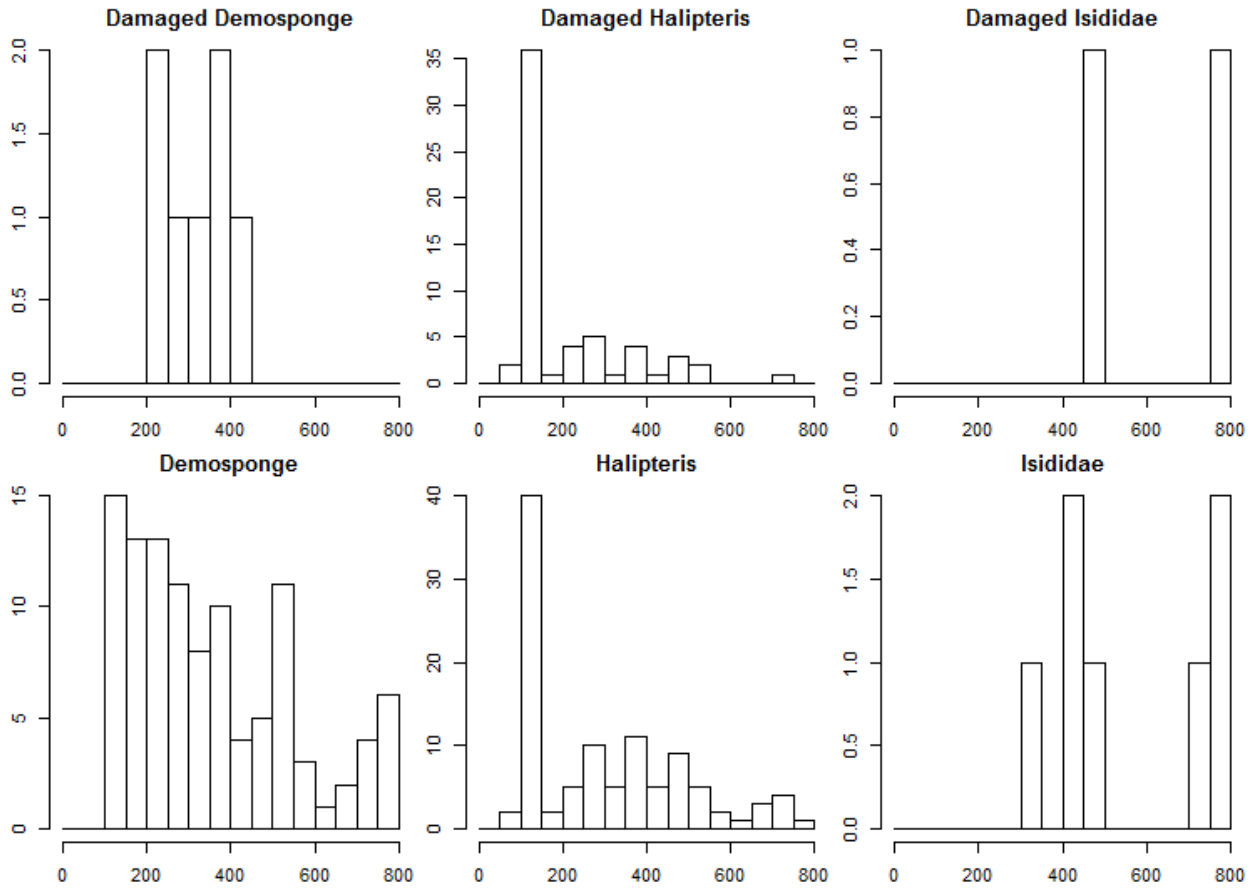


Figure 24. The depth of transects with damaged (upper) or present (lower) Demosponge, *Halipteris* sp., or Isididae

