

Predictive models of coral and sponge distribution, abundance and diversity in bottom trawl surveys of the Aleutian Islands, Alaska

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ABSTRACT: Ecosystem management requires information to determine and mitigate adverse impacts of fishing on all ecosystem components. Deep-sea coral and sponge ecosystems often co-occur with fishing activities, and there is considerable research documenting the vulnerability and slow recovery of deep-sea coral and sponge communities to damage. The objective of the present analysis was to construct models that could predict the distribution, abundance and diversity of deep sea corals and sponges in the Aleutian Islands. Generalized additive models were constructed based on bottom trawl survey data collected from 1991 to 2011 and tested on data from 2012. The results showed that deep-sea coral and sponge distributions were strongly influenced by the maximum tidal currents at bottom trawl locations, possibly indicative of reduced sedimentation or increased food-delivery processes near the seafloor in areas of moderate to high current. Depth and location were also important factors affecting the distribution of deep-sea sponges and corals. The analysis resulted in acceptable models of presence or absence for all taxonomic groups and similar fits when models were applied to test data. The best-fitting models of abundance explained between 20 and 25% of the deviance in the abundance data. Current management protects ~50% of the coral and sponge habitat in the Aleutian Islands at depths to 500 m. The models constructed here will allow managers to evaluate ecological versus economic benefits between protecting coral and sponge habitat and allowing commercial fishing by examining the effect of spatial closures on the amount of coral and sponge habitat that is protected.

KEY WORDS: Distribution modelling · General additive models · Deep-sea coral · Deep-sea sponge · Habitat · Spatial management · Alaska

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INTRODUCTION

Effective fisheries management requires the ability to identify and to characterize the adverse impacts of fishing on ecosystems and to mitigate those impacts. Considerable research exists documenting the vulnerability of deep-sea coral and sponge communities to fishing gear (van Dolah et al. 1987, Auster et al. 1996, NRC 2002, Heifetz et al. 2009). There is also a growing body of evidence that deep-

sea coral and sponge ecosystems provide important habitat to diverse marine invertebrate and fish species (Krieger & Wing 2002, Roberts et al. 2006, Marliave et al. 2009, Baillon et al. 2012, Henry et al. 2013, Beazley et al. 2013). Information that describes the intersection of fishing activities and benthic invertebrates is thus a critical component of effective fisheries management.

Many deep-sea sponge and coral species are long-lived and slow to recover from disturbance because

of their characteristic slow growth, limited reproductive output and limited dispersal (Leys & Lauzon 1998, Stone & Wing 2001, Andrews et al. 2002, Leys et al. 2007). The structure provided by sponges and corals also increases habitat complexity in otherwise uniform substrates (Tissot et al. 2006). The resulting seafloor complexity is thought to increase survival or growth for marine fish and invertebrates by providing refuge for individuals, particularly juveniles, vulnerable to predation (Ryer et al. 2004), providing substrate for spawning activities (Busby et al. 2006) or providing a source of food (van Oevelen et al. 2009). This is especially true for groundfishes such as rockfishes *Sebastes* spp. that commonly occur in coral and sponge habitats in Alaska (Heifetz 2002, Rooper & Boldt 2005, Stone 2006).

In Alaska, deep-sea coral and sponge ecosystems are widespread throughout all regions of the continental shelf and slope (Heifetz et al. 2005) at depths to >2000 m (Wing & Barnard 2004, Stone et al. 2011), but the distributions of coral and sponge are known primarily from bycatch in commercial fishing activities and research trawls (Malecha et al. 2005). The Alaska continental shelf and slope is large enough (~909 000 km²) that directed exploration to map the entire distribution of coral and sponge communities, such as a visual assessment with a remotely operated vehicle or submersible, is not feasible; however, mapping the distribution of sponge and coral ecosystems is necessary for effective management. Therefore, analysis of existing data for the construction of predictive models was undertaken as a practical alternative. A number of models of coral and sponge distribution have been attempted throughout the world's oceans, including in Alaska. Basin-wide models have often used presence data from bycatch collections or museum specimens to describe distributions (Bryan & Metaxas 2007, Tittensor et al. 2010, Davies & Guinotte 2011, Yesson et al. 2012, Taylor et al. 2013). These models are generally large-scale, encompassing entire oceans, and since only presence data are included, basin-wide models predict broader species distributions than would be predicted if absence data were available. Smaller-scale models typically use data-rich underwater video observations, but they are difficult to scale up to a regional level (Woodby et al. 2009, Kringsman et al. 2012), especially without detailed bathymetry, as is common in Alaska.

Here, we attempt a regional model for the Aleutian Islands (~74 315 km²) on a 100 m × 100 m grid size that utilizes distribution data to predict where deep-sea coral and sponge ecosystems may occur. Specifi-

cally, we constructed models of deep-sea coral and sponge that predicted presence or absence, the abundance of these taxa, and coral family diversity in the Aleutian Islands. Models of presence or absence and abundance (catch per unit of effort [CPUE]) were parameterized using bottom trawl survey data from 1991 to 2011. The models were then tested with data collected in the 2012 bottom trawl survey. The models were used to map predictions to determine where areas of high abundance or probability of occurrence can be found. The resulting models demonstrate promise with respect to spatial management and mitigation of effects of fishing on these vulnerable taxonomic groups.

MATERIALS AND METHODS

Study area

The Aleutian Islands are a series of islands that stretch westward from the Alaska Peninsula across the North Pacific Ocean, dividing the western Gulf of Alaska from the Bering Sea (Fig. 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 the many deep passes in the island chain, and tidal currents can be large (Ladd et al. 2005). A faunal division in fish and invertebrate species abundance and diversity has been noted for the area around Samalga Pass (170°W) (Heifetz et al. 2005, Logerwell et al. 2005). West of Samalga Pass, deep-sea sponge and coral diversity and abundance are greater than other areas in Alaska and many areas of the world, with 6 major taxonomic groups (Orders) and at least 50 endemic species of corals represented and 125 confirmed species or subspecies of sponges (Stone & Shotwell 2007, Stone et al. 2011).

Modeled data

The data used for these modeling analyses were collected during bottom-trawl surveys of the Aleu-

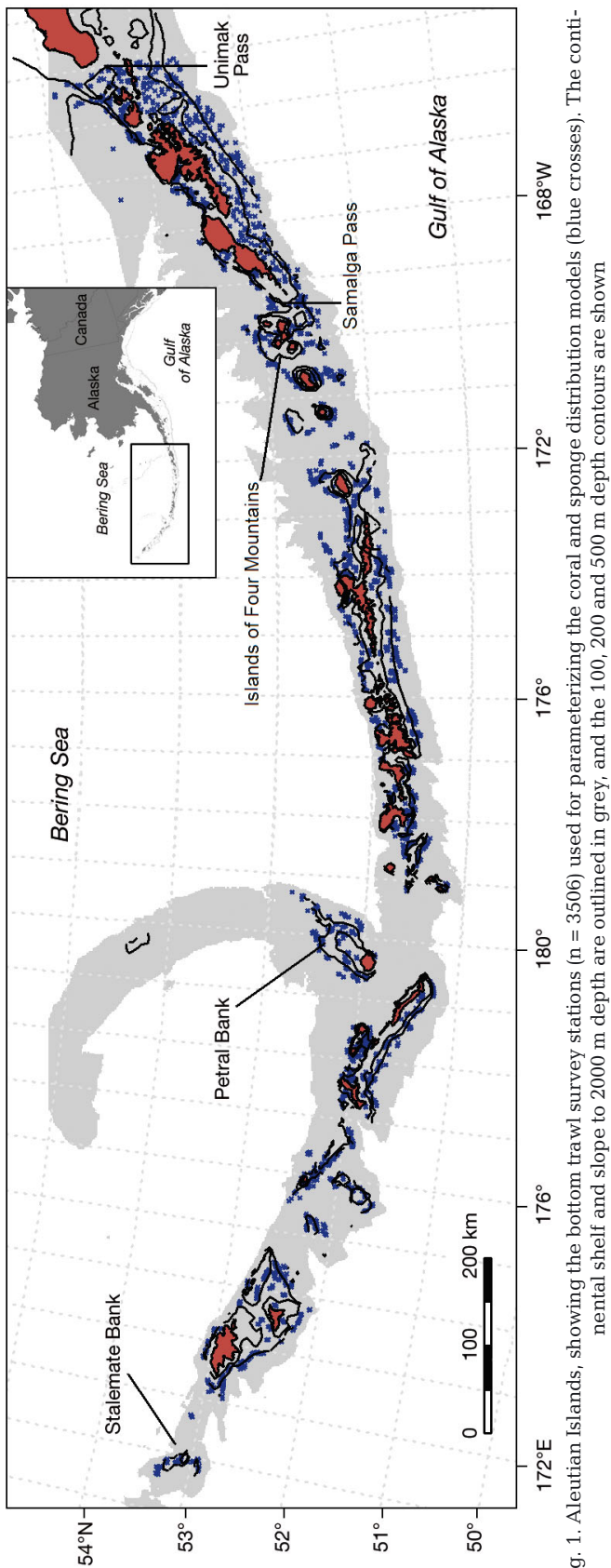


Fig. 1. Aleutian Islands, showing the bottom trawl survey stations ($n = 3506$) used for parameterizing the coral and sponge distribution models (blue crosses). The continental shelf and slope to 2000 m depth are outlined in grey, and the 100, 200 and 500 m depth contours are shown

tian Islands ecosystem and the westernmost portion of the Gulf of Alaska ecosystem. The National Marine Fisheries Service (NMFS), Alaska Fisheries Science Center (AFSC), has conducted standard bottom-trawl surveys in these ecosystems since 1980 (von Szalay et al. 2010, 2011). The Aleutian Islands bottom-trawl survey is conducted from the Islands of Four Mountains (170°W) to Stalemate Bank (170°E) (Fig. 1) on both sides of the island chain and from Unimak Pass (165°W) to the Islands of Four Mountains on the north side of the Aleutian Island chain. Surveys were conducted triennially between 1991 and 1999 and biennially thereafter ($n = 9$ surveys). In this analysis, we also used bottom trawl survey tows that occurred on the south side of the island chain in the area west of Unimak Pass to the Islands of Four Mountains that were part of the area sampled by the Gulf of Alaska bottom trawl survey ($n = 9$ surveys). The Gulf of Alaska bottom trawl survey was conducted on alternate years from the Aleutian Islands survey. Both surveys are conducted on a 5 km \times 5 km grid superimposed over the survey areas. In the Aleutian Islands, each year, ~ 420 grid cells are randomly chosen, and a bottom trawl haul is placed within the 5 km \times 5 km boundaries of the selected grid cell. In the Aleutian Islands grid cells are chosen primarily from a pool of previously trawled grid cells (~ 1200 total) with a small selection (~ 4 to 10 per year) chosen at random throughout the survey area. In the Gulf of Alaska, grid cells are chosen at random for sampling each year and include a random mix of previously sampled and unsampled grid cells. For the present analysis, AFSC bottom-trawl data in the Aleutian Islands region (Unimak Pass to Stalemate Bank) from 1991 to 2011 were combined across years. The 1991 bottom-trawl survey was the first for which accurate temperature at depth data were available for calculating water-column properties used in the modeling. The 2012 Aleutian Islands bottom-trawl data was used as a test data set for model predictions.

