



Original Article

Validation of deep-sea coral and sponge distribution models in the Aleutian Islands, Alaska

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Spatial management of vulnerable benthic ecosystem components such as deep-sea corals and sponges requires adequate maps of their distribution. These maps are often based on statistical models of survey data. The objective of this project was to validate the predictions of existing presence or absence and abundance models of deep-sea corals and sponges in the Aleutian Islands that were based on bottom trawl survey data. Model validation was conducted by comparing bottom trawl survey model predictions to the observations of an *in situ* camera survey conducted at randomly selected locations. The measures of goodness of fit (area-under-the-receiver-operator-curve, AUC) for the bottom trawl survey model predictions of camera survey observations ranged from 0.59 to 0.77 (for sponges and coral, respectively) and indicated that the bottom trawl survey models predicted the probability of presence for corals accurately across the Aleutian Islands. The bottom trawl survey models explained as little as 3% of the variability in Stylasteridae density and up to 17% of the variability in coral density. These results indicate that models of deep-sea coral distributions based on presence and absence data from bottom trawl surveys can be accurate and can provide useful information for spatial management of these vulnerable taxa. However, for some other taxa, such as sponges, care should be taken interpreting the results of bottom trawl survey models. An interesting finding of this study was that the residuals from the bottom trawl survey model-camera density relationships were negative in areas that remained open to fishing after 2005, possibly indicating an effect of continued bottom trawling on the abundance of corals in these areas. This study highlights the importance of validating models of species distribution using independent surveys, so that the results can be used with confidence to support decision-making processes.

Keywords: Alaska, Aleutian Islands, corals, habitat, model validation, species distribution, sponges, stereo camera, underwater camera.

Introduction

Deep-sea coral and sponge ecosystems throughout the world are vulnerable to climate change and fishing activity (van Dolah *et al.*, 1987; Auster *et al.*, 1996; NRC, 2002; Heifetz *et al.*, 2009). Managing these threats requires information on where deep-sea coral and sponge ecosystems occur. In most regions it is not feasible to directly sample and map these ecosystems because of the large area and consequent high cost, so alternatives, such as species distribution models, can be developed and implemented to provide information in the absence of direct measurements (Bryan and Metaxas, 2007; Davies *et al.*, 2008; Tittensor *et al.*,

2010; Kringsman *et al.*, 2012; Huff *et al.*, 2013; Guinotte and Davies, 2014). However, as with any inference-based methods, model testing and validation with independent data sets is crucial to evaluating the confidence placed in model predictions (Lobo *et al.*, 2007; Anderson *et al.*, 2016).

One area where species distribution models have been developed and used to assess managed activities is Alaska (Rooper *et al.*, 2014, 2016; Sigler *et al.*, 2015). Alaska's Aleutian Islands support some of the world's most diverse and abundant cold-water coral ecosystems (Stone, 2006). However, very little of the benthic habitat in the Aleutian Islands has been explored using *in*

situ techniques. Data on cold-water coral and sponge ecosystems in the Aleutian Islands comes mostly from bycatch in fisheries abundance surveys and commercial fisheries (Heifetz, 2002; Heifetz *et al.*, 2005; Malecha *et al.*, 2005). Based on these data, species distribution models were developed for Aleutian Islands coral and sponge (Rooper *et al.*, 2014) to predict both the probability of presence and the abundance of corals and sponges. Bottom trawl surveys for fisheries stock assessment do not supply the optimal data for use in modelling deep sea coral and sponge distributions, since the surveys do not sample well in hard, rocky habitat that is needed for coral and sponge attachment, and the catchability of coral and sponge by bottom trawls is not known but is likely low. However, at the time of model development (Rooper *et al.*, 2014), there were no data available to independently test the predictions of these models and thus to test the ability of bottom trawl survey hauls to map the distribution of deep-sea coral and sponge ecosystems.

The primary objective of this project was to validate the predictions of presence or absence and abundance of deep-sea corals and sponges in the Aleutian Islands from Rooper *et al.* (2014). In performing this model validation, we also examined the applicability of using bottom trawl surveys to determine the distribution of these vulnerable marine ecosystems. A secondary objective of this study was to examine the residuals of the relationship between model predictions and observations to determine if bottom fishing closures implemented in 2006 were effective at protecting deep-sea corals and sponges.

Methods

Study area

The Aleutian Islands archipelago stretches westward from the Alaska Peninsula across the North Pacific Ocean, dividing the western Gulf of Alaska from the Bering Sea (Figure 1). The chain consists of a series of geologically active volcanoes with a relatively deep continental shelf (250 m). The continental slope is generally steep along both the northern and southern sides of the island chain and the area west of 170°W is dominated by oceanic water temperatures and salinities (Stabeno *et al.*, 1999, 2002; Ladd *et al.*, 2005). The Alaska Coastal Stream and Alaska Coastal Current flow westward on the southern side of the Aleutian Islands, while on the Bering Sea side of the islands the dominant current flows eastward. There is extensive northward transport through deep passes in the island chain, and tidal currents can be large (Ladd *et al.*, 2005).

Study design

A total of 216 sampling stations were occupied on two research cruises in August 2012 and April–May 2014. Only 184 of the 216 occupied stations were used for this analysis because some of the stations were deeper than the 500 m depth limit of the models produced in Rooper *et al.* (2014). Stations were initially chosen at random from three depth strata ($n=250$ in 20–200 m, $n=100$ in 200–500 m, and $n=85$ in 500–900 m) from a regularly spaced grid (100 m×100 m) overlaid on the Aleutian Islands shelf and slope (20–900 m). Initially, 435 stations were chosen; however due to time constraints 135 stations were dropped at random after the first year and an additional 84 stations were not sampled due to weather constraints.

The primary sampling tool for this study was a stereo drop-camera system (Rooper *et al.*, 2016; Goddard *et al.*, 2016, 2017)

deployed from a chartered fishing vessel. The electronic components of the drop-camera were protected from physical damage by a cage constructed from aluminum tubing. Two machine-vision cameras spaced ~30 cm apart in underwater housings were connected via Ethernet cables to a computer that was also in an underwater housing. One of the paired cameras recorded monochromatic still images sized at 1.45 megapixels (JAI, CM-140GE), while the other camera collected 1.73 megapixel colour still images (JAI, AB-201GE). Lighting was provided by four strobe lights constructed of four Bridgelux® BXRA LED arrays capable of producing 1300 lumens at 10.4 W. The computer, cameras, and lights were powered by a 28-V NiMH battery pack. Synchronous images were taken at a rate of four images per second for real-time viewing on a monitor mounted to an electric winch at the surface. This allowed active control to maintain a consistent camera height off the seafloor and avoidance of obstacles. A 0.64 cm (1/4 inch) diameter coaxial cable provided the connection from the drop-camera system to the winch at the surface. Synchronous images from each camera were recorded at a rate of one image per second to the computer onboard the drop-camera system at depth.

The camera was deployed at the centre of the grid cell at each station and lowered to the seafloor. During each deployment, the drop-camera system was allowed to drift or was towed lightly through the water column at a speed of 0.08–6.07 km h⁻¹ (0.05–3.28 knots) in the direction of the prevailing current. The camera was held ~1–2 m above the substrate with the cameras pointed slightly downward at an angle of ~35° off parallel to the seafloor. The position of the camera throughout the deployment was assumed to be the same as the vessel GPS. The deployment cable was held as near vertical as possible to improve positional accuracy, given weather and wind conditions. The distances travelled during deployments ranged from 21 to 1476 m (mean = 411 m, SE = 14.4). Five tows were <100 m in length and were the result of equipment failure (such as dying batteries), whereas over 80% of the deployment distances were between 200 and 1000 m.