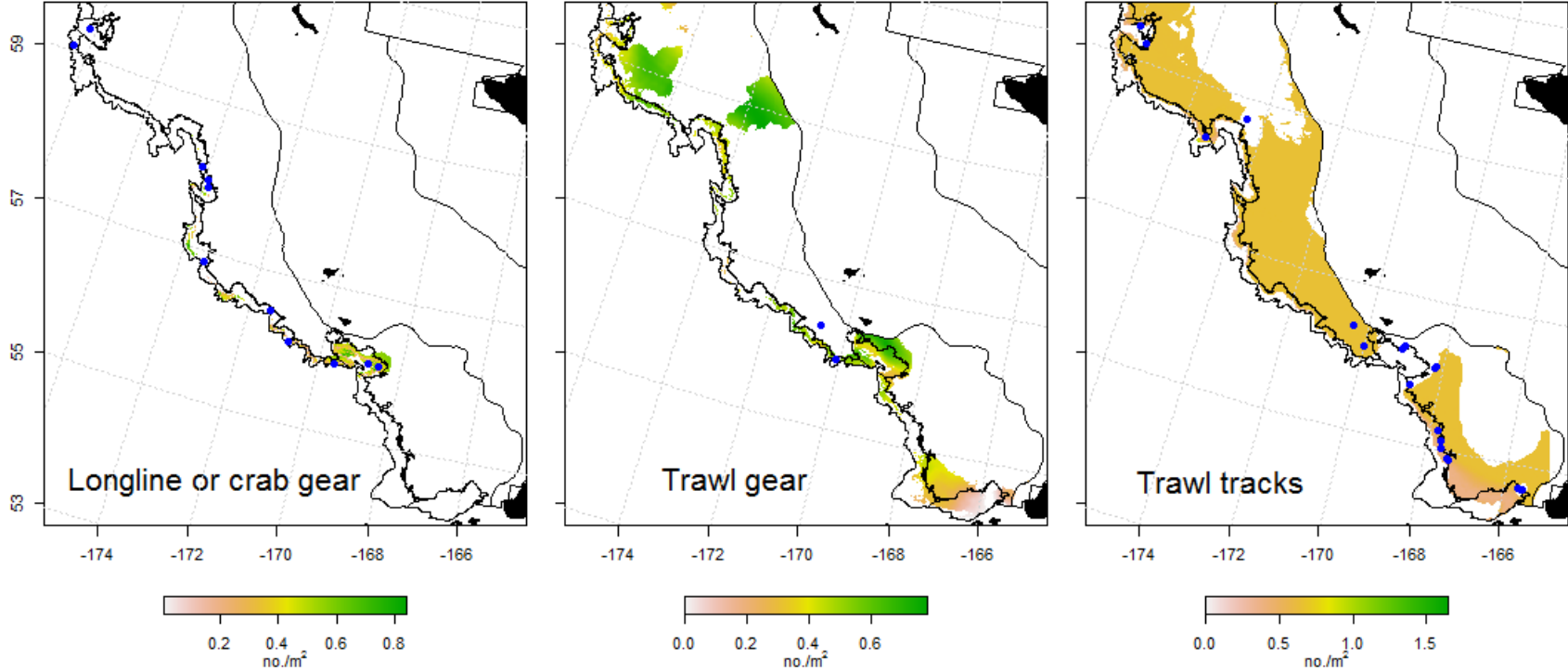


Figure 25. The location of transects with evidence of fishing (e.g., lost gear) indicated by blue dots. The dots are overlaid on predicted density for the coral, sponge and sea whip models (from left to right).