The Aleutian Islands and Gulf of Alaska bottom trawl surveys utilize a poly Nor'Eastern high-opening bottom trawl with 24.2 m roller gear constructed with 36 cm rubber bobbins separated by 10 cm rubber disks (Stauffer 2004). Trawl tows were conducted at a target speed of 5.6 km h⁻¹ (3 knots) for 15 or 30 min. Bottom contact and net dimensions were recorded throughout each trawl using net mensuration equipment. The net width averaged 15.8 m across all bottom trawl hauls. For these analyses, data were only used if trawl performance was satisfactory and if the distance fished, geographic posi-

tion, average depth and water temperature profile were recorded. Tows were deemed satisfactory if the net opening was within a predetermined normal range, the roller gear maintained contact with the seafloor, and the net suffered little or no damage during the tow. Data from a total of 3506 bottom-trawl tows were used. All coral and sponge captured during a survey tow were sorted either by species or into larger taxonomic groups, and the total weight in the catch was determined. The CPUE (kg ha^{-1}) for each taxonomic group was calculated using the area swept, which was computed from the net width for each tow multiplied by the distance towed recorded with GPS.

Some sponge and coral species are difficult to identify as some taxa have cryptic species and there is confusion with distinguishing features between closely related species as well as species that are currently undescribed. Sponges are especially difficult to identify to species and often require microscopic examination of spicules (Stone et al. 2011) to be certain at the species level, which is not possible during AFSC bottom trawl surveys. In addition, sponge identifications by scientists aboard the bottom trawl surveys have been historically inconsistent, leading to additional uncertainty. Because we were only interested in sponges that provide structural habitat for fishes and are most vulnerable to damage, we divided the identified sponge in the catch records into upright types (i.e. vases) and non-upright types (i.e. ball sponges). We assumed upright-type sponges were more likely to both be vulnerable to damage by fishing gear (e.g. Freese 2001) and form fish habitat (Tissot et al. 2006). Since identified sponges are usually accompanied by an additional amount of unidentified sponge from each tow, we divided the catch (kg) of upright sponge types by the total identified sponge catch for each tow and assumed this was the proportion of upright sponge in the unidentified catch in that tow. In the 18 individual bottom trawl surveys of the 2 regions, the average proportion of sponges (by weight) that could be identified as either upright or not-upright morphology was 0.46 (SE = 0.05). The other 54% of sponge material caught in the bottom trawl hauls was unidentifiable, either being intact sponges where the species or taxonomic group was unknown or damaged or broken sponges that were unidentifiable when retrieved from the trawl. For bottom trawl tows where none of the sponge catch was identified to species or morphotype, an overall survey average percentage of upright sponge (56%) was applied to the sponge catch. This correction was made in 203 of 2730 bottom trawl

hauls where sponges were captured (7.4%) from 1991 to 2012.

Coral taxonomy in Alaska is better known, and the identification of coral species captured in bottom trawl surveys has been better than for sponge, especially with the publication of a coral identification guide (Wing & Barnard 2004). Even with these resources, field identification to species is often difficult, but identification to family has been consistent. However, some families are rarely caught in the survey. Therefore, for this analysis, CPUE of coral species was combined by family for the 2 most common Families (Primnoidae and Stylasteridae), and CPUE for these and the other species of gorgonian and hydrocorals were also combined into a total coral grouping. Since coral diversity is also important, we counted the number of coral families represented in each bottom trawl haul and used this as a dependent variable in distribution modeling.

Sponge and coral presence and absence as well as abundance in bottom trawl survey catches were modeled. Thus, 4 models were developed with presence or absence for upright sponge, total coral, Primnoidae and Stylasteridae as dependent variables. There were 4 corresponding models of CPUE as well, with the CPUE of each of these taxonomic groupings as dependent variables. Finally, we modeled the coral family diversity (number of coral families occurring in the bottom trawl catch) as a dependent variable.

Habitat variables

Independent variables for modeling included the standard suite of habitat variables typically collected on the bottom trawl survey as well as a few derived and modeled variables (Table 1). Haul position and depth were collected during each bottom trawl haul. A start and end position for the vessel during the on-bottom portion of the tow were collected using the vessel-mounted GPS receiver. Vessel position was corrected for the position of the bottom trawl itself by triangulating how far the net was behind the vessel (based on the seafloor depth and the wire out) and subtracting this distance from the vessel position in the direction of the bottom trawl haul. We assumed that the bottom trawl was directly behind the vessel during the tow and that all bottom trawl tows were conducted in a straight line from the beginning point to the end point. The mid-point of the start and end positions of the net was used as the location variable in the modeling. The longitude and latitude data for

Table 1. Variables used in the generalized additive modeling of coral and sponge presence or absence and abundance and coral family diversity. For each variable, the unit of measure (where applicable) and the definition are given. The method used to interpolate the variable from points to the 100 m \times 100 m raster grid is also provided, as well as the source of the original data. NOS: National Ocean Service, ROMS: Regional Ocean Model System

Variable	Unit	Definition	Interpolation method	Source
Location	eastings, northings	Latitude and longitude of bottom trawl hauls in Alaska, Albers projection corrected for the position of the trawl net relative to the vessel	—	DGPS collected at bottom trawl hauls
Depth	m	Bathymetry of the seafloor based on digitized and position-corrected NOS charts	Linear interpolation	Mean depth of bottom trawl hauls (modeling), Zimmermann et al. (2013) (prediction)
Slope	%	Maximum difference between a depth measurement and its adjoining cells	—	Zimmermann et al. (2013)
Rugosity	—	Ratio of the surface area of each grid cell and its nearest neighbors to the planar area of the grid cell and its nearest neighbors	—	—
Bottom temperature	$^{\circ}\text{C}$	Mean summer bottom temperature for the region measured during bottom trawl surveys from 1991 to 2011	Ordinary kriging	Temperature data collected at bottom trawl hauls
Ocean color	$\text{mg C m}^{-2} \text{d}^{-1}$	Net primary production in surface waters in May to September averaged by 1080 \times 2160 grid cells then averaged across years (2003 to 2011)	Inverse distance weighting	Behrenfeld & Falkowski (1997)
Mean ocean current	m s^{-1}	Ocean current speed predicted from the ROMS model during the years 1970 to 2004 and averaged on a 10 km \times 10 km grid	Inverse distance weighting	Danielson et al. (2011)
Maximum tidal current	cm s^{-1}	Maximum of the predicted tidal current at each bottom trawl location over a 1 yr cycle	Ordinary kriging	Egbert & Erofeeva (2002)
Aspect relative to mean current	degrees	Absolute difference between the direction of the current and the aspect of the bathymetry	—	Derived from mean current variable and bathymetry variable
Area open or closed to fishing	—	Polygon coverage describing whether the bottom trawl haul was open or closed to mobile bottom-contact gear	—	Area closures designated by the North Pacific Fishery Management Council

each tow (and all other geographical data including the raster layers described below) were projected into Alaska Albers Equal Area Conic projection (center latitude: 50 $^{\circ}$ N, center longitude: 154 $^{\circ}$ W), and degrees of latitude and longitude were transformed into 100 m \times 100 m square grids of eastings and northings for modeling. In the maps, a center longitude of 175 $^{\circ}$ W was used to show the Aleutian Island arc on a single long panel (e.g. Fig. 1). The location variable was used to capture any significant spatial trends across the Aleutian Islands region in coral and sponge bottom trawl survey catches.

The depth for each tow was estimated from a Sea-Bird SBE-39 microbathythermograph attached to the headrope of the net plus the measured net height. Mean depth during the tow was calculated for inclusion as an explanatory variable in the modeling. A bathymetry raster for the entire Aleutian Islands region was also produced for this analysis (Zimmermann et al. 2013; Fig. 2A). This raster was used for prediction but not for parameterizing the models. Bathymetric point data were derived from soundings ($n > 2.1$ million soundings) on NOS smooth sheets that were digitized and compiled according to the meth-

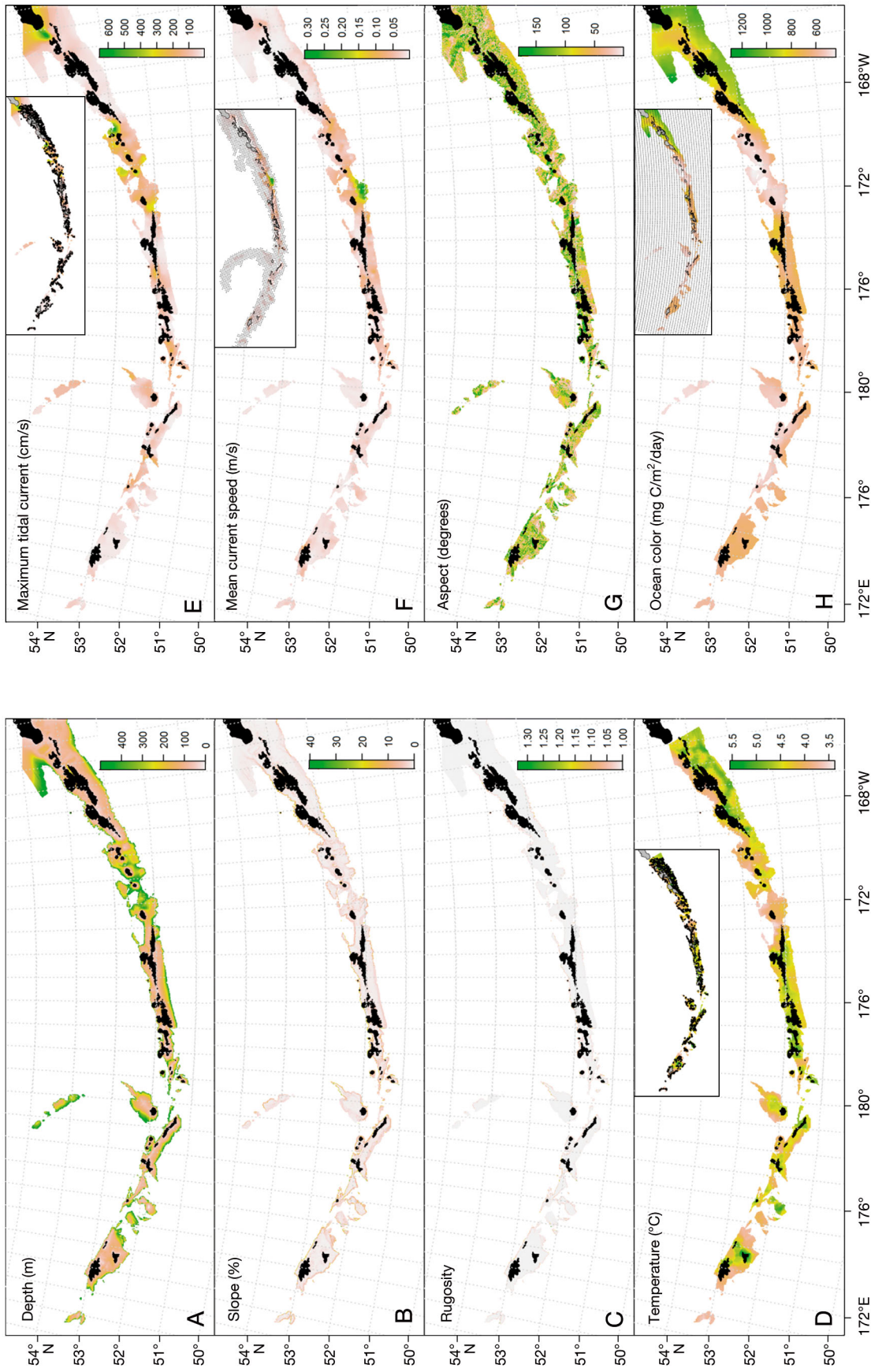


Fig. 2. Explanatory variables used in modeling coral and sponge abundance in the Aleutian Islands. Each variable is mapped on a 100 m × 100 m grid. Inset maps are shown for those variables that were interpolated (temperature, mean current speed, maximum tidal current and ocean color), showing the distribution of the data points used for interpolation

ods in Zimmermann et al. (2013). These point data were linearly interpolated from a triangular irregular network (TIN) layer to a 100 m × 100 m raster grid. This interpolation was conducted using the Spatial Analyst package in ArcGIS software (ESRI 2009).