Image analyses

Post-cruise image analysis was conducted to determine substrate types, species abundance and size. Image pairs collected during each deployment were viewed using stereo image processing software developed in the Python programming language (Williams *et al.*, 2016). To compute range and size information, the cameras were calibrated to correct for image distortion due to the lens and viewport optics, and to solve for the epipolar geometry between the two cameras (Williams *et al.*, 2010, 2016). The image analysis software then determined the three-dimensional coordinates of corresponding points identified in stereo-image pairs using a stereo-triangulation function.

All structure-forming invertebrates (corals, sponges, sea pens, and sea whips), fishes, and crabs were identified to the lowest possible taxonomic level and counted for each transect. The lowest possible taxonomic level was typically genus for corals and sea whips and class for sponges (Stone *et al.*, 2011; Stone, 2014; R. Stone, AFSC, pers. comm.). Careful examination and accounting of individual targets in adjacent frames ensured that objects were only counted once and all groups were enumerated fully for each transect. Because demosponges on 34 transects, corals on 20 transects, and stylasterids on one transect were too numerous to count individually, 135 image pairs were randomly subsampled

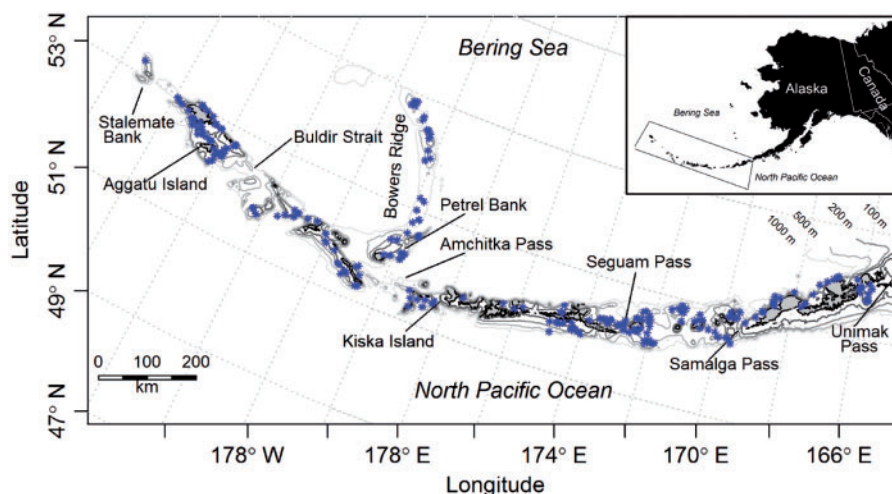


Figure 1. Map of the Aleutian Islands showing the locations of camera transects ($n = 216$) occupied in 2012 and 2014.

for complete enumeration of all individual sponges, corals, and stylasterids and counts from these frames were expanded to the unsampled frames. Sponges < 20 cm in height were difficult to discern from other small white- or yellow-coloured items on the seafloor, so these were excluded from the counts and analyses.

Densities of individual taxa were calculated by dividing transect counts by the area swept (distance of seafloor observed \times path width observed). The path width observed was calculated from the median range (in cm) from the camera to all objects counted on a transect. It was assumed that 100% of fishes and invertebrates within this range were detectable during image analysis. Combining the known viewing angle for each camera (fixed by the camera lens) and the median range to objects on a transect, a path width observed at the median range was calculated. The mean path width across all transects was 3.80 m (SE = 0.06), with a minimum of 1.82 m and a maximum of 6.32 m for any individual transect. The area viewed on each transect ranged from 80 to 4197 m² and averaged 1531 m² (SE = 56).

Bottom trawl survey models

The initial distribution modelling was carried out using data collected on the NOAA Fisheries, Alaska Fisheries Science Center, Aleutian Islands bottom trawl surveys and Gulf of Alaska trawl surveys during 1991–2011 (9 surveys total, Rooper *et al.*, 2014). Briefly, the invertebrate probability of presence and catch-per-unit-effort (CPUE; kg/ha) in bottom trawl hauls were predicted using generalized additive models (GAM) to determine the relationships between environmental variables (latitude \times longitude, depth, slope, long-term average bottom temperature, ocean colour, mean current speed and maximum tidal current speed) and presence or abundance. All modelling was carried out with R software using the mgcv package (Wood, 2006). Model validation in Rooper *et al.* (2014) was carried out by predicting the observations of coral and sponge distribution and CPUE from the 2012 bottom trawl survey, a year that was not included in the model parameterization and instead was held back for model testing. The best-fitting models of abundance explained from 20% to 25% of the variability in abundance and models of presence absence had area-under-the-receiver-operator-curve (AUC) values of between 0.67 (for sponges) and 0.78 (for stylasterid corals).

Table 1. Species and numbers of specimens used to calculate height–weight conversions for sponges and corals.

Taxa group	Species	Number
Hexactinellidae	<i>Acanthacus</i> sp.	4
Hexactinellidae	<i>Aphrocallistes vastus</i>	9
Hexactinellidae	<i>Aulosaccus schulzei</i>	2
Hexactinellidae	<i>Rhabdocalyptus</i> sp.	7
Demospongiae	<i>Artemisia</i> sp.	1
Demospongiae	<i>Cladocroce attu</i>	1
Demospongiae	<i>Cladocroce kiska</i>	2
Demospongiae	Demosponge unid.	48
Demospongiae	<i>Neoesperiopsis rigida</i>	4
Demospongiae	<i>Tedania kagalaskai</i>	1
Acanthogorgiidae	<i>Calcigorgia spiculifera</i>	7
Paragorgiidae	<i>Paragorgia arborea</i>	10
Plexauridae	<i>Alaskagorgia</i> sp.	4
Plexauridae	<i>Cryogorgia</i> sp.	2
Plexauridae	<i>Muriciedes nigra</i>	29
Primnoidae	<i>Fanellia compressa</i>	2
Primnoidae	<i>Plumarella</i> sp.	72
Primnoidae	<i>Plumarella superba</i>	1
Primnoidae	<i>Fanellia</i> sp.	75
Primnoidae	<i>Primnoa</i> sp.	13
Primnoidae	<i>Thouarella</i> sp.	8
Hydrocoral	Stylasteridae	1

Model validation and residual comparisons

To validate bottom trawl survey models (BTS models) from Rooper *et al.* (2014), observations from the underwater camera survey (UCS observations) were compared with predictions from BTS models. Taxa observed in the underwater camera survey were grouped the same as the bottom trawl survey data (upright sponges, all corals, and corals from the families Primnoidae and Stylasteridae). Only corals from the order Antipatharia, suborders Holaxonia (families Plexauridae, Acanthogorgiidae), Calcaxonina (families Primnoidae and Isidiidae), Scleraxonia (family Paragorgiidae), family Paramuriceidae, and hydrocorals from the family Stylasteridae were modelled in Rooper *et al.* (2014). In Rooper *et al.* (2014) models were produced for Primnoidae, Stylasteridae and combined corals, however the combined coral