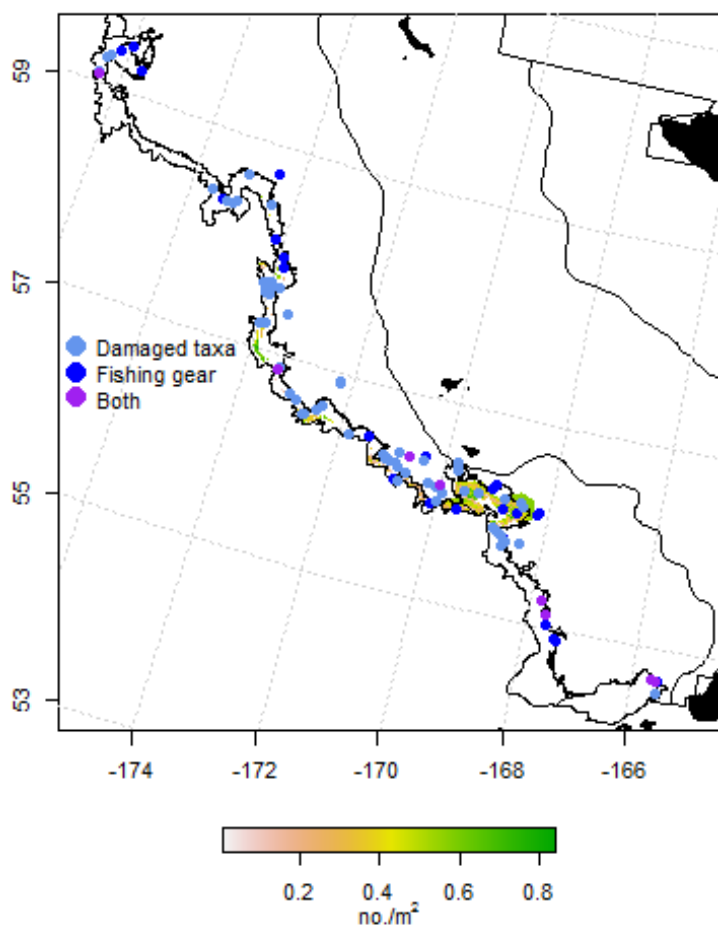


Figure 26. The location of transects with damaged coral, sponge, or sea whip or evidence of fishing (e.g., lost gear). The dots are overlaid on predicted density for the coral model.