Slope and rugosity were 2 habitat variables derived from the 100 m × 100 m bathymetry raster. Slope for each raster grid cell was computed as the maximum difference between the depth at a cell and its surrounding cells. Slope was computed using the Spatial Analyst package in ArcGIS software (ESRI 2009). Rugosity (or roughness of the seafloor) was estimated as the ratio of the surface area of each grid cell and its nearest neighbors to the planar area of the grid cell and its nearest neighbors. Rugosity was estimated for the 100 m × 100 m raster using the DEM Surface Tools add-on to ArcGIS (Jenness 2013), and rugosity values ranged from 1 to 2.24. The maximum rugosity and the mean slope underneath each bottom trawl tow path were used as habitat variables in the modeling. The 100 m × 100 m raster layers of slope and rugosity were used for prediction (Fig. 2B,C).

The average summer temperature at each site was estimated from data collected during Aleutian Islands bottom trawl surveys from 1991 to 2011. Bottom temperatures are collected during each bottom trawl tow using the SBE-39 attached to the headrope of the net (Fig. 2D). Mean bottom temperatures for each haul were interpolated to the 100 m × 100 m grid for the entire Aleutian Islands region. These data were interpolated using ordinary kriging (Venables & Ripley 2002) with a spherical semi-variogram model. This resulted in a single temperature raster layer that reflects the average temperature conditions in surveys from 1991 to 2011 (Fig. 2D). When evaluated using leave-one-out cross-validation, the kriging model was a statistically significant fit to the observations ($n = 2814$, mean squared error = 0.19, $R^2 = 0.38$), capturing the spatial trend in the temperature data. Historical mooring data have indicated that summer temperatures vary by ~2 to 3°C at depths ≤ 100 m, while at deeper depths, annual temperature variations are generally < 1°C (Stabeno et al. 2002). The temperature data used in our models were primarily designed to reflect long-term averages that could be compared spatially to the distribution of corals and sponges. Mean bottom temperature underneath each bottom trawl tow path was used as a habitat variable in the modeling. The 100 m × 100 m raster layers of average temperature were used for prediction.

Three measures of water movement and its potential interaction with the seafloor were used as habitat variables in modeling and prediction. The first vari-

able was the maximum tidal current speed at the site of each bottom trawl haul. Tidal speeds were estimated for 368 consecutive days (1 January 2009 to 3 January 2010) using a tidal inversion program parameterized for the Aleutian Islands on a 1 km × 1 km grid (Egbert & Erofeeva 2002). This tidal prediction model was used to produce a time series of 1 yr of tidal currents for spring and neap cycles at each bottom trawl survey location. The maximum of the time series of predicted tidal current was then extracted for the position of each bottom trawl survey haul. This maximum value was used as a habitat variable in the modeling. Maximum currents at each bottom trawl survey site were also interpolated to the entire Aleutian Islands using ordinary kriging and a spherical semi-variogram. When evaluated using leave-one-out cross-validation, the kriging model fit the observations very well ($n = 3051$, mean squared error = 407, $R^2 = 0.93$). The kriging model was then used to interpolate a raster of maximum current values on a 100 m × 100 m cell size that was used for prediction (Fig. 2E).

The second water-movement variable was the predicted bottom water layer current speed from the Regional Ocean Modeling System (ROMS) model runs from 1970 to 2004 (Danielson et al. 2011). These long-term current speed and direction values were available as points on a 10 km × 10 km grid. The ROMS model was based on a 3-dimensional grid with 60 depth tiers for each grid cell. For example, a point at 60 m water depth would have 60 depth bins at 1 m intervals, while a point at 120 m depth would have 60 depth bins at 2 m depth intervals, etc. The current speed and direction for the deepest depth bin at each point (closest to the seafloor) was used in this analysis. These regularly spaced data were interpolated to a 100 m × 100 m cell size raster covering the entire Aleutian Islands using inverse distance weighting (Fig. 2F). Then, the values from this raster at each of the bottom trawl survey haul locations were extracted, and the mean value was computed for the path of each bottom trawl survey tow. The raster was also used for prediction.

The final water current variable used in the modeling was the aspect of the seafloor relative to the mean current direction. The aspect of the seafloor (the angle the seafloor faces) in degrees relative to north (0°) was computed using the Spatial Analyst package in ArcGIS (ESRI 2009). This data was produced on a 100 m × 100 m raster grid, the same as the bathymetry data (Fig. 2G). The current direction used was the mean current direction from the long-term model output from the ROMS model (Danielson et al. 2011). The absolute value of the difference between the

current direction and the aspect of the seafloor at the position of each bottom trawl haul was used as a habitat variable in the modeling. This value ranged from 0° (where the currents were flowing in the same direction the seafloor was facing) to 180° (where the mean current was flowing directly opposite the aspect of the seafloor). The raster grid of the aspect variable (on the 100 m × 100 m grid) was used in the prediction.

To reflect average ocean productivity ($\text{mg C m}^{-2} \text{d}^{-1}$) at each of the bottom trawl survey sites, we used MODIS ocean color data for 5 spring-summer months (May to September) that encompass the spring and summer phytoplankton blooms over 9 yr (2003 to 2011) for the Aleutian Islands region (Behrenfeld & Falkowski 1997). These data were downloaded from the Oregon State University Ocean Productivity website and were averaged by cell and by month and then averaged again by cell and by year (to account for differences in the number of samples within each cell). The averages were then interpolated to 100 m × 100 m raster grids using inverse distance weighting (Fig. 2H). The mean value in this grid underlying each bottom trawl survey tow was extracted from this raster. The raster was used for prediction.

The final independent variable used in the model was whether the bottom trawl haul fell within the boundary of an area that was open for bottom trawl fishing or closed to bottom trawl fishing. In 2006, much of the Aleutian Islands region was closed to mobile fishing gear as part of deep-sea coral protection efforts (Hourigan 2009). Each bottom trawl tow site was classified as either occurring within a closed area or in an area open to fishing using the position of the tow, and this classification was included as an explanatory variable in the models of presence or absence and abundance of sponge and coral.

There was some collinearity in the habitat variables included in the model (Table 2). Eastings (longitude) and northings (latitude) were very strongly correlated ($R^2 = 0.59$) because of the geographical shape of the Aleutian Islands and as such were included as a bivariate term (location) in the model. Although many other correlations among variables were statistically significant, all had $R^2 < 0.44$, and the vast majority were not very well correlated ($R^2 < 0.10$). Thus, the remaining habitat variables used in the models were in a univariate form.

Model fitting

Generalized additive models (Hastie & Tibshirani 1990) using the *mgcv* package in R (Wood 2006) were used to predict the dependent variables with the suite of untransformed habitat variables included, so that the full model was as follows:

$$y = s(\text{location}) + s(\text{depth}) + s(\text{temperature}) \\ + s(\text{slope}) + s(\text{rugosity}) + s(\text{maximum tidal current}) \\ + s(\text{mean current speed}) + s(\text{ocean color}) \\ + s(\text{aspect}) + \text{open or closed} + \varepsilon$$

where y was the dependent variable presence or absence (for sponge, coral, Primnoidae or Stylasteridae), abundance (for sponge, coral, Primnoidae or Stylasteridae) or coral family diversity, and s indicates a thin plate regression spline smoothing function (Wood 2006). In each case, the basis degrees of freedom used in the smoothing function was limited to ≤ 4 for univariate variables and ≤ 30 for the bivariate term (location). For presence or absence models, a binomial distribution was used for the fitting, while for diversity data (counts), a Poisson distribu-

Table 2. Correlations (r) among explanatory habitat variables used in the model of coral and sponge distribution in the Aleutian Islands bottom trawl surveys (1991 to 2011)

	Longitude	Latitude	Depth	Rugosity	Slope	Maximum tidal current	Ocean color	Mean current speed	Mean bottom temperature
Latitude	-0.77	1							
Depth	-0.12	-0.02	1						
Rugosity	-0.04	0.03	0.20	1					
Slope	-0.15	0.07	0.47	0.66	1				
Maximum tidal current	0.23	-0.26	0.08	-0.03	-0.02	1			
Ocean color	0.60	-0.27	-0.23	0.01	-0.12	-0.35	1		
Mean current speed	0.04	-0.28	0.21	-0.01	0.01	0.35	-0.26	1	
Mean bottom temperature	0.05	-0.21	-0.44	-0.10	-0.23	-0.09	0.16	-0.02	1
Aspect	0.01	0.06	-0.10	0.03	-0.04	0.01	0.03	-0.02	-0.02

tion was used. During initial analyses, a number of distribution combinations and data transformations were explored to use with the CPUE data, including the Gaussian (Wood 2006), gamma (Wood 2006), and Tweedie distributions (Shono 2008) and both the square and fourth root transformations. The log transformation with constants of 1, 10% of the mean CPUE and half of the smallest positive value were also evaluated. Residuals from each distribution and data transformation were visually compared to the normal distribution using quantile-quantile plots to determine which combination best approximated normality for each response variable. The Gaussian distribution with log-transformed CPUE data and a constant of half of the smallest positive value proved to best approximate normality for the analyses of sponge, coral and Primnoidae abundance. The Tweedie distribution with the power parameter set to 1.9 and untransformed CPUE data proved to be closest to normality for the Stylasteridae models.

A factorial analysis was used to reduce the number of variables in each model. Initially, a full model containing the entire variable suite was fit to the data. Then, the least significant variable was removed from the model, provided it met 2 of the 3 criteria set out by Wood (2003): $p > 0.05$ or 95% confidence intervals about the predicted curve contain 0, the generalized cross-validation (GCV) score for CPUE models or the unbiased risk estimator (UBRE) score for binomial models was lower with the elimination of the variable, or the effective degrees of freedom are close to 1.0 for the univariate smooth of the variable. Then, the reduced model was re-fit to the data. Stepwise variable removal was continued until a final best-fitting model that included only significant variables was reached.

To test the performance of the best-fitting models, the predictions were compared to the observations. For presence and absence models, the area under the receiver operating characteristic curve (AUC) was computed to judge model performance. The AUC calculates the probability that a randomly chosen presence observation would have a higher probability of presence than a randomly chosen absence observation, using rank data. We used the scale of Hosmer & Lemeshow (2005), where an AUC value > 0.5 is estimated to be better than chance, a value > 0.7 is estimated to be acceptable, and values > 0.8 and > 0.9 are excellent and outstanding, respectively. Confidence intervals for the AUC (95%) were calculated according to the methodology of DeLong et al. (1988). For abundance and diversity models, the performance was directly tested by correlating the predictions with the observations.

Model validation and predictions

Model validation and testing was performed on data collected during the 2012 Aleutian Islands bottom trawl survey. In 2012, the bottom trawl survey was conducted at 408 stations covering the entire Aleutian Island chain. These data were held back from model formulation, and the best-fitting models for each taxonomic grouping of sponge and coral were used to predict the presence or absence and abundance from the 2012 survey data. The model predictions were then compared to the observed data from the 2012 bottom trawl survey. The AUC was computed for the presence or absence predictions, while the correlation between observed and predicted abundance was used to compare the abundance data.