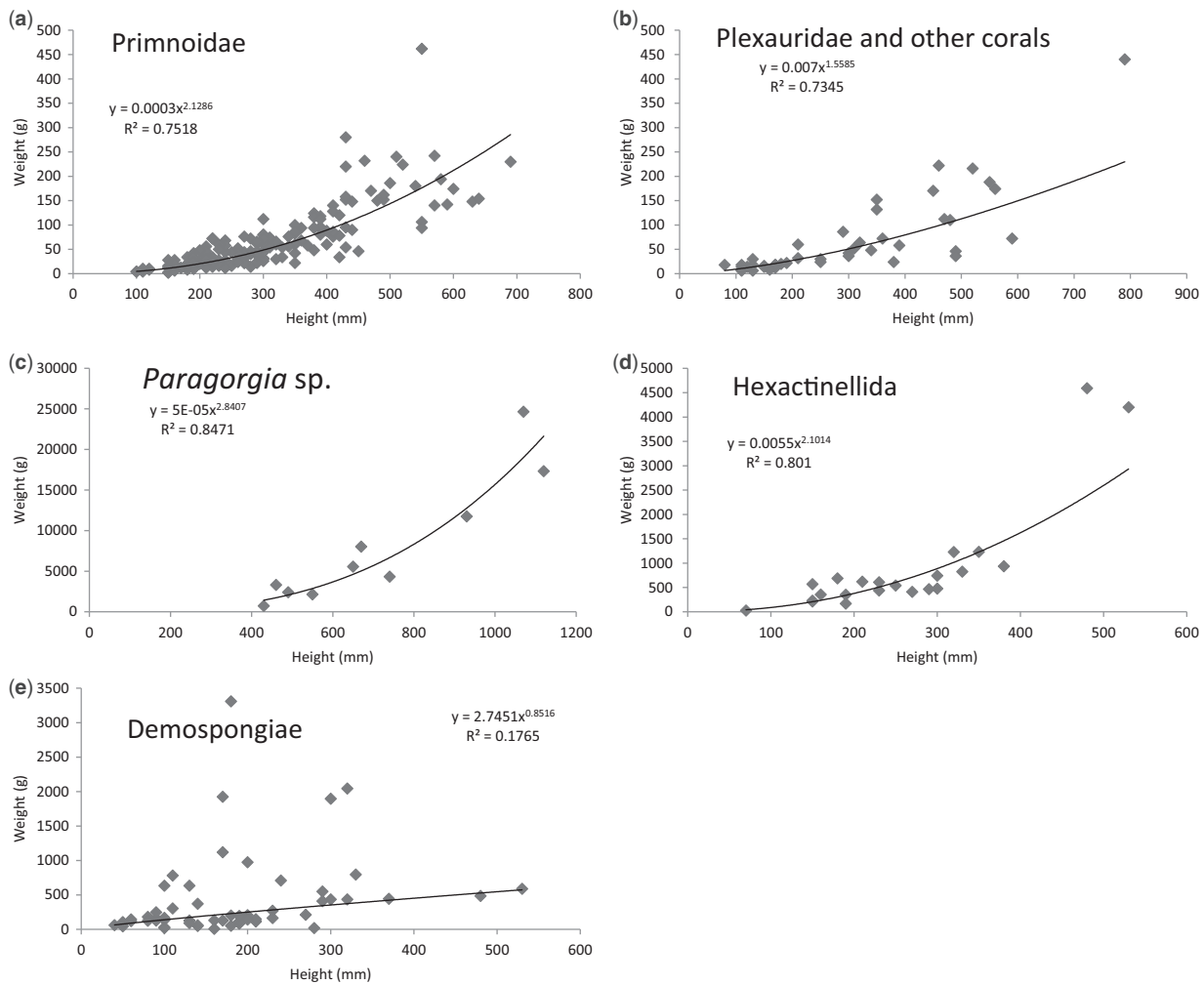


Figure 2. Height–weight conversions for primnoid corals (a), plexaurid and other corals (b), *Paragorgia* sp. (c), hexactinellid sponges (d) and demosponges (e) used to convert to CPUE in kg/ha for comparison with bottom trawl survey catches.

model largely reflected the dominant family in trawl catches (Primnoidae). Thus, although model validation was performed for the Primnoidae model, for the sake of brevity, it is not reported here as the results were the same as for combined corals.

For the probability of presence, the predictions from the BTS model at the camera survey locations were extracted and AUC values and Spearman's rank correlation values between the BTS model probabilities and UCS observations of presence or absence were computed. As a performance measure, AUC has been found to be problematic for model evaluation where absences are not accurately known, the geographic area over which the model is evaluated is not fully sampled and where errors of omission and commission are not of equal value (Lobo *et al.*, 2007). The UCS observations provided accurate presence and absence information throughout the model domain and errors were examined spatially. These data also comprise an independently collected data set for testing as suggested by Lobo *et al.* (2007). As a secondary test of the BTS model fit, a threshold probability was calculated where the predicted prevalence from the model was equal to the observed prevalence for the UCS observations, in order to portray unbiased estimates of species prevalence (Freeman and Moisen,

2008). This threshold probability was applied to all the UCS sites to produce a matrix of presence or absence predictions for each observation. From this matrix, we calculated threshold dependent metrics of true skill statistic (Allouche *et al.*, 2006), sensitivity (prediction of presence where presence occurred) and specificity (prediction of absence where absence occurs).

The BTS CPUE models estimated the $\log(\text{CPUE})$ in kg/ha for the Aleutian Islands, while the UCS observations measured densities in no. of individual sponges or coral colonies per metre square. To convert densities to kg/ha, samples of corals captured in the bottom trawl surveys in 2014 and 2016 were measured for individual height and weight (Table 1). Separate relationships between invertebrate height and weight were developed for corals and sponges independently. The average height for sponges and corals measured in the stereo video and the height–weight relationship were used to estimate the weight of coral and sponge observed in camera transects in kg/ha. In cases where no sponges ($n = 46$ transects) or corals ($n = 34$ transects) were measured on a transect where the taxa occurred, the overall average individual height in camera transects was used to make the conversion to weight. The CPUE predicted by the BTS model was then

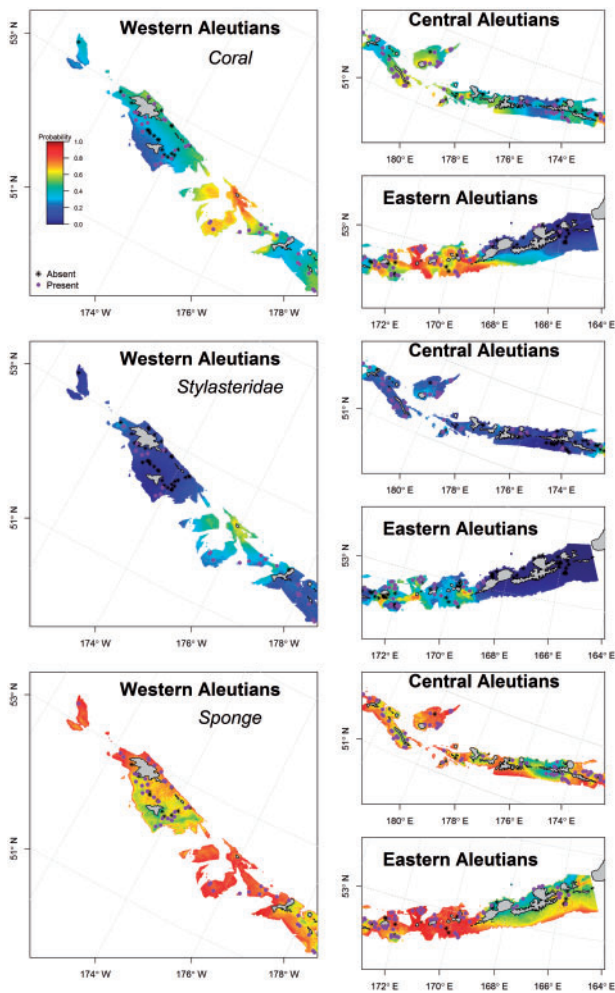


Figure 3. Plots of predicted probability of presence of corals, Stylasteridae and sponges in the Aleutian Islands with observations of presence or absence. Sponges are combined classes (Hexactinellida and Demospongiae) and corals include the order Antipatharia, suborders Holaxonia (families Plexauridae, Acanthogorgiidae), Calcaxonina (families Primnoidae and Isididae), Scleraxonia (family Paragorgiidae), family Paramuriceidae, and hydrocorals from the family Stylasteridae.

compared with observations of UCS density using R^2 as a goodness of fit criterion. All analyses, modelling and mapping were carried out using R software (R Core Development Team, 2013).

