Environmental factors that influence the distribution, size, and biotic relationships of the Christmas tree coral *Antipathes dendrochristos* in the Southern California Bight

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ABSTRACT: The Christmas tree coral *Antipathes dendrochristos* is a recently discovered black coral species that represents a habitat associated with numerous sensitive taxa in the Southern California Bight. We evaluated whether broad-scale oceanographic features influence coral density and size by selecting from among generalized additive models (for density) and generalized linear models (for size) that represented competing hypotheses. We constructed models to predict coral density and size using depth, seafloor slope, surface primary productivity, bottom currents, ocean temperature, salinity, and dissolved oxygen as candidate covariates. Specifically, we evaluated hypothesized links between pelagic production and benthic coral utilization and between bottom currents and larval coral dispersal. Our analysis revealed that high surface primary productivity in combination with depth and January currents are important predictors of Christmas tree coral density. Higher coral density coincided with greater chlorophyll persistence and optimal depths near 400 m. Surface productivity increasingly was associated with Christmas tree corals at shallower depths. Our results supported the hypothesis that ocean currents affect coral density via larval dispersal mechanisms. The selected coral size models responded to similar covariates, corroborating coral density results. Fish and invertebrate ordinations indicated that Christmas tree corals were widely distributed across environmental gradients and that Christmas tree corals co-occurred with several demersal fish and invertebrates. Several predicted coral hotspots remain unprotected from fishing, particularly in areas adjacent to highly populated portions of the Southern California Bight. These regions should be targeted by future studies to confirm the presence of Christmas tree coral communities and to evaluate their vulnerability.

KEY WORDS: Antipatharia · Black corals · Deep sea corals · Cold-water corals · ROMS · Predictive modeling · Indirect gradient analysis

INTRODUCTION

The black corals (order: Antipatharia) represent one of the least studied groups of non-scleractinian corals, and until recently, data regarding their distri-

bution and environmental associations along the continental Pacific coast of North America were largely unavailable (Yoklavich & Love 2005, Tissot et al. 2006, Lundsten et al. 2009). Although cold-water black corals include many commercially valuable

species, they may also occupy important habitats that support a variety of co-occurring taxa (Stone 2006, Bo et al. 2008, 2012). Opresko (2005) recently published a new black coral species description, the Christmas tree coral *Antipathes dendrochristos* (Fig. 1), that was collected from the Southern California Bight. The Christmas tree coral is an uncommon, long-lived, colonial coral that typically supports a diverse biological assemblage and may represent a habitat that is acutely vulnerable to benthic fishing activities and other anthropogenic disturbances (Yoklavich & Love 2005, Tissot et al. 2006, Love et al. 2007).

The distribution and habitat associations of many coral species are poorly understood. Describing these relationships advances progress toward ecosystem-based resource management (Pikitch et al. 2004), marine spatial planning, and sustainable fisheries practices (Crowder et al. 2006, Halpern et al. 2008). This is especially true in the Southern California Bight, which is among the most heavily exploited areas on the west coast of North America for purposes such as commercial shipping, coastal development, recreational boating, fishing, and municipal discharge. However, characterizing cold-water coral habitats is inherently difficult because of the complex nature of marine ecosystems in which multiple factors affect coral–habitat associations, the range of spatial and temporal scales over which habitat

Fig. 1. *Antipathes dendrochristos. In situ* red and white color variants of Christmas tree coral colonies within the Southern California Bight. These coral colonies were found at 300 m depth and were approximately 50 cm tall

features are relevant, and the practical difficulties of sampling deep-sea habitats. Increased use of manned submersibles and remotely operated vehicles to survey deep-sea fisheries habitat has provided unique and valuable data sets that have been gleaned from archived video (Yoklavich & O'Connell 2008). These spatially explicit data include numerous species of fishes and invertebrates, their sizes, densities, and associated habitat components. A challenge in modeling coral distribution and abundance has been the dearth of environmental data that are relevant to corals on a spatial scale needed to characterize components of coral habitat across broad regions. Methodological advances in oceanographic modeling, such as regional oceanographic modeling systems (ROMS), provide environmental parameters near the seafloor that are relevant to benthic species (Shchepetkin & McWilliams 2005). This information is available over a number of time intervals and across expansive seafloor landscapes. Combining visual observations with oceanographic model output or other broad-scale data may greatly contribute to the emerging body of research into regional and global predictive habitat modeling for cold-water corals, many of which remain among the most enigmatic organisms in the deep ocean (Davies & Guinotte 2011, Manderson et al. 2011).