For each taxonomic grouping of sponge and coral, predictions of the presence or absence and abundance were also made for the entire Aleutian Islands region. Predictions of coral family diversity were also made for the entire Aleutian Islands region. Interpolated raster layers of each of the habitat variables were constructed on a $100 \text{ m} \times 100 \text{ m}$ grid for the region, as described above. The best-fitting GAM models for each dependent variable were applied to the habitat raster layers to make predictions over the entire Aleutian Islands region on a $100 \text{ m} \times 100 \text{ m}$ grid. Summaries of these prediction layers are presented graphically. The predicted abundance and suitable habitat for each of the sponge and coral taxonomic groupings was also summed for areas closed and open to fishing.

RESULTS

Presence and absence models

The best-fitting models of presence or absence all contained the bivariate location term as the most significant factor (Table 3). For all presence or absence models, the next most important variable was the maximum tidal current. For coral, Primnoidae and Stylasteridae presence or absence models, the probability of presence had a dome-shaped relationship with maximum tidal currents, with a peak at $\sim 350 \text{ cm s}^{-1}$ (Fig. 3). For upright sponge presence or absence models, a dome-shaped relationship with maximum tidal current was still apparent, but it peaked at $\sim 300 \text{ cm s}^{-1}$ (Fig. 3). The probability of sponge presence increased with increasing depth, but depth was not included in the

Table 3. Best-fitting generalized additive model results for each dependent variable modeled for Aleutian Islands bottom trawl survey data (1991–2011). Significant variables are listed in order of their significance (highest to lowest) in the model. The R^2 value is listed for the relationship between the modeled data (1991–2011) and the corresponding model predictions, as well as for the test data set (2012). AUC: area under the receiver operating characteristic curve, edf: estimated degrees of freedom. Variables are location (long,lat), the maximum tidal current (max_tide, cm s^{-1}), aspect (degrees), ocean color (color, $\text{mg C m}^{-2} \text{d}^{-1}$), seafloor slope (slope, %), mean current speed (mean_current, m s^{-1}), depth (m) and temperature (temp, $^{\circ}\text{C}$)

Response variable (presence or absence)	With/without location	Model	Modeled data (1991–2011)			Test data (2012)	
			Deviance explained (%)	edf	AUC (95% CI)	AUC (95% CI)	
Upright sponge	With	s(long,lat)+s(max_tide)+s(depth)+s(temp)+s(aspect)	8	27.9; 2.6; 1.4; 2.4; 2.7	0.73 (0.71–0.74)	0.67 (0.61–0.73)	
	Without	s(max_tide)+s(depth)+s(temp)+s(aspect)	4	2.2; 2.8; 1.7; 2.8	0.62 (0.60–0.64)		
Coral	With	s(long,lat)+s(max_tide)+s(color)+s(slope)	16	27.2; 2.9; 2.3; 1.6	0.75 (0.74–0.77)	0.74 (0.69–0.79)	
	Without	s(max_tide)+s(color)+s(slope)	6	2.8; 3.0; 1.0	0.66 (0.64–0.68)		
Primnoidae	With	s(long,lat)+s(max_tide)+s(color)	18	27.2; 2.8; 2.6	0.77 (0.76–0.79)	0.76 (0.72–0.81)	
	Without	s(max_tide)+s(color)	6	2.6; 2.9	0.66 (0.64–0.68)		
Stylasteridae	With	s(long,lat)+s(max_tide)+s(mean_current)+s(aspect)	19	25.1; 2.5; 2.9; 2.6	0.80 (0.78–0.82)	0.78 (0.73–0.83)	
	Without	s(max_tide)+s(mean_current)+s(aspect)	8	2.8; 2.9; 2.7	0.68 (0.66–0.71)		

best-fitting models for any of the coral groupings. Temperature was another variable that was only included in the best-fitting model of sponge presence or absence, where the relationship was dome shaped with a peak probability of presence at $\sim 4^{\circ}\text{C}$ (Fig. 3). Aspect was the final variable included in the best-fitting model of sponge presence or absence. Aspect was also included in the best-fitting model for Stylasteridae, and for both groups, there were peak probabilities of presence at 90 and 180° . The coral and Primnoidae best-fitting models both included a significant effect of ocean color, where the probability of presence decreased with increasing ocean color to a minimum around $250 \text{ mg C m}^{-2} \text{d}^{-1}$ and then increased almost linearly at higher levels of production (Fig. 3). Seafloor slope had a non-linear negative effect on the probability of presence of coral but was insignificant for all other groups. Mean current speed was significant in the Stylasteridae best-fitting model, with a dome-shaped relationship peaking at 0.15 m s^{-1} (Fig. 3). Seafloor rugosity and whether the trawl haul occurred in an open or closed area were not significant in determining presence or absence in any of the best-fitting models.

The location variable was significant in all the best-fitting models of presence or absence (Table 3). The predictions mapped throughout the Aleutian Islands shows that there was a relatively high probability (>0.50) of sponges being present in most areas of the Aleutian Islands, reflecting their widespread distribution in bottom trawl survey catches (Fig. 4). Notable areas of low predicted presence occurred near Agattu Island (174°E) and on the western side of Atka Island (175°W). Coral was predicted to occur over a smaller area than sponge (Fig. 4). There were predicted 'hotspots' of coral in a large area centered around Tahoma Bank (175 to 177°E), throughout the central Aleutian Islands ($\sim 178^{\circ}\text{E}$ to 176°W) and in the area between Amlia Island and Samalga Pass (173 to 170°W). Primnoidae exhibited a similar distribution to the combined coral category (Fig. 4), possibly reflecting the fact that this species is the predominant coral family in the Aleutian Islands. For Stylasteridae, the least common taxonomic group examined, presence was predicted for the area around Tahoma Bank (175 to 177°E) and in a narrow band between Seguam Island and Amukta Island (172.5 to 170.5°W ; Fig. 4).

The best-fitting models for presence or absence explained between 8 and 19% of the deviance in

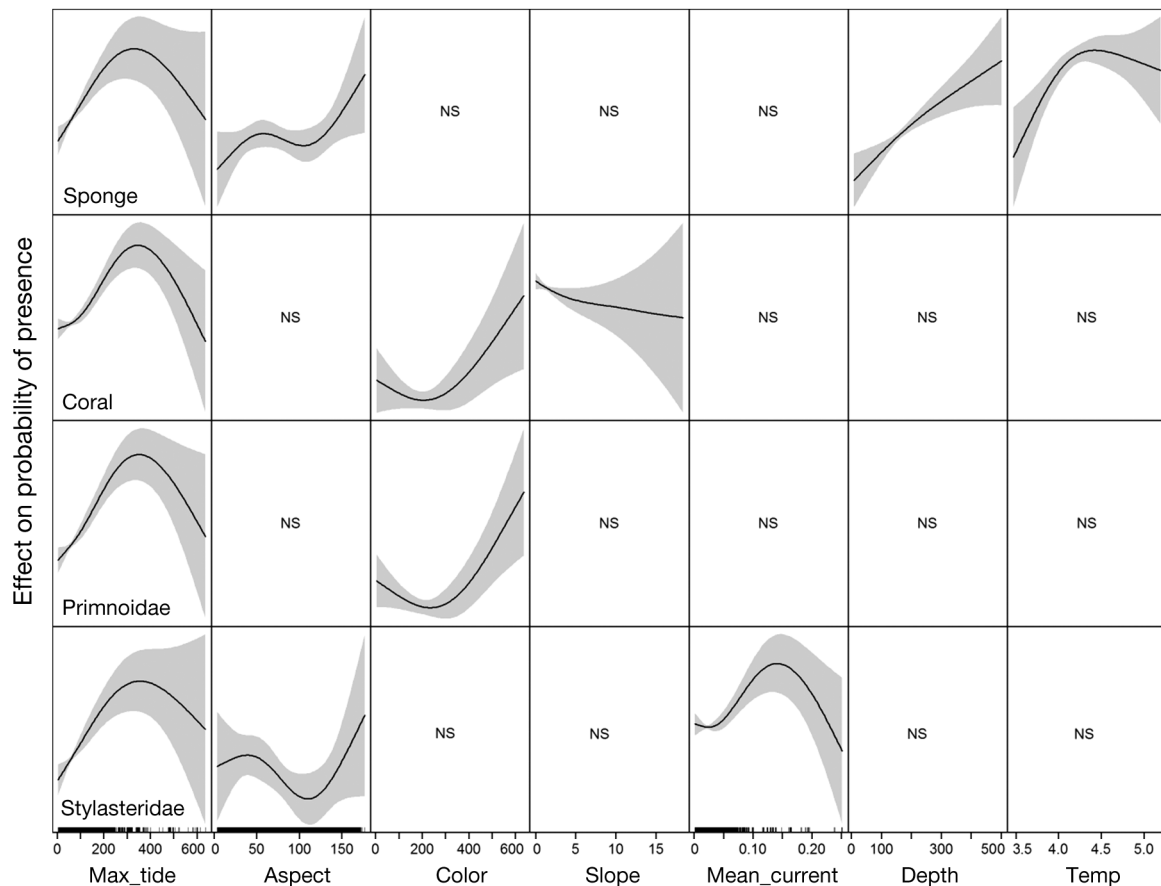


Fig. 3. Partial effects of significant univariate variables in the best-fitting model of upright sponge, coral, Primnoidae and Stylasteridae presence or absence in the Aleutian Islands, shown in rows. In the univariate plots, the line is the smoothed model fit, and the grey area is the 95% confidence interval. Tick marks on the x-axis indicate where samples occurred, and 'NS' indicates the variable was not significant in the model. Variables shown in the columns from left to right are the maximum tidal current (Max_tide, cm s^{-1}), aspect (degrees), ocean color (Color, $\text{mg C m}^{-2} \text{d}^{-1}$), seafloor slope (Slope, %), mean current speed (Mean_current, m s^{-1}), depth (m) and temperature (Temp, $^{\circ}\text{C}$)

observed presence or absence (Table 3). The AUC values for each of the models ranged from 0.73 for sponge to 0.80 for Stylasteridae, and all the 95% confidence intervals of the AUC indicated the models were within the acceptable range (0.70 to 0.79). When the location variable was removed from the best-fitting models, the deviance explained and the AUC values dropped precipitously, with AUC values ranging from 0.62 for sponge to 0.68 for Stylasteridae (Table 3). Although this result is considerably better than predicted from chance (0.50), models without the location variable were not in the acceptable range.