Results

A total of 304 individual height–weight combinations were collected for various species of deep-sea corals and sponges (Table 1). The height–weight relationships were best fit with a power function for all species, with weight increasing approximately as the square of the height for hexactinellid sponges and most coral groupings (Figure 2). *Paragorgia* sp. weight increased as the cube of height. Demosponges represented a very diverse group, in which most individuals could not be identified to family, genus or species. Height–weight relationships for this group were therefore highly variable (Figure 2). For hydrocorals, height–weight information was only collected for a single specimen (Table 1).

The probability of coral presence was predicted to be highest in and around Samalga pass (~169 W–172 W longitude) and west of Kiska Island to Agattu Island (175–177 W longitude) (Rooper *et al.*, 2014) (Figure 3). Coral was present and identified in 87% of the UCS observations in these areas. The AUC for the BTS model predicting the camera survey presence or absence of coral was very good (AUC = 0.77, TSS = 0.34, Table 2). Coral presence was correctly predicted 79% of the time, while absence was correctly predicted only 55% of the time with a threshold probability of 0.36. Coral was observed at 27 of the 59 locations where coral absence was predicted in the BTS model.

The stylasterid BTS model predicting presence or absence of hydrocorals also performed well in predicting the UCS observations (Table 2). The model AUC was 0.72 and the TSS was 0.38. In the case of stylasterids, a probability threshold for presence of 0.17 resulted in the correct prediction of 72% of stylasterid absences in the UCS and 66% of stylasterid presence at UCS stations. This was the opposite result from the other two coral groupings where presence was predicted more effectively. Stylasterids were predicted by the BTS model to occur in much the same regions as the general coral category, but at lower probabilities overall (Figure 2).

Sponges were predicted to occur at relatively high probabilities throughout the Aleutian Islands by BTS models, with the exception of areas around Kiska, Umnak, and Unalaska Islands (Figure 3). However, there were multiple observations of sponges in the camera survey in all of these areas, which probably accounted for the low (19%) ability of the BTS model to predict absences in the UCS observations (Figure 4). The BTS model predicted absence of sponge at 25 camera survey sites in the Aleutian Islands, but absence was only observed at six of these sites during the UCS. This discrepancy led to a relatively poor AUC (0.59) and TSS (0.03) for the BTS model predicting presence of the sponges.

The BTS model predicting coral density using bottom trawl survey data (Rooper *et al.*, 2014) indicated that coral densities would be highest in Seguam Pass and west of Kiska Island. Densities of coral > 1 kg/ha were found both in these areas and in isolated locations on and around Petrel Bank (Figure 5). Correlation between predicted coral CPUE in the BTS model and observed density from the UCS was significant ($p < 0.001$, Figure 6), but only 17% of the variability in observed density was explained by the BTS model (Table 3). Residuals for the fit of density observed in the UCS to the BTS model predictions were mostly positive (Figure 7), indicating that the model generally underestimated the density of coral at camera survey locations.

The Stylasteridae BTS model performed the worst of all the BTS models in terms of predicting stylasterid density in the UCS observations. The areas of predicted high density from the BTS model were in Samalga Pass and Seguam Pass, but neither of these areas had the highest densities in the UCS (Figure 5). The relationship between UCS observations and BTS model predictions was not significant (Table 3) and the two did not even appear to be related (Figure 6).

In the case of sponges, the BTS model predicted high CPUE's throughout the Aleutian Islands, and high densities were observed throughout the Aleutian Islands in the UCS (Figure 5). Although the BTS model predictions were significantly correlated to the UCS observations (Table 3), the model explained only ~6% of the variability in sponge densities observed in the camera survey (Figure 6). For sponges, the majority of residuals of the UCS observations of density vs. the BTS model-predicted CPUEs were negative, which

Table 2. Model diagnostics for each taxonomic grouping of benthic invertebrates.

Taxa	AUC	Spearman's Rank Correlation	Suitable habitat threshold	True Skill Statistic	Percent correct—present (Sensitivity)	Percent correct—absent (Specificity)
Sponge	0.588	0.114	0.570	0.030	83.7%	19.4%
Coral	0.772	0.438	0.360	0.337	78.6%	55.2%
Stylasteridae	0.724	0.388	0.170	0.376	65.9%	71.7%

Values are for the comparison of predicted probability of presence from the bottom trawl survey models to the observed presence or absence from the camera survey. Sponges are combined classes (Hexactinellida and Demospongiae) and corals include the order Antipatharia, suborders Holaxonia (families Plexauridae, Acanthogorgiidae), Calcaxonina (families Primnoidae and Isididae), Scleraxonia (family Paragorgiidae), family Paramuriceidae, and hydrocorals from the family Stylasteridae.

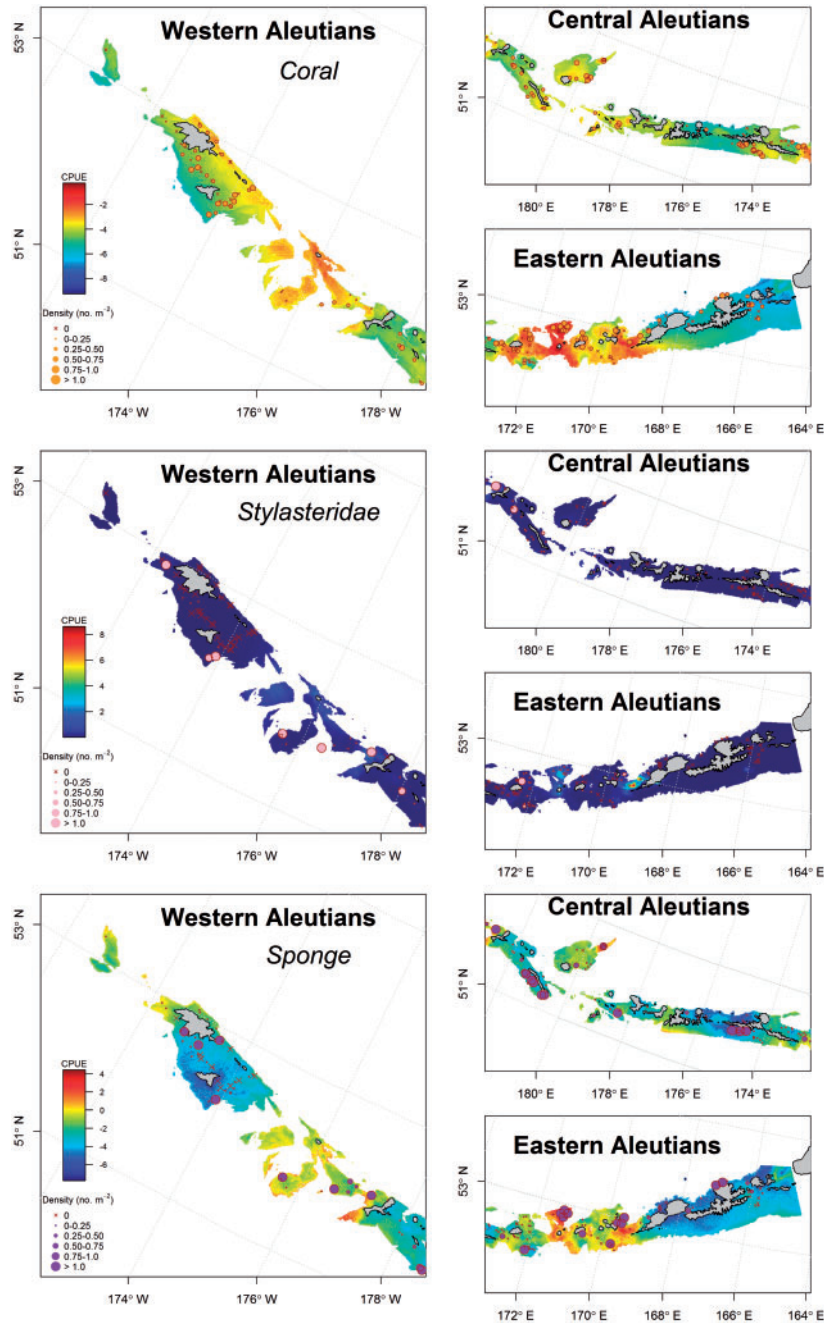


Figure 4. Plots of predicted log(CPUE) of coral, sponge and Stylasteridae in the Aleutian Islands overlaid with observations of density (kg/ha). Sponges are combined classes (Hexactinellida and Demospongiae) and corals include the order Antipatharia, suborders Holaxonia (families Plexauridae, Acanthogorgiidae), Calcaxonina (families Primnoidae and Isididae), Scleraxonia (family Paragorgiidae), family Paramuriceidae, and hydrocorals from the family Stylasteridae.