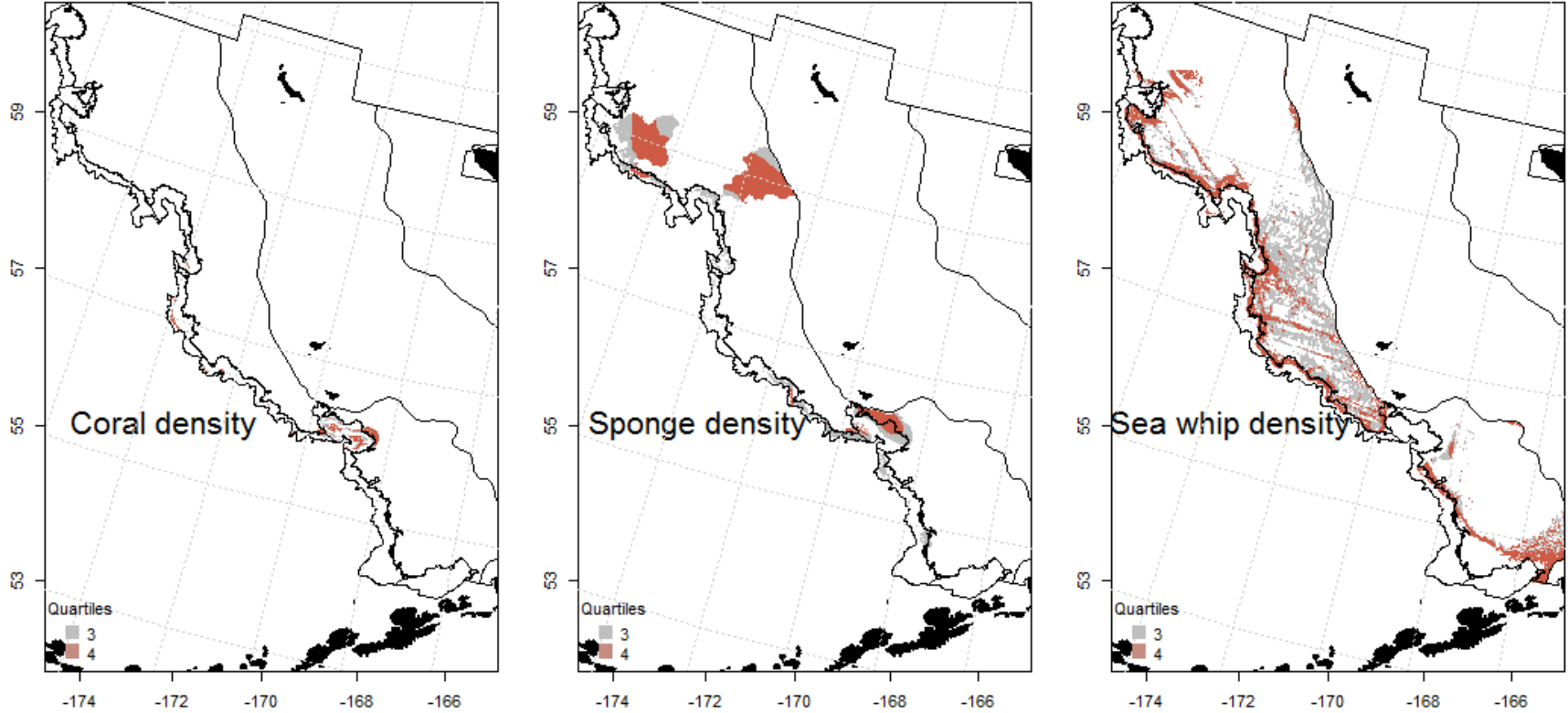


Figure 27. Plots of the upper two quartiles of predicted density for structure-forming invertebrates based on the density model for the eastern Bering Sea slope and outer shelf.