Abundance models

The best-fitting models for invertebrate abundance were similar to the models of presence or absence. Location was the most significant variable for all

abundance models (Table 4). Maximum tidal current was included in best-fitting models of all groups (Table 4). A familiar dome-shaped relationship between maximum tidal current and abundance was found, with peak abundance at $\sim 350 \text{ cm s}^{-1}$ for coral, Primnoidae and Stylasteridae and a peak at $\sim 300 \text{ cm s}^{-1}$ for sponge (Fig. 5). Mean current speed was also included in the best-fitting models for each taxonomic grouping. For this variable, peaks in abundance were generally found at currents between 0.1 and 0.2 m s^{-1} (Fig. 5), although Stylasteridae abundance had a bimodal relationship with mean current exhibiting peaks near 0.0 m s^{-1} as well. Depth and temperature were again included in the best-fitting models of upright sponge abundance, with sponge abundance increasing non-linearly with increasing depth and peaking at temperatures around 4°C . The relationship between sponge abundance and aspect was the same as the relationship

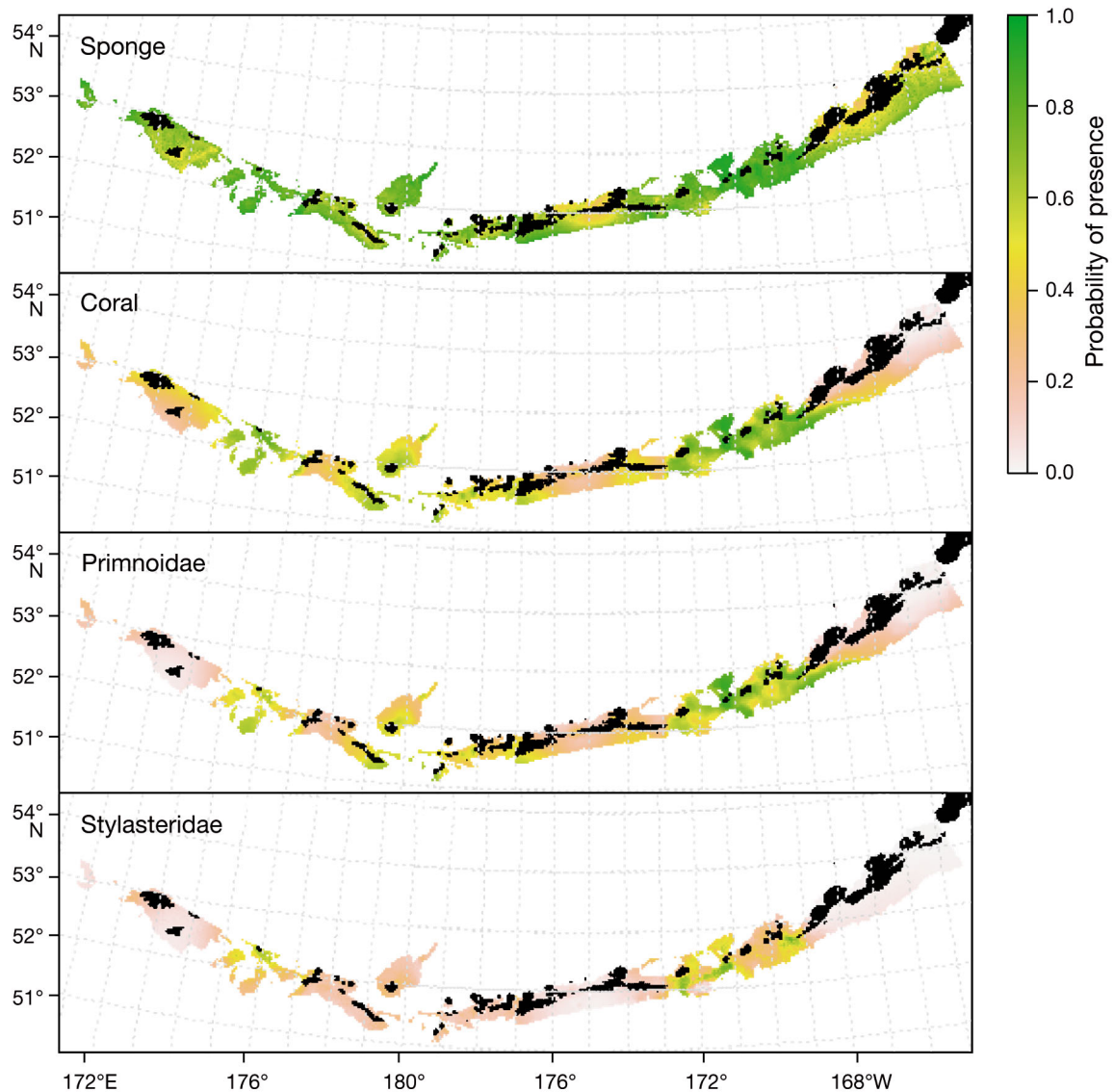


Fig. 4. Predictions of the best-fitting generalized additive model for upright sponge, coral, Primnoidae and Stylasteridae predicting the probability of presence in the Aleutian Islands bottom trawl surveys

between sponge presence and aspect, with peaks at ~ 90 and 180° . The best-fitting coral, Primnoidae and Stylasteridae abundance models contained the ocean color variable as well, although the shapes of the relationships were not entirely consistent (Fig. 5). The abundance of coral and Primnoidae was low at low levels of productivity and then increased rapidly at productivity levels $> 700 \text{ mg C m}^{-2} \text{ d}^{-1}$. Interestingly, the abundance of Stylasteridae showed the exact opposite trend. An effect of slope on coral abundance was also significant, with lower abundance at low slope values and little effect (either positive or negative) at higher slopes. A single linear term was significant in the best-fitting model of Prim-

noidae, where there was a linear decrease in abundance with depth. Seafloor rugosity and whether the trawl haul occurred in an open or closed area were not significant in any of the best-fitting abundance models.

The location variable was highly significant in each of the best-fitting models of abundance (Table 4). Areas of predicted high upright sponge abundance occurred on the northern edge of Stalemate Bank ($\sim 170.5^\circ\text{E}$) and to the east of Attu Island (172°E) and Kiska Island (177°E) (Fig. 6). The largest area of predicted high sponge abundance was found in the area from Samalga Pass (170°W) to the west side of Amlia Island (173°W). For coral, predicted abundance fol-

Table 4. Best-fitting generalized additive model results for each dependent variable modeled for Aleutian Islands bottom trawl survey data (1991–2011). Significant variables are listed in order of their significance (highest to lowest) in the model, the deviance explained and the estimated degrees of freedom (edf) of the best fitting models are also provided. The R^2 value is listed for the correlation between the modeled data (1991–2011) and the corresponding model predictions as well as for the test data (2012). Variables are location (long,lat), the maximum tidal current (max_tide, cm s^{-1}), aspect (degrees), ocean color (color, $\text{mg C m}^{-2} \text{d}^{-1}$), seafloor slope (slope, %), mean current speed (mean_current, m s^{-1}), depth (m), rugosity (rug), and temperature (temp, $^{\circ}\text{C}$)

Response variable	With/without location	Model	— Modeled data (1991–2011) —			Test data (2012) R^2
			Deviance explained (%)	edf	R^2	
Upright sponge abundance	With	s(long,lat)+s(max_tide)+s(depth)+s(temp)+s(aspect)+s(mean_current)	20	28.5; 2.8; 1.8; 2.4; 2.8; 2.7	0.198	0.199
	Without	s(max_tide)+s(depth)+s(temp)+s(aspect)+s(mean_current)	9	2.5; 2.6; 2.2; 2.9; 2.0	0.086	
Coral abundance	With	s(long,lat)+s(max_tide)+s(slope)+s(mean_current)+s(color)	21	28.1; 2.9; 2.7; 2.8, 2.1	0.205	0.196
	Without	s(max_tide)+s(slope)+s(mean_current)+s(color)	11	2.9; 2.5; 2.5; 2.9	0.107	
Primnoidae abundance	With	s(long,lat)+s(max_tide)+depth+s(color)+s(mean_current)	22	28.3; 2.9; 2.4; 2.8	0.214	0.228
	Without	s(max_tide)+depth+s(color)+s(mean_current)	11	2.8; 2.6; 2.4	0.106	
Stylasteridae abundance	With	s(long,lat)+s(color)+s(max_tide)+s(mean_current)	25	29.0; 3.0; 2.4; 2.9	0.047	0.003
	Without	s(color)+s(max_tide)+s(mean_current)	10	2.9; 3.0; 2.9	0.084	
Coral family diversity	With	s(long,lat)+s(max_tide)+temp+s(color)+s(mean_current)+s(rug)	25	27.6; 2.6; 2.7; 2.8; 2.7	0.236	0.279
	Without	s(max_tide)+temp+s(color)+s(mean_current)+s(rug)	13	2.3; 2.9; 2.4; 1.8	0.136	

lowed a similar pattern as sponges, with high abundance generally occurring from Attu Island (172°E) to Kiska Island (177°E) and from Samalga Pass (170°W) to the west side of Amlia Island (173°W) (Fig. 6). Primnoidae abundance was predicted to be highest from Samalga Pass (170°W) to the west side of Amlia Island (173°W) and on Tahoma Bank (175°E). The best-fitting abundance model did not predict many contiguous areas of Stylasteridae abundance (Fig. 6), but the areas of predicted higher abundance were the same as for Primnoidae.

The best-fitting models of abundance explained between 20 and 25% of the deviance in the abundance data (Table 4). The R^2 between observed and predicted values was 0.20 for sponge, 0.21 for coral and 0.21 for Primnoidae, but this value was much lower at 0.03 for Stylasteridae (Table 4). When the location variable was removed from the best-fitting models of abundance, the amount of deviance explained and the R^2 between observed and predicted values each dropped by $\sim 50\%$ (Table 4), indicating the importance of the bivariate location variable in the models.

Diversity model

Coral family diversity was best explained by location, maximum tidal current, temperature, ocean color, mean current and rugosity at each of the bottom trawl sites (Table 4). The best-fitting model explained 25% of the deviance in the data set. The relationships between diversity and the explanatory variables followed similar patterns as the trends in coral abundance and coral presence or absence (Fig. 5). Diversity was predicted to be highest at maximum tidal current speeds of $\sim 350 \text{ cm s}^{-1}$. The relationships of coral family diversity with ocean color and mean current speed were similar to those found for the coral and Primnoidae taxonomic groupings, with increasing coral family diversity at productivity levels $> 700 \text{ mg C m}^{-2} \text{d}^{-1}$ and peak diversity at mean current speeds of $\sim 0.15 \text{ m s}^{-1}$ (Fig. 5). For coral family diversity, there was a significant linear decrease in the number of families present with increasing temperature. The final significant variable in the modeling was a decrease in coral family diversity with increasing rugosity (Fig. 5); however, this relation-