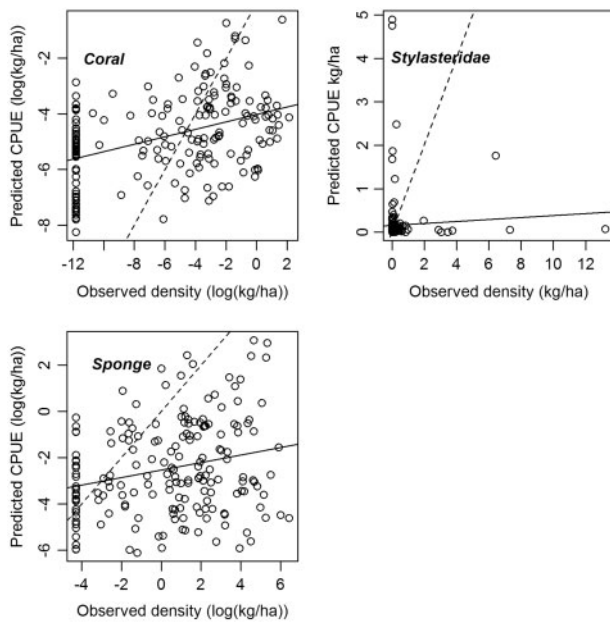


Figure 5. Plots of observed density in the camera surveys against predictions of CPUE from the bottom trawl survey model. Dashed lines indicate the 1:1 relationship line, solid lines indicate the fit to observed and predicted values. Sponges are combined classes (Hexactinellida and Demospongiae) and corals include the order Antipatharia, suborders Holaxonia (families Plexauridae, Acanthogorgiidae), Calcaxonina (families Primnoidae and Isididae), Scleraxonia (family Paragorgiidae), family Paramuriceidae, and hydrocorals from the family Stylasteridae.

contrasts with the majority positive residuals for the coral group (Figure 6). This indicated that the BTS model likely over-predicted the abundance of sponge at camera survey locations.

Residuals for the BTS model fit to the UCS presence or absence observations were not significantly different between areas that were open or closed to fishing ($p > 0.20$ in all cases). The spatial pattern of residuals for the presence and absence models indicated that errors were spread throughout the surveyed area (Figure 4). However, the BTS models of coral and sponges were particularly accurate in the region from Kiska Island to Agattu Island. The sponge model showed some indication of over-predicting the probability of sponge presence (indicated by negative residuals) in the area west of Agattu Island (Figure 4).

Spatial patterns in residuals for the UCS density observations compared with the BTS models indicated some areas of similarly poor fits (Figure 7). For example, Stylasteridae densities were over-predicted throughout the Aleutian Islands with a couple of exceptions near Kiska Island and Seguam Pass. Corals and sponges were all over-predicted in the eastern Aleutian Islands and west from Petrel Bank to Kiska Island, but they were under-predicted in the area between Samalga Pass and Seguam Pass (Figure 7). Residuals for the CPUE BTS model fit to the UCS density data were significantly lower for corals in areas that were open to bottom trawling ($p = 0.006$). This indicates that the BTS model predicted a higher density of corals than were observed in the UCS. The trend was the same for sponges, although differences in residuals were not significant ($p = 0.10$ and $p = 0.70$). For these taxonomic groups, the trend was for over-prediction of density in areas where commercial fishing was ongoing; however,

in the case of Stylasteridae, an opposite, but insignificant ($p = 0.54$) pattern was observed.

Discussion

Goodness of fit measurements of the original BTS models to the bottom trawl survey data (Rooper *et al.*, 2014) were generally similar to the goodness of fit measurements of the BTS models to the UCS data. For example, AUC values ranged from 0.73 to 0.80 for the trawl survey presence–absence training data and from 0.67 to 0.78 for the bottom trawl presence–absence test data set (2012 bottom trawl survey data). The AUC's for the BTS models predicting the UCS presence–absence data ranged from 0.72 to 0.81, with the exception of sponge (AUC = 0.59).

Measures of fit for the abundance models were also similar between the BTS models (Rooper *et al.*, 2014) and the UCS data. The BTS models explained between 5% and 21% of the variability in the bottom trawl training data and between 3% and 23% of the variability in the test data from 2012, with Stylasteridae the worst performer and Primnoidae the best performer (Rooper *et al.*, 2014). The BTS models performed about the same for Stylasteridae in the UCS data (explaining 3% of the variability in density) and the BTS model fit the UCS density data better than the original training and testing data from the bottom trawl survey (explaining 33% of the data variability). However, the performance of the BTS model in predicting sponge density was much poorer, 5% for the UCS data compared with 20% for both the training and testing data sets from the bottom trawl survey. Overall, with the exception of the model of sponge abundance, the BTS models performed about the same at predicting the camera survey data as for predicting bottom trawl survey data.

The results of this study indicate that the catchability for sponges (and likely corals too) in the bottom trawl survey is probably low, implying that the bottom trawl survey abundance estimates may be negatively biased. Beyond poor catchability for sponges, there were a number of other differences between the two data sets. The sponge data used in the BTS model was a reconstruction of upright shaped sponges from trawl catches, where the proportion of identified upright morphologies (i.e. vase sponges) was applied to the unidentified proportion of sponge in the catch. The proportion of upright sponges may have been overestimated as smaller non-erect sponges may have been less likely to be identified than other morphologies. In addition, only sponges taller than 20 cm were counted in the camera survey image analyses. There was evidence that the BTS model for sponges overpredicted the abundance of sponge in the camera survey, which could have been a result of these differences. This mismatch in the data may have resulted in additional unexplained variability between the model predictions or the camera survey model observations.

The coral and sponge groupings modelled in the Rooper *et al.* (2014) study lumped many species together into large taxonomic groups. We reproduced the same taxonomic groupings for the model validation study, but it is important to note that although necessary, this is less than ideal. For example, at least some of the species that are combined in the sponges category are likely to have very different habitat preferences from one another. For corals, this may be less of an issue, since the coral assemblage was dominated by a single family (Primnoidae) and thus, the larger coral taxonomic grouping had essentially the same distribution as the Primnoidae. Since the taxonomic groupings were held the same between this study and the Rooper *et al.* (2014) modelling