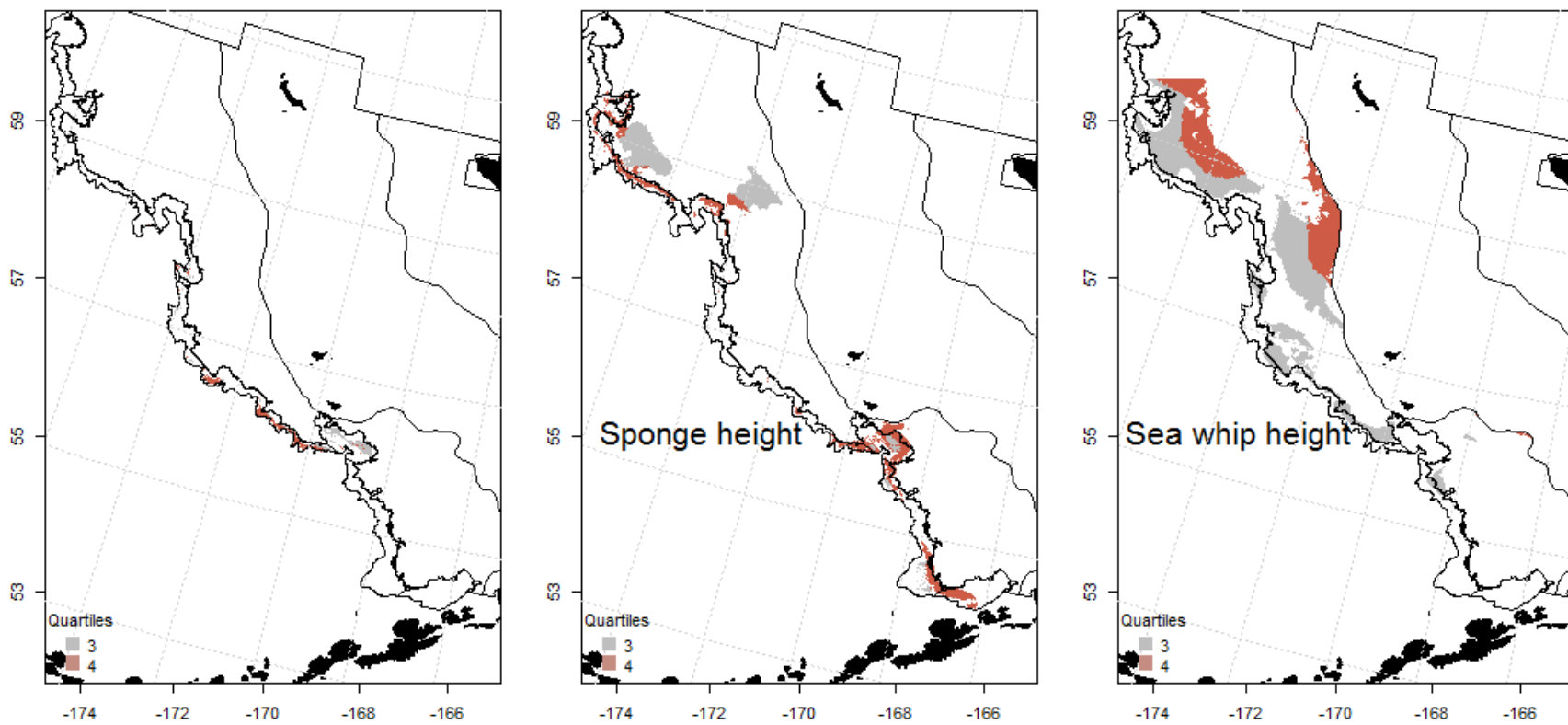


Figure 28. Plots of the upper two quartiles of predicted height for structure-forming invertebrates based on the height model for the eastern Bering Sea slope and outer shelf.

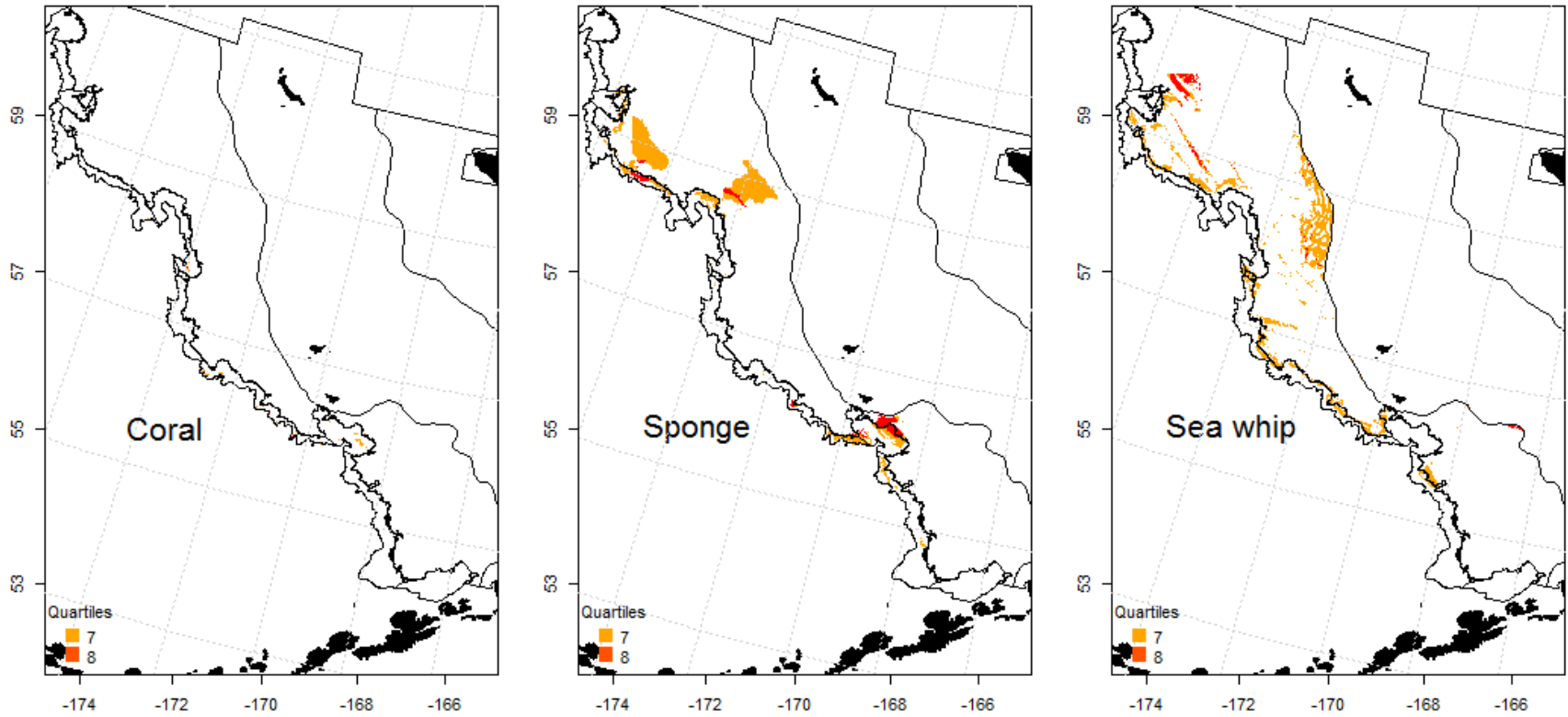


Figure 29. Plots of the upper two quartiles of predicted height for structure-forming invertebrates based on the height model for the eastern Bering Sea slope and outer shelf.