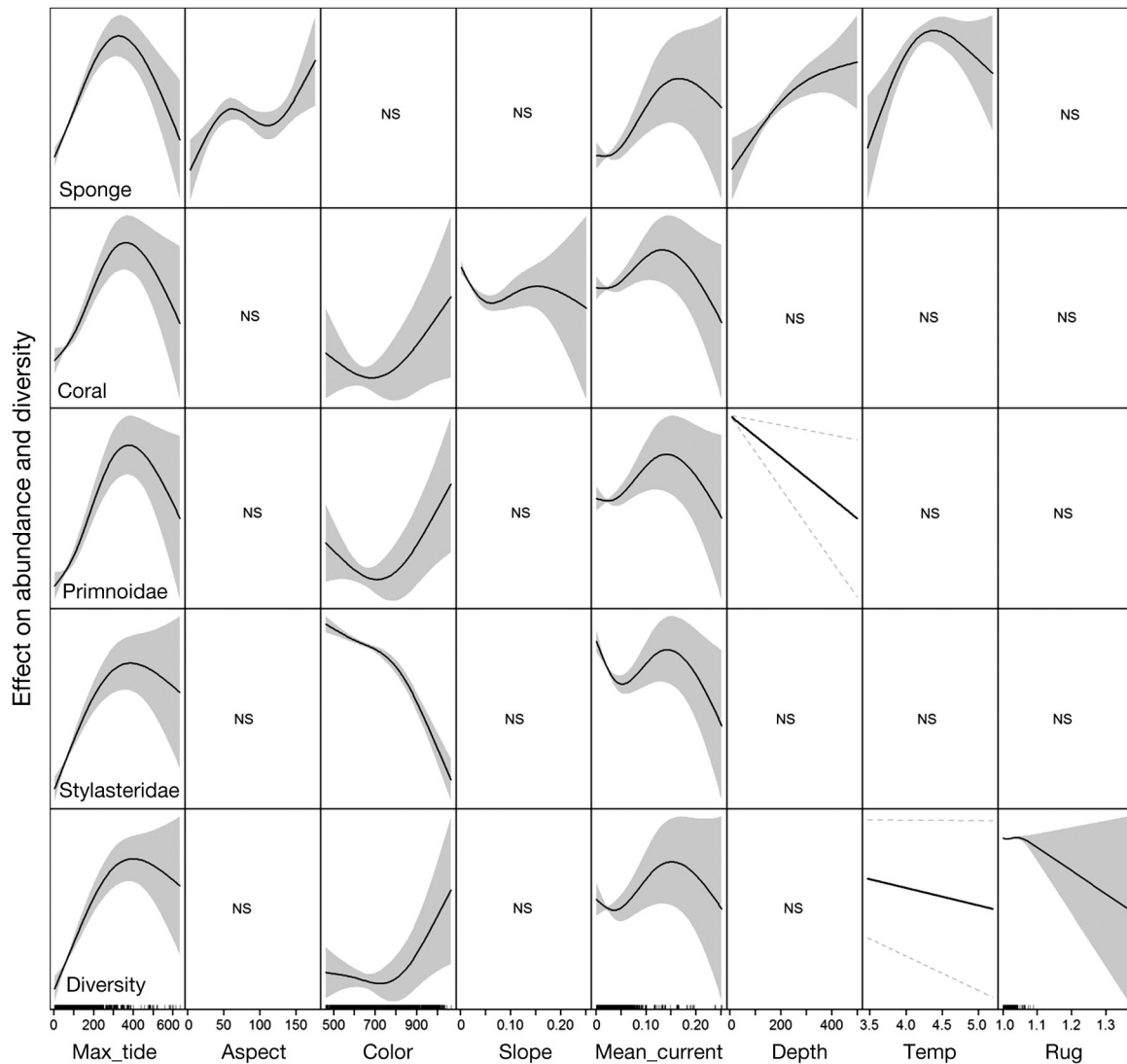


Fig. 5. Partial effects of significant univariate variables in the best-fitting model of upright sponge, coral and Primnoidae abundance (log-transformed catch per unit of effort [CPUE]), Stylasteridae abundance (CPUE) and coral family diversity (number of families) in the Aleutian Islands, shown in rows. In the univariate plots, the line is the smoothed model fit, and the grey area is the 95% confidence interval. Variables with strictly linear relationships to CPUE are shown as straight lines, with grey dashed lines indicating standard errors. Tick marks on the x-axis indicate where samples occurred, and 'NS' indicates the variable was not significant in the model. Variables shown in the columns from left to right are the maximum tidal current (Max_tide, cm s^{-1}), aspect (degrees), ocean color (Color, $\text{mg C m}^{-2} \text{d}^{-1}$), seafloor slope (Slope, %), mean current speed (Mean_current, m s^{-1}), depth (m), rugosity (Rug) and temperature (Temp, $^{\circ}\text{C}$)

ship was driven by a single high rugosity value, and the relationship between rugosity and diversity was flat through the bulk of the observations (Fig. 5).

Areas of predicted high coral family diversity were near Buldir Island (176°E) and in the area around Seguam Pass (173 to 171°W ; Fig. 7), a result that is similar to both the presence and abundance models for the 3 coral taxonomic groupings. The number of coral families predicted to occur in the Aleutians outside of the 2 hotspots was generally < 1 . Location was again important in the best-fitting models of coral

family diversity (Table 4). When the location variable was removed from the models, the deviance explained and the R^2 between observed and predicted values decreased by half.

Model testing

The model predictions for the bottom trawl survey data collected in 2012 indicated good agreement for the presence-absence models (Table 3). The AUC for

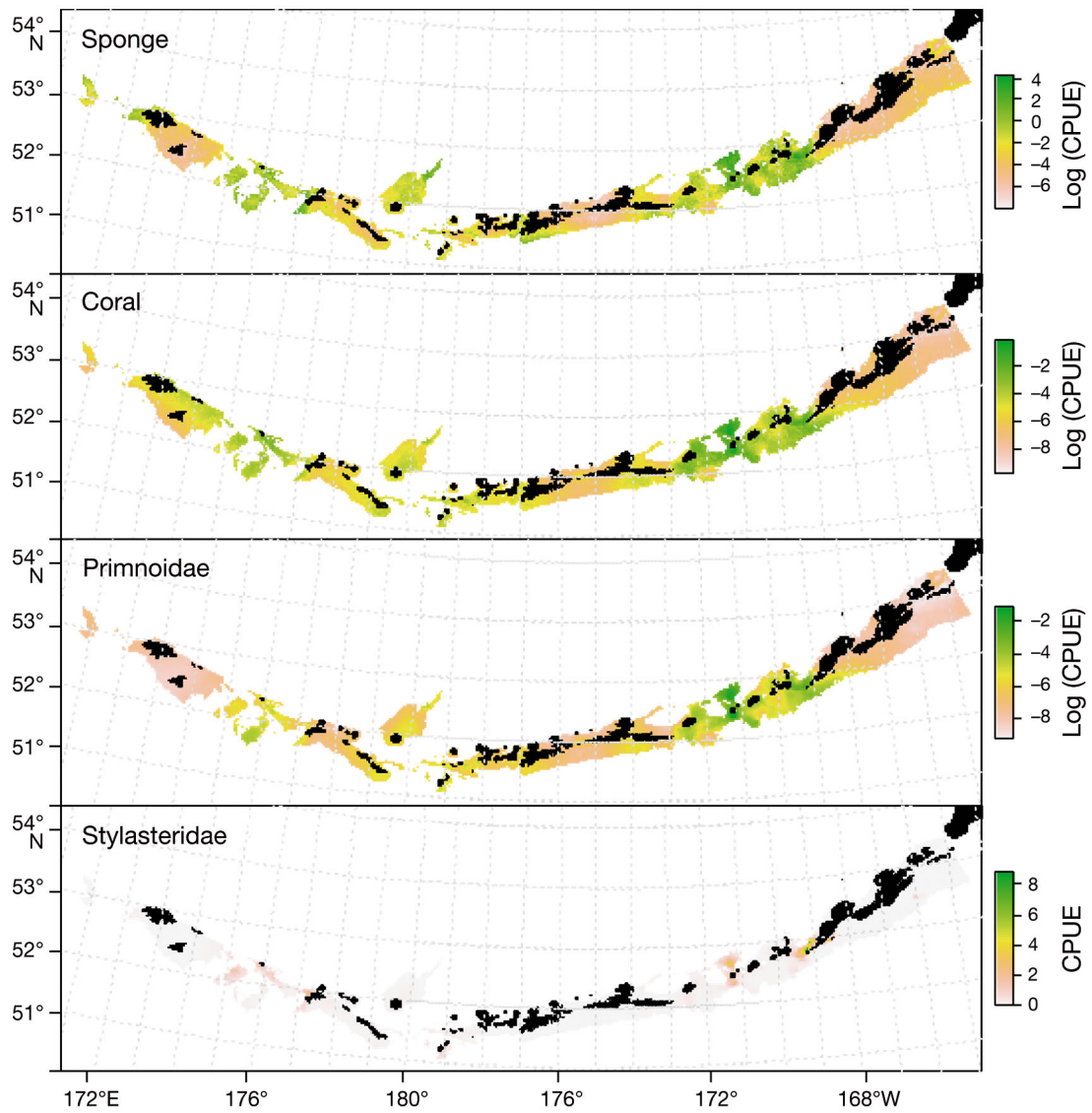


Fig. 6. Predictions of the best-fitting generalized additive model for predicting the abundance of upright sponge, coral, Primnoidae (log-transformed catch per unit of effort [CPUE]) and Stylasteridae (CPUE) in the Aleutian Islands bottom trawl surveys

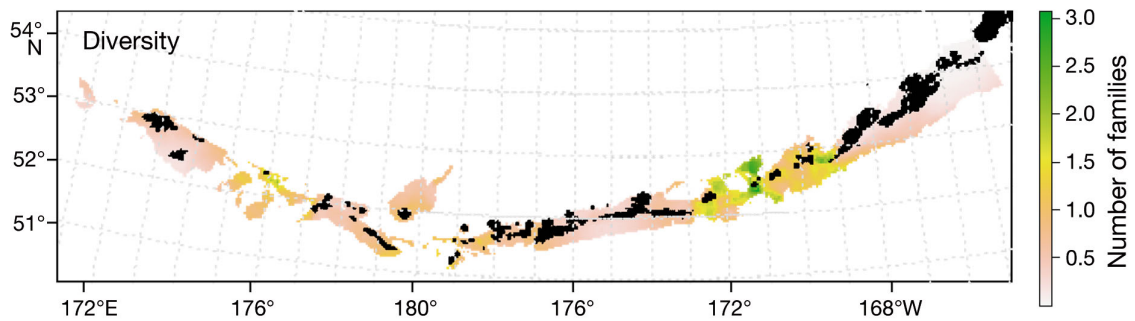


Fig. 7. Predictions of the best-fitting generalized additive model for coral diversity predicting the number of families of coral represented in bottom trawl hauls during the Aleutian Islands bottom trawl surveys

prediction of presence or absence for sponge decreased slightly for each of the coral taxonomic groupings by a minimal amount (0.01 to 0.02) when the 1991–2011 model was applied to the 2012 data, but all models were still in the acceptable range. The AUC for the sponge model decreased from 0.73 to 0.67, slightly below the acceptable range but far better than chance.

Results were similar for the abundance models and the coral diversity models, except for Stylasteridae (Table 4). The abundance models data explained about the same amount of variance (measured by the R^2 between observations and predictions) in the abundance data for the 2012 test data set as the 1991–2011 data on which they were parameterized. In 3 cases (sponge, Primnoidae and coral family diversity), the R^2 between observed and predicted increased slightly when applied to the 2012 data set. The percentages of variance in the 2012 data explained ranged from 20 to 23% for coral and Primnoidae respectively (Table 4). For Stylasteridae abundance, the best-fitting model parameterized on the 1991–2011 data did not explain any of the deviance in the 2012 data, meaning this model was not helpful in explaining any patterns in the test data set. For diversity, the variance explained increased from 24% for the 1991–2011 data to 28% for the 2012 test data set.

DISCUSSION

The modeling presented here indicates that coral and sponge presence, abundance and diversity are all strongly influenced by location and maximum tidal currents. The models predicting presence or absence were accurate (AUC > 0.70) in most instances for both the modeled data and the independently collected test data. The models predicting abundance explained roughly similar proportions (~20 to 25%) of the log-transformed CPUE data in both the test data set and the modeled data set. Similar results were found for the prediction of the diversity of coral families in the bottom trawl survey hauls. The location variable was included in the modeling to capture spatial trends in coral and sponge presence or absence and abundance throughout the Aleutian Islands, and this variable was important in all models and accounted for ~50% of the explanatory power of most models. Since the distribution of deep-sea coral and sponge ecosystems reflect the combination of both geographic and habitat factors, both relevant geographical and environmental variables were important to include (Elith & Leathwick 2009). Spatial

modeling exercises such as those presented here commonly use a location variable to represent geographical position and incorporate potential spatial autocorrelation in the residuals (Swartzman et al. 1992, Denis et al. 2002, Knapp et al. 2003, Ciannelli et al. 2008, Politou et al. 2008, Boldt et al. 2012). However, use of the location variable precludes extension of this modeling outside the area of interest for the present study (the Aleutian Islands to 500 m depth). It is important to note that the habitat variables used in the models of coral and sponge were somewhat limited; for example, the ocean color variable was based on productivity at the ocean surface, whereas coral and sponge are found exclusively attached to the seafloor. The ocean color variable would best be considered a proxy variable for production occurring at the seafloor. The location variable may have accounted for some of the variability due to habitat variables such as ocean color that may not have been well represented. The location variable may have also accounted for other processes that were not represented in the models, such as spatial patterns in historical recruitment or spatial patterns in historical fishing activity. The sampling scheme whereby stations on the 5 km × 5 km grid could be sampled multiple times during the course of the 9 yr of bottom trawl surveys could also have increased the importance of the location variable. Since the purpose of the modeling was to accurately predict the distribution and abundance of coral and sponge in the Aleutian Islands, we chose to explicitly include location in the habitat models. There is likely some spatial autocorrelation in other explanatory variables as well. For example, individuals that occurred at closely located stations would likely experience similar temperature and current patterns. Thus, some of the variance accounted for by location may have been due to individual stations experiencing similar environmental conditions, and some of the variance accounted for by environmental variables may have been due to spatial processes that were unaccounted for in the model (such as recruitment processes). It was impossible to completely distinguish the effect of location from environmental variables using the data we had available. It is likely in this analysis that the location variable is acting as a proxy for imperfect variables or variables that were not included in the model as well as accounting for some of the spatial autocorrelation in coral and sponge distributions. However, there were also important geographic trends that were obvious in the data, such as the contiguous region of relatively high probability of coral presence centered around 176°E in the Aleutian Islands (Fig. 4).