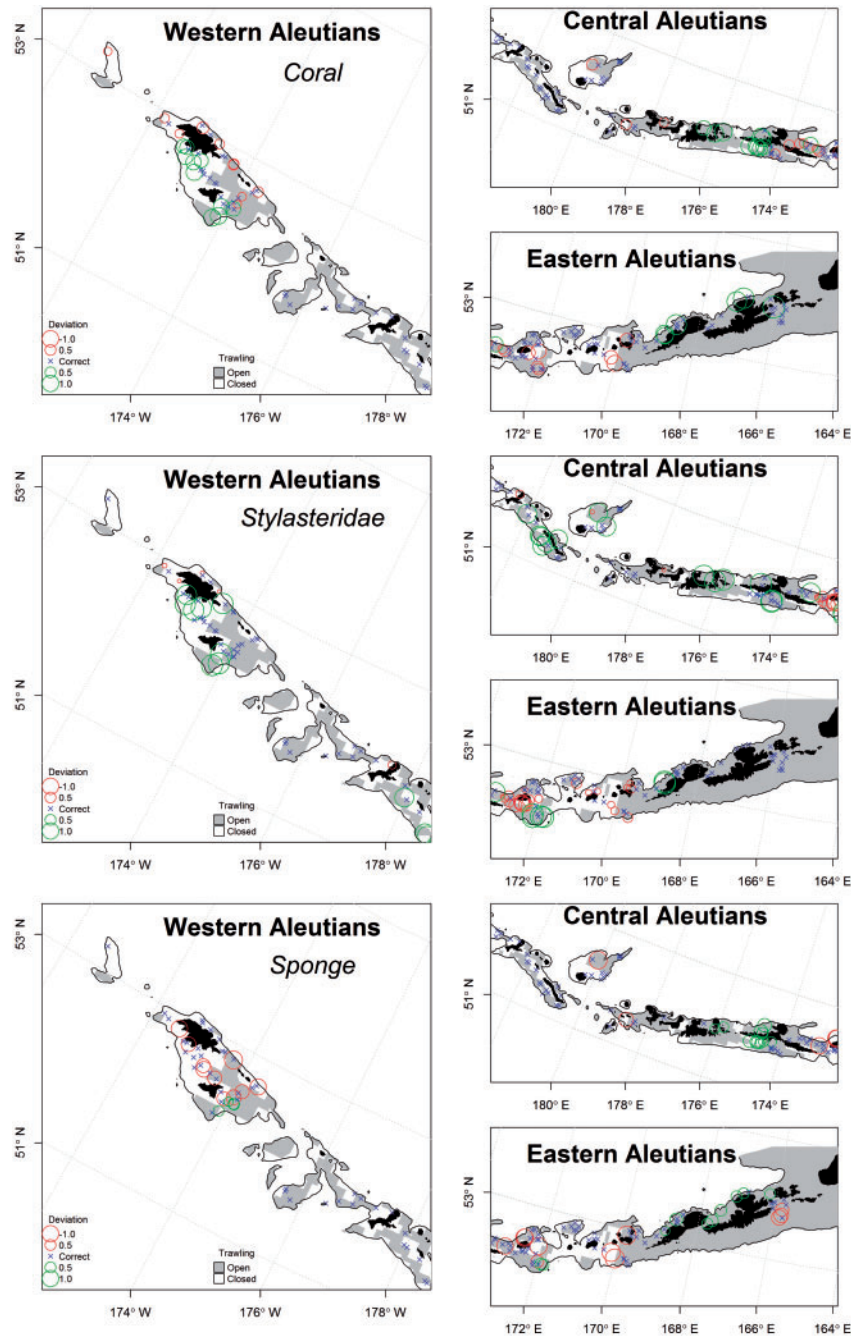


Figure 6. Residuals of the relationship between bottom trawl-predicted probability of presence and observed presence or absence in the camera survey for each group of structure forming invertebrate in the Aleutian Islands. Crosses indicate the prediction and observation matched; circles indicate the observation of presence (0 or 1) minus the predicted probability. Sponges are combined classes (Hexactinellida and Demospongiae) and corals include the order Antipatharia, suborders Holaxonia (families Plexauridae, Acanthogorgiae), Calcaxonina (families Primnoidae and Isididae), Scleraxonia (family Paragorgiae), family Paramuriceidae, and hydrocorals from the family Stylasteridae.

study, the taxonomic groupings do not necessarily impact the model validation results reported here, but they may be another reason for unexplained variability in both presence and density for the original BTS models.

Another potential reason for the mismatch in predicted and observed density is the history of commercial fishing in the Aleutian Islands. Stone (2006) indicated that ~39% of the seafloor showed evidence of disturbance by fishing gear and 8.5% of

corals were observed to be damaged. Since 2006, about 1/2 of the shelf and upper slope area of the Aleutian Islands has been closed to mobile bottom contact fishing gear. This closure to mobile bottom contact gear essentially froze the footprint of the existing bottom trawl fisheries. Thus, the closures protected areas that were likely to have seen light historical trawling effort, while allowing continued fishing in areas that were being utilized by the fishery. Given the long lifespan and potential decadal-scale

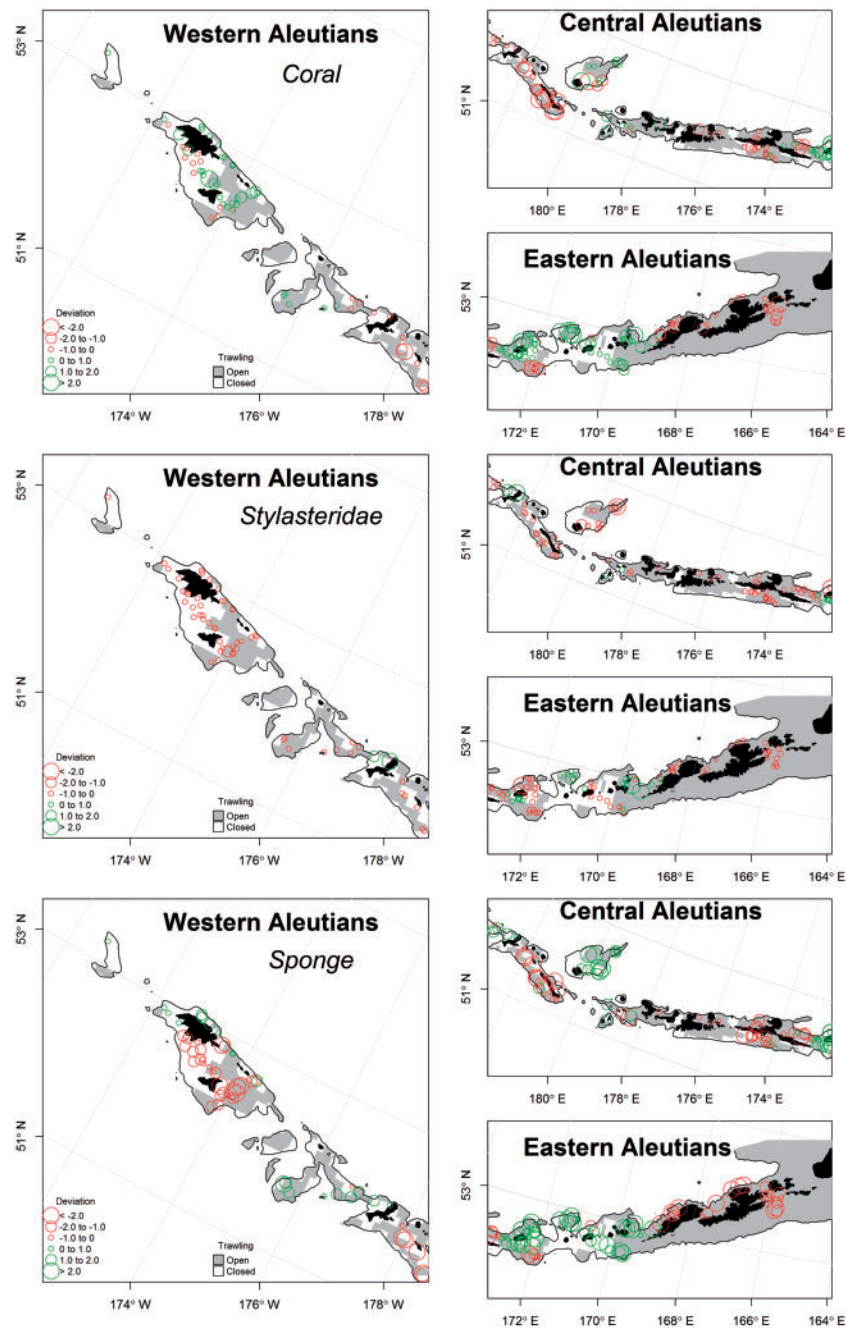


Figure 7. Residuals of the relationship between bottom trawl-predicted density and observed density in the camera survey for each group of structure forming invertebrate in the Aleutian Islands. Sponges are combined classes (Hexactinellida and Demospongiae) and corals include the order Antipatharia, suborders Holaxonia (families Plexauridae, Acanthogorgiidae), Calcaxonia (families Primnoidae and Isididae), Scleraxonia (family Paragorgiidae), family Paramuriceidae, and hydrocorals from the family Stylasteridae.