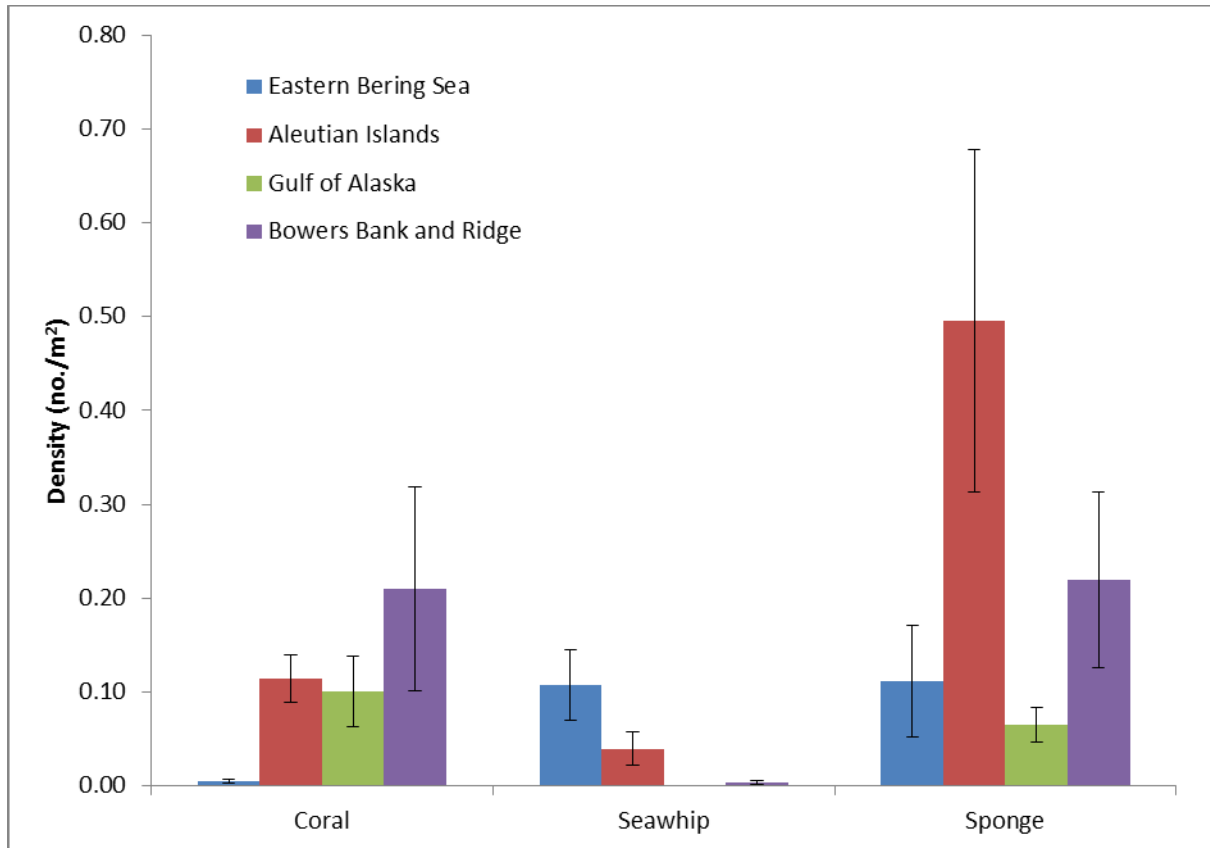


Figure 30. Densities (SE bars) of structure-forming invertebrates from four areas where the same type of study was conducted using randomly selected camera transects.