Two potential mechanisms by which maximum tidal current may be influencing the distribution of corals and sponges could be through the delivery of food to these filter-feeding organisms or through the reduction of sedimentation in high-current areas that would be reflected in exposed patches of hard seafloor. In the deep-sea area of Porcupine Bight, dense aggregations of sponges have been observed in areas adjacent to areas of high current speeds (Rice et al. 1990, White 2003). This distribution has been hypothesized to reflect patterns of the re-suspension of detrital material in the high-current areas and then delivery to adjacent low-current areas where sponges can maintain their attachment to the substrate while benefitting from delivery of food items. In theory, this explanation would be consistent with our finding of increased sponge and coral presence and abundance at intermediate levels of maximum tidal current (~ 300 to 350 cm s^{-1}). There have also been studies that show sponges can adapt their morphology to local current conditions and mitigate some of the potential disadvantages of differential current regimes where the volume of water moving past the organism may not provide adequate food resources (Bell et al. 2002). Flow-mediated competition for food resources has been observed to occur in these epibenthic taxa (Kim & Lasker 1997), so it is likely that current speed is important in determining where corals and sponges can obtain enough food to survive.

There is a strong relationship between the amount of exposed bedrock and the current regime near the seafloor, as currents can scour and re-suspend sediments, moving them away from the seafloor and exposing bedrock and other hard substrates. Upright sponges have been shown to inhabit a variety of substrates, especially exposed rock with little sedimentation but also flat silty seafloors possibly with hard substrate beneath (Freese 2001). Corals in Alaska appear to be more directly tied to hard substrates, such as boulders and exposed bedrock (Cimberg et al. 1981, Krieger 2001), and are not often found on sandy or silty seafloors. In addition to studies in Alaska, researchers in other areas have found relationships between exposed hard substrate and recruitment and abundance of corals and sponges (Gotelli 1988, Leys & Lauzon 1998). One of the interesting results of our modeling was the importance of the aspect variable in 3 of the models (sponge and Stylasteridae presence or absence and sponge abundance). The shape of the relationship was the same for all 3 models, with peaks at 90° and 180° and the minimum at 0° . This was generally what would be expected if delivery of food items were an important factor in the

model. At 0° aspects, the predominant currents flow with the slope of the seafloor, which might tend to reduce the amount of food delivered to a stationary benthic invertebrate, while at 180° , the flow into a stationary benthic invertebrate would be maximized. Some combination of a diet-based and substrate-based mechanism likely causes the strong relationship between maximum tidal current and coral and sponge presence or abundance.

Comparisons with other methods

Other models have found a variety of important variables determining the distribution of sponges and corals. Depth is the most commonly occurring variable in most models predicting habitat suitability for corals (Davies & Guinotte 2011), in part because of its availability but also because of the relationship of depth to other habitat factors. Other variables, such as temperature, aragonite saturation (Tittensor et al. 2010), water column productivity (Bryan & Metaxas 2007, Tittensor et al. 2010), slope and current (Bryan & Metaxas 2007) have also been found to be important in determining coral presence. These modeling efforts did not have the luxury of the wide variety of location-specific habitat variables, as most were informed through remotely sensed data rather than field observations. We used a combination of remotely sensed data, predictions from oceanographic models and data collected over many years during the trawl survey to inform our models of distribution and abundance of corals and sponges. Because of their slow growth, limited reproductive output and dispersal (Leys & Lauzon 1998, Stone & Wing 2001, Andrews et al. 2002, Leys et al. 2007), we felt that longer term average values for temperature, currents and ocean color were probably more appropriate for modeling coral and sponge distributions, as opposed to short term fluctuations that might be present only ephemerally at each site.

Our model is also different from previous regional-scale modeling efforts in that we predicted presence or absence and abundance as opposed to presence-only models. For deep-water corals, it has been more common to estimate habitat suitability for entire ocean basins (Bryan & Metaxas 2007, Davies et al. 2008, Tittensor et al. 2010, Davies & Guinotte 2011), based on presence data only. Where both presence and absence data are available, as was the case for the present study and other studies using underwater video methodology, standard statistical models predicting the binomial response of presence or absence

may be preferable in predicting the distribution of deep-water invertebrates (Woodby et al. 2009, Kringsman et al. 2012). The studies by Woodby et al. (2009) and Kringsman et al. (2012) were comparable in objectives and statistical methods to our study, although the independent variables were different. Woodby et al. (2009) used backscatter data collected from multi-beam surveys to predict where coral were present or absent. They found that corals and sponges were predictable based on depth, rugosity and slope. Kringsman et al. (2012) used a geological interpretation of substrate type based on multibeam surveys to make predictions about the distribution of corals, hydroids, sea pens and brittlestars. Both these approaches used generalized linear models to characterize the relationships between the binomial presence or absence of coral and substrate characteristics. Our approach was similar, but we used a generalized additive model approach rather than the linear model approach.

Unexplained variability

There was a substantial portion of variance in abundance, presence or absence and diversity of corals unexplained by the best-fitting models. Two contributing factors to the reduced explanatory power of the models could be the necessary lumping of species into taxonomic groups and important but unrepresented variables in the analysis. Because of the previously mentioned difficulties with sponge and coral taxonomy, only major groupings (sponges, corals, Primnoidae and Stylasteridae) were used in the modeling. The use of higher-order taxonomic groupings as dependent variables in spatial models of coral and sponges is not uncommon (Bryan & Metaxas 2007, Woodby et al. 2009, Yesson et al. 2012, Taylor et al. 2013). However, this practice has implications for the resulting models in that species within these groupings undoubtedly vary in terms of their specific life history and habitat requirements. A large portion of the unexplained variability in the best-fitting models may be due to the lumping of species with different habitat requirements into larger taxonomic groups. In this case, better methods for identifying cryptic species and a more fully resolved taxonomy of especially sponges would no doubt result in better model power.

A second source of unexplained variability in the modeling may be due to missing, yet important, variables necessary for predicting coral and sponge spatial distributions. The most important of these missing variables is probably seafloor substrate types. Al-

though the bottom trawl survey data is the most comprehensive data set available for examining the distribution of corals and sponges, it is likely that not all areas within the Aleutians had an equal probability of being sampled in the survey. The bottom trawl used in the Aleutian Islands survey is fairly lightly constructed and as such does not have large tire gear that would enable the gear to be deployed in rough terrain (Stauffer 2004). This limits the data collection to relatively flat smooth seafloor areas. The rocky areas unexamined by the bottom trawl survey are likely to be excellent coral and sponge habitat given the predilection of these groups for hard-bottom seafloor. Maps of substrate types do not currently exist for the Aleutian Islands, but these would certainly improve our ability to predict where corals and sponges occur.

Management implications

Our results clearly demonstrate that current management protects a large fraction of deep-sea coral and sponge in the Aleutian Islands west of Samalga Pass (170°W). For example, in a recent petition to list 44 species of deep-sea coral in Alaska, petitioners indicated that although >950 000 km² had been protected from mobile fishing gear in 2006 (Hourigan 2009), much of this area was 'mudflats' and did not constitute coral habitat. Overall, 46.5% of the Aleutian Islands region of <500 m depth is protected in the 2006 closure. Using the coral presence or absence model developed from trawl survey data, the total area where coral was predicted to be present (in <500 m water depth) is 26158 km². Of this total, 50.7% is protected by the 2006 bottom trawl closures. Using the upper quantile of coral abundance predicted by the model as an indicator of prime coral habitat, 51.0% of prime coral habitat was closed to bottom trawling in 2006. The amount of habitat where sponge is predicted to be present in the Aleutian Islands is 53527 km². Of this total, 45.2% falls within areas closed to bottom trawling. Using the upper quantile of sponge abundance predicted by the model as an indicator of prime sponge habitat, 51.9% of prime sponge habitat was closed to bottom trawling in 2006. In areas where coral diversity is predicted to be > 1 family, 46.9% of the area is protected by the 2006 bottom trawl closure. Thus, the area closures protected ~50% of the total area where coral and sponge were predicted to be present, the prime coral and sponge habitat where abundances are predicted to be high, and the area where diversity of coral families was > 1. Since ~50% of the total

area was protected (46.5%), the closures may have been distributed randomly relative to the distribution coral and sponge. Conversely, ~50% of the area that is currently protected is probably not important coral and sponge habitat, according to the model results. Further evaluation of these models would allow managers to consider trade-offs between protecting coral and sponge and allowing commercial fishing by examining the effect of spatial closures on the amount of coral and sponge habitat that is protected. The model results could potentially be used to create new closures or modify existing closures to maximize the area available to fishing activities while minimizing the potential interactions with deep-sea coral and sponge ecosystems.