recovery times for corals and sponges (Andrews *et al.*, 2002, 2009; Rooper *et al.*, 2011), it is likely that some of the patterns in observed density reflect historical patterns of fishing activity. The trend found in this study of overprediction of density for three taxonomic groups where commercial fishing activity is ongoing was statistically weak (significant for only coral, but not sponges), but suggests a causal relationship. If this is true, the trend in residuals would indicate that the closures to mobile bottom fishing gear have been effective at preserving higher densities of coral

where they are predicted to occur. Positive residuals would indicate more than anticipated sponge or coral density occurred based on the model predictions, while negative residuals would indicate the opposite. Thus, positive residuals within closed areas would indicate that higher densities than predicted were observed, possibly as a result of limited fishing impacts within closed areas.

Models of coral and sponge distributions have been developed for many regions (Bryan and Metaxas, 2007; Davies *et al.*, 2008;

Table 3. Correlations and significance for the regression of the observed density of each taxonomic grouping of benthic invertebrates in the camera survey and the prediction for that grouping from the model based on bottom trawl survey data ($n = 184$ observations).

Taxa	R ²	p-value
Sponge	0.057	0.001
Coral	0.172	<0.001
Stylasteridae	0.003	0.483

Sponges are combined classes (Hexactinellida and Demospongiae) and corals include the order Antipatharia, suborders Holaxonia (families Plexauridae, Acanthogorgiidae), Calcaxonia (families Primnoidae and Isididae), Scleraxonia (family Paragorgiidae), family Paramuriceidae, and hydrocorals from the family Stylasteridae.

Tittensor *et al.*, 2010; Krigsman *et al.*, 2012; Huff *et al.*, 2013; Guinotte and Davies, 2014). However, model validation with independently collected survey data are rare for deep-sea corals and sponges (Abecasis *et al.*, 2014; Anderson *et al.*, 2016). Other model validation studies have also shown better results for corals than sponges when comparing predictions of invertebrate distributions with independent model validation surveys. In a similar study in the eastern Bering Sea, model validation results were similar to the results found here for coral models, with AUC values of 0.73 for bottom trawl survey models predicting camera survey presence or absence (Rooper *et al.*, 2016). The presence-absence bottom trawl model was less accurate for sponges than for coral in the eastern Bering Sea, with an AUC of 0.63. A similar pattern was found for this study, where the coral models tended to fit the camera survey data better than the sponge models. Anderson *et al.* (2016) also attempted to validate a habitat distribution model for deep-sea corals. The authors found that occurrence of corals in the validation survey was less than expected from the model results and the patterns of the observed and predicted species distributions were not well correlated. However, the initial models in the Anderson *et al.* (2016) study were presence-only models which likely biased the results towards higher probabilities of presence; and additionally, the authors point out the potential for spatial bias in their data due to the uneven sampling across the study area. The wider implication of this study and that of Anderson *et al.* (2016) is that model validation with independent data is a crucial part of the process if models are to be used for regional or global management decisions (Guisan *et al.*, 2013). There are many easily accessible tools available to model species distributions (Phillips *et al.*, 2006; Elith *et al.*, 2008) and as such, they are commonly used. However, distribution models can result in biased or poor predictions (Barry and Elith, 2006; Yackulic *et al.*, 2013) and as with all models, they have difficulty predicting observations outside of the observed data (Huff *et al.*, 2013). Cross-validation techniques using resubstitution or randomized subsets of the data are a commonly used tool to assess issues with model performance (Bryan and Metaxas, 2007; Krigsman *et al.*, 2012; Franklin *et al.*, 2013). However, a test with independently collected data across the spatial domain of the model will provide the best indication of model performance (Elith *et al.*, 2006).

In summary, we found that the bottom trawl survey model of probability of presence developed in Rooper *et al.* (2014) realistically fit new data points collected using a randomized underwater

camera survey for three different groupings of corals. The bottom trawl survey model predicting probability of presence for sponges performed poorly. Models of abundance based on bottom trawl surveys for corals and Stylasteridae performed with similar accuracy on the camera survey data as they did for the original bottom trawl survey data. Again, however, sponge abundance in the camera survey was not predicted well by the bottom trawl survey models. These results indicate that models of deep-sea coral distributions based on presence and absence data from bottom trawl surveys can be accurate and can provide useful information for spatial management of these vulnerable taxa. Density predictions may be biased by catchability issues with the bottom trawl, as was observed in the under-prediction of coral density. However, for some other taxa, such as sponges, care should be taken in interpreting the results of bottom trawl survey models. This study also showed the importance of independent model validation studies that can be used to assess the level of confidence in model results that are necessary for decision-making.

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References

- Abecasis, D., Aronso, P., and Erzini, K. 2014. Combining multispecies home range and distribution models aids assessment of MPA effectiveness. *Marine Ecology Progress Series*, 513: 155–169.
- Allouche, O., Tsoar, A., Kadmon, R. 2006. Assessing the accuracy of species distribution models: prevalence, kappa and the true skill statistic (TSS). *Journal of Applied Ecology*, 43: 1223–1232.
- Anderson, O. F., Guinotte, J. M., Rowden, A. A., Clark, M. R., Mormede, S., Davies, A. J., and Bowden, D. A. 2016. Field validation of habitat suitability models for vulnerable marine ecosystems in the South Pacific Ocean: implications for the use of broad-scale models in fisheries management. *Ocean and Coastal Management*, 120: 110–126.
- Andrews, A. H., Cordes, E. E., Mahoney, M. M., Munk, K., Coale, K. H., Cailliet, G. M., and Heifetz, J. 2002. Age, growth and radiometric age validation of a deep-sea, habitat-forming gorgonian (*Primnoa resedaeformis*) from the Gulf of Alaska. *Hydrobiologia*, 471: 101–110.
- Andrews, A. H., Stone, R. P., Lundstrom, C. C., and DeVogelaere, A. P. 2009. Growth rate and age determination of bamboo corals from the northeastern Pacific Ocean using refined 210Pb dating. *Marine Ecology Progress Series*, 397: 173–185.
- Auster, P. J., Malatesta, R. J., Langton, R. W., Watling, L. and others. 1996. The impacts of mobile fishing gear on seafloor habitats in the Gulf of Maine (northwest Atlantic): implications for conservation of fish populations. *Reviews in Fisheries Science*, 4: 185–202.
- Barry, S., and Elith, J. 2006. Error and uncertainty in habitat models. *Journal of Applied Ecology*, 43: 413–423.
- Bryan, T. L., and Metaxas, A. 2007. Predicting suitable habitat for deep-water gorgonian corals on the Atlantic and Pacific Continental Margins of North America. *Marine Ecology Progress Series*, 330: 113–126.
- Davies, A. J., Wisshak, M., Orr, J. C., and Roberts, J. M. 2008. Predicting suitable habitat for the cold-water reef framework-