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LITERATURE CITED

- Andrews AH, Cordes EE, Mahoney MM, Munk K, Coale KH, Cailliet GM, 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
- Auster PJ, Malatesta RJ, Langton RW, 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. *Rev Fish Sci* 4:185–202
- Baillon S, Hamel JF, Wareham VE, Mercier A (2012) Deep cold-water corals as nurseries for fish larvae. *Front Ecol Environ* 10:351–356
- Beazley LI, Kenchington EL, Murillo FJ, del Mar Sacau M (2013) Deep-sea sponge grounds enhance diversity and abundance of epibenthic megafauna in the Northwest Atlantic. *ICES J Mar Sci* 70:1471–1490
- Behrenfeld MJ, Falkowski PG (1997) Photosynthetic rates derived from satellite-based chlorophyll concentration. *Limnol Oceanogr* 42:1–20
- Bell J, Barnes D, Turner J (2002) The importance of micro and macro morphological variation in the adaption of a sublittoral demosponge to current extremes. *Mar Biol* 140:75–81
- Boldt JL, Buckley TW, Rooper CN, Aydin K (2012) Factors influencing cannibalism and abundance of walleye pollock (*Theragra chalcogramma*) on the eastern Bering Sea shelf, 1982–2006. *Fish Bull* 110:293–306
- Bryan TL, Metaxas A (2007) Predicting suitable habitat for deep-water gorgonian corals on the Atlantic and Pacific Continental Margins of North America. *Mar Ecol Prog Ser* 330:113–126
- Busby MS, Orr JW, Blood DM (2006) Eggs and late-stage embryos of *Allocareproctus unangas* (family Liparidae) from the Aleutian Islands. *Ichthyol Res* 53:423–426
- Ciannelli L, Fauchald P, Chan KS, Agostini VN, Dingsør GE (2008) Spatial fisheries ecology: recent progress and future prospects. *J Mar Syst* 71:223–236
- Cimberg RL, Gerrodette T, Muzik K (1981) Habitat requirements and expected distribution of Alaska coral. Final Report, Research Unit 601, VTN Oregon, US Dept Commerce, NOAA, OCSEAP Final Report 54 (1987):207–308
- Danielson S, Curchitser E, Hedstrom K, Weingartner T, Stabeno P (2011) On ocean and sea ice modes of variability in the Bering Sea. *J Geophys Res* 116:C12034, doi: 10.1029/2011JC007389
- Davies AJ, Guinotte JM (2011) Global habitat suitability for framework-forming cold-water corals. *PLoS One* 6:e18483
- Davies AJ, Wisshak M, Orr JC, Roberts JM (2008) Predicting suitable habitat for the cold-water coral *Lophelia pertusa* (Scleractinia). *Deep-Sea Res I* 55:1048–1062
- DeLong ER, DeLong DM, Clarke-Pearson DL (1988) Comparing the areas under two or more correlated receiver operating characteristic curves: a nonparametric approach. *Biometrics* 44:837–845
- Denis V, Lejeune J, Robin JP (2002) Spatio-temporal analysis of commercial trawler data using general additive models: patterns of Loliginid squid abundance in the north-east Atlantic. *ICES J Mar Sci* 59:633–648
- Egbert GD, Erofeeva SY (2002) Efficient inverse modeling of barotropic ocean tides. *J Atmos Ocean Technol* 19:183–204
- Elith J, Leathwick JR (2009) Species distribution models: ecological explanation and prediction across space and time. *Annu Rev Ecol Evol Syst* 40:677–697
- ESRI (Environmental Systems Research Institute) (2009) ArcGIS Desktop: release 9.2. Environmental Systems Research Institute, Redlands, CA
- Freese JL (2001) Trawl-induced damage to sponges observed from a research submersible. *Mar Fish Rev* 63:7–13
- Gotelli NJ (1988) Determinants of recruitment, juvenile growth, and spatial distribution of a shallow-water gorgonian. *Ecology* 69:157–166
- Hastie TJ, Tibshirani RJ (1990) Generalized additive models. Chapman & Hall, London
- Heifetz J (2002) Coral in Alaska: distribution, abundance, and species associations. *Hydrobiologia* 471:19–28
- Heifetz J, Wing BL, Stone RP, Malecha PW, Courtney DL (2005) Corals of the Aleutian Islands. *Fish Oceanogr* 14: 131–138
- Heifetz J, Stone RP, Shotwell SK (2009) Damage and disturbance to coral and sponge habitat of the Aleutian Archipelago. *Mar Ecol Prog Ser* 397:295–303
- Henry LA, Navas JM, Hennige SJ, Wicks LC, Vad J, Roberts JM (2013) Cold-water coral reef habitats benefit recreationally valuable sharks. *Biol Conserv* 161:67–70
- Hosmer DW, Lemeshow S (2005) Assessing the fit of the model in applied logistic regression, 2nd edn. John Wiley & Sons, Hoboken, NJ
- Hourigan TF (2009) Managing fishery impacts on deep-water coral ecosystems of the USA: emerging best practices. *Mar Ecol Prog Ser* 397:333–340
- Jenness J (2013) DEM Surface Tools for ArcGIS (surface_area.exe). Jenness Enterprises, Flagstaff, AZ, available at www.jennessent.com/arcgis/surface_area.htm
- Kim K, Lasker HR (1997) Flow-mediated resource competition in the suspension feeding gorgonian *Plexaura homomalla* (Esper). *J Exp Mar Biol Ecol* 215:49–64
- Knapp KA, Matthews KR, Preisler HK, Jellison R (2003) Developing probabilistic models to predict amphibian site occupancy in a patchy landscape. *Ecol Appl* 13: 1069–1082

- Krieger KJ (2001) Coral (*Primnoa*) impacted by fishing gear in the Gulf of Alaska. In: Willison JHM, Hall J, Gass SE, Kenchington ELR, Butler M, Doherty P (eds) Proceedings of the first international symposium on deep-sea corals. Ecology Action Centre, Dalhousie University and Nova Scotia Museum, Halifax, p 106–116
- Krieger KJ, Wing BL (2002) Megafauna associations with deepwater corals (*Primnoa* spp.) in the Gulf of Alaska. *Hydrobiologia* 471:83–90
- Krigsman LM, Yoklavich MM, Dick EJ, Cochrane GR (2012) Models and maps: predicting the distribution of corals and other macro-invertebrates in shelf habitats. *Ecosphere* 3:art3
- Ladd C, Hunt GL Jr, Mordy CW, Salo SA, Stabeno PJ (2005) Marine environment of the eastern and central Aleutian Islands. *Fish Oceanogr* 14:22–38
- Leys SP, Lauzon NRJ (1998) *Hexactinellid* sponge ecology: growth rates and seasonality in deep water sponges. *J Exp Mar Biol Ecol* 230:111–129
- Leys SP, Mackie GO, Reiswig HM (2007) The biology of glass sponges. *Adv Mar Biol* 52:1–245
- Logerwell EA, Aydin K, Barbeaux S, Brown E and others (2005) Geographic patterns in the demersal ichthyofauna of the Aleutian Islands. *Fish Oceanogr* 14:93–112
- Malecha PW, Stone RP, Heifetz J (2005) Living substrate in Alaska: distribution, abundance and species associations. *Am Fish Soc Symp* 41:289–299
- Marliave JB, Conway KW, Gibbs DM, Lamb A, Gibbs C (2009) Biodiversity and rockfish recruitment in sponge gardens and bioherms of southern British Columbia, Canada. *Mar Biol* 156:2247–2254
- NRC (National Research Council) (2002) Effects of trawling and dredging on seafloor habitat. National Academy Press, Washington, DC
- Politou CY, Tserpes G, Dokos J (2008) Identification of deep-water pink shrimp abundance distribution patterns and nursery grounds in the eastern Mediterranean by means of generalized additive modeling. *Hydrobiologia* 612:99–107
- Rice AL, Thurston MH, New AL (1990) Dense aggregations of the *hexactinellid* sponge, *Pheronema carpentier*, in the Porcupine Sea bight (northeast Atlantic Ocean), and possible causes. *Prog Oceanogr* 24:179–196
- Roberts JM, Wheeler AJ, Friewald A (2006) Reefs of the deep: the biology and geology of cold-water coral ecosystems. *Science* 312:543–547
- Rooper CN, Boldt JL (2005) Distribution of juvenile Pacific ocean perch (*Sebastes alutus*) in the Aleutian Islands in relation to benthic habitat. *Alsk Fish Res Bull* 11:102–112
- Ryer CH, Stoner AW, Titgen RH (2004) Behavioral mechanisms underlying the refuge value of benthic habitat structure for two flatfishes with differing anti-predator strategies. *Mar Ecol Prog Ser* 268:231–243
- Shono H (2008) Application of the Tweedie distribution to zero-catch data in CPUE analysis. *Fish Res* 93:154–162
- Stabeno PJ, Schumacher JD, Ohtani K (1999) The physical oceanography of the Bering Sea. In: Loughlin TR, Ohtani K (eds) Dynamics of the Bering Sea: a summary of physical, chemical, and biological characteristics, and a synopsis of research on the Bering Sea. North Pacific Marine Science Organization (PICES), University of Alaska Sea Grant, AK-SG-99-03, Fairbanks, AK, p 1–59
- Stabeno PJ, Reed RK, Napp JM (2002) Transport through Unimak Pass, Alaska. *Deep-Sea Res II* 49:5919–5930
- Stauffer G (2004) NOAA protocols for groundfish bottom trawl surveys of the nation's fishery resources. US Dept Commerce, NOAA Tech Memo NMFS-F/SPO-65
- Stone RP (2006) Coral habitat in the Aleutian Islands off Alaska: depth distribution, fine-scale species associations, and fisheries interactions. *Coral Reefs* 25:229–238
- Stone RP, Shotwell SK (2007) State of deep coral ecosystems in the Alaska Region: Gulf of Alaska, Bering Sea and Aleutian Islands. In: Lumsden SE, Hourigan TF, Bruckner AW, Dorr G (eds) The state of deep coral ecosystems of the United States. US Dept Commerce, NOAA Tech Memo CRCP-3, p 65–108
- Stone R, Wing B (2001) Growth and recruitment of an Alaskan shallow water gorgonian. In: Willison JHM, Hall J, Gass SE, Kenchington ELR, Butler M, Doherty P (eds) Proceedings of the first international symposium on deep-sea corals. Ecology Action Centre, Dalhousie University and Nova Scotia Museum, Halifax, p 88–94
- Stone RP, Lehnert H, Reiswig H (2011) A guide to the deep-water sponges of the Aleutian Island Archipelago. US Dept Commerce, NOAA Professional Paper, NMFS-12
- Swartzman G, Huang C, Kaluzny S (1992) Spatial analysis of Bering Sea groundfish survey data using generalized additive models. *Can J Fish Aquat Sci* 49:1366–1378
- Taylor ML, Yesson C, Agnew DJ, Mitchell RE, Rogers AD (2013) Using fisheries by-catch data to predict octocoral habitat suitability around South Georgia. *J Biogeogr* 40: 1688–1701
- Tissot BN, Yoklavich MM, Love MS, York K, Amend M (2006) Benthic invertebrates that form habitat structures on deep banks off southern California, with special reference to deep sea coral. *Fish Bull* 104:167–181
- Tittensor DP, Baco AR, Hall-Spencer JM, Orr JC, Rogers CAD (2010) Seamounts as refugia from ocean acidification for cold-water stony corals. *Mar Ecol* 31:212–225
- van Dolah RF, Wendt PH, Nicholson N (1987) Effects of a research trawl on a hard-bottom assemblage of sponges and corals. *Fish Res* 5:39–54
- van Oevelen D, Duineveld G, Lavaleye M, Soetaert K, Heip CHR (2009) The cold-water coral community as a hot spot for carbon, cycling on continental margins: a food web analysis from Rockall Bank (northeast Atlantic). *Limnol Oceanogr* 54:1829–1844
- Venables WN, Ripley BD (2002) Modern applied statistics with S, 4th edn. Springer Science+Business Media, New York, NY
- von Szalay PG, Raring NW, Shaw FR, Wilkins ME, Martin MH (2010) Data report: 2009 Gulf of Alaska bottom trawl survey. US Dept Commerce, NOAA Tech Memo NMFS-AFSC-208
- von Szalay PG, Rooper CN, Raring NW, Martin MH (2011) Data report: 2010 Aleutian Islands bottom trawl survey. US Dept Commerce, NOAA Tech Memo NMFS-AFSC-215
- White M (2003) Comparison of near seabed currents at two locations in the Porcupine Sea Bight—implications for benthic fauna. *J Mar Biol Assoc UK* 83:683–686
- Wing BL, Barnard DR (2004) A field guide to Alaskan corals. US Dept Commerce, NOAA Tech Memo, NMFS-AFSC-146
- Wood SN (2003) Thin-plate regression splines. *J R Stat Soc B* 65:95–114
- Wood SN (2006) Generalized additive models: an introduction with R. Chapman & Hall/CRC Press, Boca Raton, FL
- Woodby D, Carlile D, Hurlburt L (2009) Predictive modeling of coral distribution in the Central Aleutian Islands, USA. *Mar Ecol Prog Ser* 397:227–240
- Yesson C, Taylor ML, Tittensor DP, Davies AJ and others (2012) Global habitat suitability of cold-water octocorals. *J Biogeogr* 39:1278–1292
- Zimmermann M, Prescott MM, Rooper CN (2013) Smooth sheet bathymetry of the Aleutian Islands. US Dep Commerce, NOAA Tech Memo NMFS-AFSC-250