- forming coral *Lophelia pertusa* (Scleractinia). *Deep-Sea Research I*, 55: 1048–1062.
- Elith, J., Graham, C. H., Anderson, R. P., Dudi, K. M., Ferrier, S., Guisan, A., Hijmans, R. J. *et al.* 2006. Novel methods improve prediction of species' distributions from occurrence data. *Ecography*, 29: 129–151.
- Elith, J., Leathwick, J. R., and Hastie, T. 2008. A working guide to boosted regression trees. *Journal of Animal Ecology*, 77: 802–813.
- Franklin, E. C., Jokiel, P. L., and Donahue, M. J. 2013. Predictive modeling of coral distribution and abundance in the Hawaiian Islands. *Marine Ecology Progress Series*, 481: 121–132.
- Freeman, E. A. and Moisen, G. G. 2008. A comparison of the performance of threshold criteria for binary classification in terms of predicted prevalence and kappa. *Ecological Modelling*, 217: 48–58.
- Goddard, P., Wilborn, R., Rooper, C., Williams, K., Towler, R., Sigler, M., and Malecha, P. 2016. Results of the 2014 underwater camera survey of the eastern Bering Slope and Outer Shelf. U.S. Department of Commerce, NOAA Technical Memorandum. NMFS-AFSC-313, 304 p.
- Goddard, P., Wilborn, R. E., Rooper, C. N., Williams, K., Towler, R. 2017. Results of the 2012 and 2014 underwater camera surveys of the Aleutian Islands. U.S. Department of Commerce, NOAA Technical Memorandum. NMFS-AFSC-351, 505 p.
- Guinotte, J. M., and Davies, A. J. 2014. Predicted deep-sea coral habitat suitability for the U.S. west coast. *PLoS One*, 9: e93918.
- Guisan, A., Tingley, R., Baumgartner, J. B., Naujokaitis-Lewis, I., and Sutcliffe, P. R. 2013. Predicting species distributions for conservation decisions. *Ecology Letters*, 16: 1424–1435.
- Heifetz, J. 2002. Coral in Alaska: distribution, abundance, and species associations. *Hydrobiologia*, 471: 19–28.
- Heifetz, J., Stone, R. P., and Shotwell, S. K. 2009. Damage and disturbance to coral and sponge habitat of the Aleutian Archipelago. *Marine Ecology Progress Series*, 397: 295–303.
- Heifetz, J., Wing, B. L., Stone, R. P., Malecha, P. W., and Courtney, D. L. 2005. Corals of the Aleutian Islands. *Fisheries Oceanography*, 14: 131–138.
- Huff, D. D., Yoklavich, M. M., Love, M. S., Watters, D. L., Chai, F., and Lindley, S. T. 2013. Environmental factors that influence the distribution, size, and biotic relationships of the Christmas tree coral *Antipathes dendrochristos* in the Southern California Bight. *Marine Ecology Progress Series*, 494: 159–177.
- Krigsman, L. M., Yoklavich, M. M., Dick, E. J., and Cochrane, G. R. 2012. Models and maps: predicting the distribution of corals and other macro-invertebrates in shelf habitats. *Ecosphere*, 3: 1–16.
- Ladd, C., Hunt, Jr, G. L., Mordy, C. W., Salo, S. A., and Stabeno, P. J. 2005. Marine environment of the eastern and central Aleutian Islands. *Fisheries Oceanography*, 14: 22–38. –
- Lobo, J. M., Jiménez-Valverde, A., and Real, R. 2007. AUC: a misleading measure of the performance of predictive distribution models. *Global Ecology and Biogeography*, 17: 145–151.
- Malecha, P. W., Stone, R. P., and Heifetz, J. 2005. Living substrate in Alaska: distribution, abundance and species associations. *American Fisheries Society Symposium*, 41: 289–299.
- NRC (National Research Council). 2002. *Effects of Trawling and Dredging on Seafloor Habitat*. National Academy Press, Washington, DC.
- Phillips, S. J., Anderson, R. P., and Schapire, R. E. 2006. Maximum entropy modeling of species geographic distributions. *Ecology Model*, 190: 231–259.
- R Development Core Team. 2013. *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing, Vienna. www.R-project.org.
- Rooper, C. N., Sigler, M. F., Goddard, P., Malecha, P., Towler, R., Williams, R., Wilborn, R. *et al.* 2016. Validation and improvement of species distribution models for structure forming invertebrates in the eastern Bering Sea with an independent survey. *Marine Ecology Progress Series*, 551: 117–130.
- Rooper, C. N., Wilkins, M. E., Rose, C., and Coon, C. 2011. Modeling the impacts of bottom trawling and the subsequent recovery rates of sponges and corals in the Aleutian Islands, Alaska. *Continental Shelf Research*, 31: 1827–1834.
- Rooper, C. N., Zimmermann, M., Prescott, M. M., and Hermann, A. J. 2014. Predictive models of coral and sponge distribution, abundance and diversity in bottom trawl surveys of the Aleutian Islands, Alaska. *Marine Ecology Progress Series*, 503: 157–176.
- Sigler, M. F., Rooper, C. N., Hoff, G. R., Stone, R. P., McConnaughey, R. A., and Wilderbuer, T. K. 2015. Faunal features of submarine canyons on the eastern Bering Sea slope. *Marine Ecology Progress Series*, 526: 21–40.
- Stabeno, P. J., Reed, R. K., and Napp, J. M. 2002. Transport through Unimak Pass, Alaska. *Deep-Sea Research II*, 49: 5919–5930.
- Stabeno, P. J., Schumacher, J. D., and Ohtani, K. 1999. The physical oceanography of the Bering Sea. *In Dynamics of the Bering Sea: A Summary of Physical, Chemical, and Biological Characteristics, and A Synopsis of Research on the Bering Sea*, pp. 1 – 59. Ed. by T. R. Loughlin and K. Ohtani. North Pacific Marine Science Organization (PICES), University of Alaska Sea Grant, AK-SG-99-03, Fairbanks, AK.
- Stone, R. P. 2006. Coral habitat in the Aleutian Islands of Alaska: depth distribution, fine-scale species associations, and fisheries interactions. *Coral Reefs*, 25: 229–238.
- Stone, R. P. 2014. *The Ecology of Deep-Sea Coral and Sponge Habitats of the Central Aleutian Islands of Alaska*. NOAA Professional Paper NMFS 16. U.S. Department of Commerce, Seattle, WA.
- Stone, R. P., Lehnert, H., and Reisinger, H. 2011. *A Guide to the Deepwater Sponges of the Aleutian Island Archipelago*. NOAA Professional Paper NMFS 12. U.S. Department of Commerce, Seattle, WA.
- Tittensor, D. P., Baco, A. R., Hall-Spencer, J. M., Orr, J. C., and Rogers, C. A. D. 2010. Seamounts as refugia from ocean acidification for cold-water stony corals. *Marine Ecology*, 31: 212–225.
- van Dolah, R. F., Wendt, P. H., and Nicholson, N. 1987. Effects of a research trawl on a hard-bottom assemblage of sponges and corals. *Fisheries Research*, 5: 39–54.
- Williams, K., Rooper, C. N., and Towler, R. 2010. Use of stereo camera systems for assessment of rockfish abundance in untrawlable areas and for recording pollock behavior during midwater trawls. *Fishery Bulletin*, 108: 352–362.
- Williams, K., Towler, R., Goddard, P., Wilborn, R., and Rooper, C. 2016. SEBASTES stereo image analysis software. AFSC Processed Rep. 2016-03, 42 p. Alaska Fisheries Science Center, NOAA, National Marine Fisheries Service, 7600 Sand Point Way NE, Seattle WA 98115.
- Wood, S. N. 2006. *Generalized Additive Models: An Introduction with R*. Chapman & Hall/CRC Press, Boca Raton, FL.
- Yackulic, C. B., Chandler, R., Zipkin, E. F., Royle, J. A., Nichols, J. D., Cambell Grant, E. H., and Veran, S. 2013. Presence-only modelling using MAXENT: when can we trust the inferences?. *Methods in Ecology and Evolution*, 4: 236–243.