The geographic distribution of Christmas tree corals may be influenced by various habitat features. Hard substratum is a basic requirement that provides an attachment surface, which must be stable in strong currents and large enough to support colonies up to 2.5 m in height. Seafloor slope measurements may distinguish features such as ridges and mounts that are associated with hard substratum. Water temperature is perhaps the most significant feature that influences cold-water coral distribution; species tend to colonize at depths that have an optimal temperature range (Roberts et al. 2009). While the majority of black coral species occur in deep water (down to 8600 m), Christmas tree corals occur shallower from 50 to 860 m (this study). Although direct studies of calcification rates and environmental growth controls are limited, it is likely that food availability also affects the geographic range of corals (Sherwood et al. 2005). Corals in deeper waters that are farther from surface production have been demonstrated to grow more slowly than those in shallow waters closer to the euphotic zone (Roberts et al. 2009). Therefore, habitat features that approximate surface production or link pelagic production to benthic coral consumption may serve as predictors of coral distribution and growth (Frederiksen et al. 1992, Klitgaard et al. 1997, Bryan & Metaxas
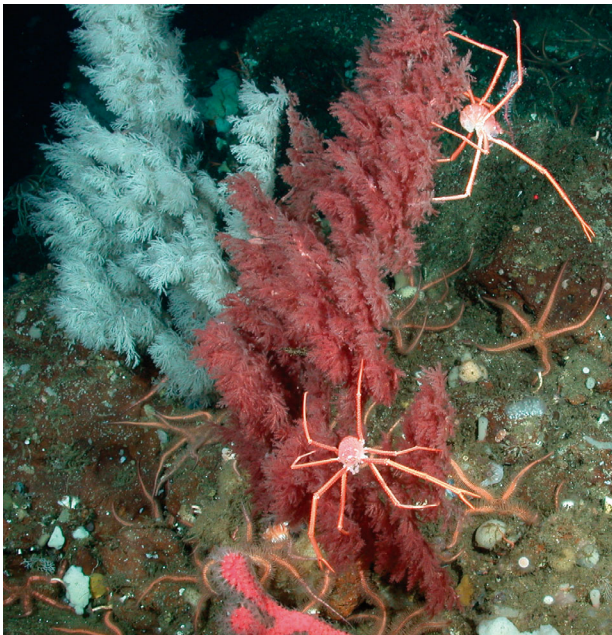
2007). Water currents are also an important environmental factor because they may (1) affect the routes by which the corals receive food particles, (2) prevent fouling of corals with sediment or cause physical damage, and (3) influence larval dispersal and connectivity among suitable habitat patches (Scheltema 1986, White et al. 2005, Davies et al. 2009). Dissolved oxygen and salinity also may affect cold-water coral distributions, but these variables are expected to have less direct impact than the other habitat components because salinity is relatively constant in deep water, and cold-water corals generally are able to tolerate a broad range of oxygen levels (Childress & Seibel 1998). On a global scale, ocean chemistry may control the distribution patterns of cold-water scleractinian corals in particular, relative to the depth of the aragonite saturation horizon (Clark et al. 2006, Guinotte et al. 2006, Yesson et al. 2012).

In the present study, we developed predictive models to geographically delineate areas in the Southern California Bight that coincided with hypothesized Christmas tree coral environmental constraints. We used data on size and density of corals from archived video surveys, together with potentially relevant environmental features that included depth, seafloor slope, surface primary productivity, bottom currents, ocean temperature, salinity, and dissolved oxygen. We modeled the density and size of Christmas tree corals using generalized additive models (GAMs; coral density) and generalized linear models (GLMs; coral size). Specifically, we assessed the support of our statistical models for hypotheses regarding food availability and coral dispersal. We examined response curves derived from selected model covariates, and identified patterns in covariate distributions that were likely to comprise important environmental constraints. We also described some of the biotic associations of Christmas tree corals relative to predictive model covariates by constructing non-metric multidimensional scaling (NMS) plots that depicted benthic community structure in the context of environmental gradients.

MATERIALS AND METHODS

Study area

Our study area in the Southern California Bight lies from just south of Point Conception to San Diego, California, USA (approximately 121° W, 34.5° N to 117° W, 32° N); it encompasses the Channel Islands and numerous ridges and seamounts (Fig. 2). The interior of the Southern California Bight comprises surface water with lower chlorophyll concentrations bounded by frontal regions on the northern and western margins that are adjacent to cooler and more chlorophyll-rich water (Eppley 1992). At the southern boundary of the Bight, a chlorophyll gradient known as the Ensenada Front separates relatively higher chlorophyll waters in the colder water directly to the north of the front and lower chlorophyll waters to the south (Moser & Smith 1993). Wind stress and Ekman transport are minimal in the Bight relative to the rest of the California Current region, and stratification may be substantial in both winter and summer (Husby & Nelson 1982). The areas adjacent to the coast commonly exhibit colder surface water and greater chlorophyll concentrations that are indicative of local upwelling; suspended organic matter concentrations are consistently higher inshore than farther offshore in the Bight (Mullin 1986, Barnett & Jahn 1987). Circulation in the Southern California Bight is generally cyclonic, a result of the interaction between the southeastward California Current and Southern California Countercurrent. However, most of the Bight is characterized by complex current circulation patterns. Large variations in current strength have been observed over the course of weeks to months, and it is possible that during occasional extreme fluctuations the entire Bight could be flushed within a few weeks (Hickey 1992). More than 5000 benthic invertebrate species and approximately 500 fish species inhabit this region, presumably because the Bight comprises ocean conditions representative of both the northern Oregonian and southern San Diegan provinces and because a wide variety of marine habitat types are found in this area (Dailey et al. 1993).

Data sources

We conducted 457 underwater video transect surveys of demersal communities in the Southern California Bight using a manned submersible ('Delta') and a remotely operated vehicle ('Kraken 2') during September and October from 1999 to 2010 (see Tissot et al. 2006 and Love et al. 2009 for details on the 'Delta' survey vehicle and methods). Seafloor maps of substratum types and other past geophysical surveys were used to identify and select locations with rocky habitats (Greene et al. 1999, 2003). Location, habitat features (seafloor depth and substratum type), Christmas tree corals, sponges, other coral taxa, and fishes were recorded and quantified for each 2 m wide
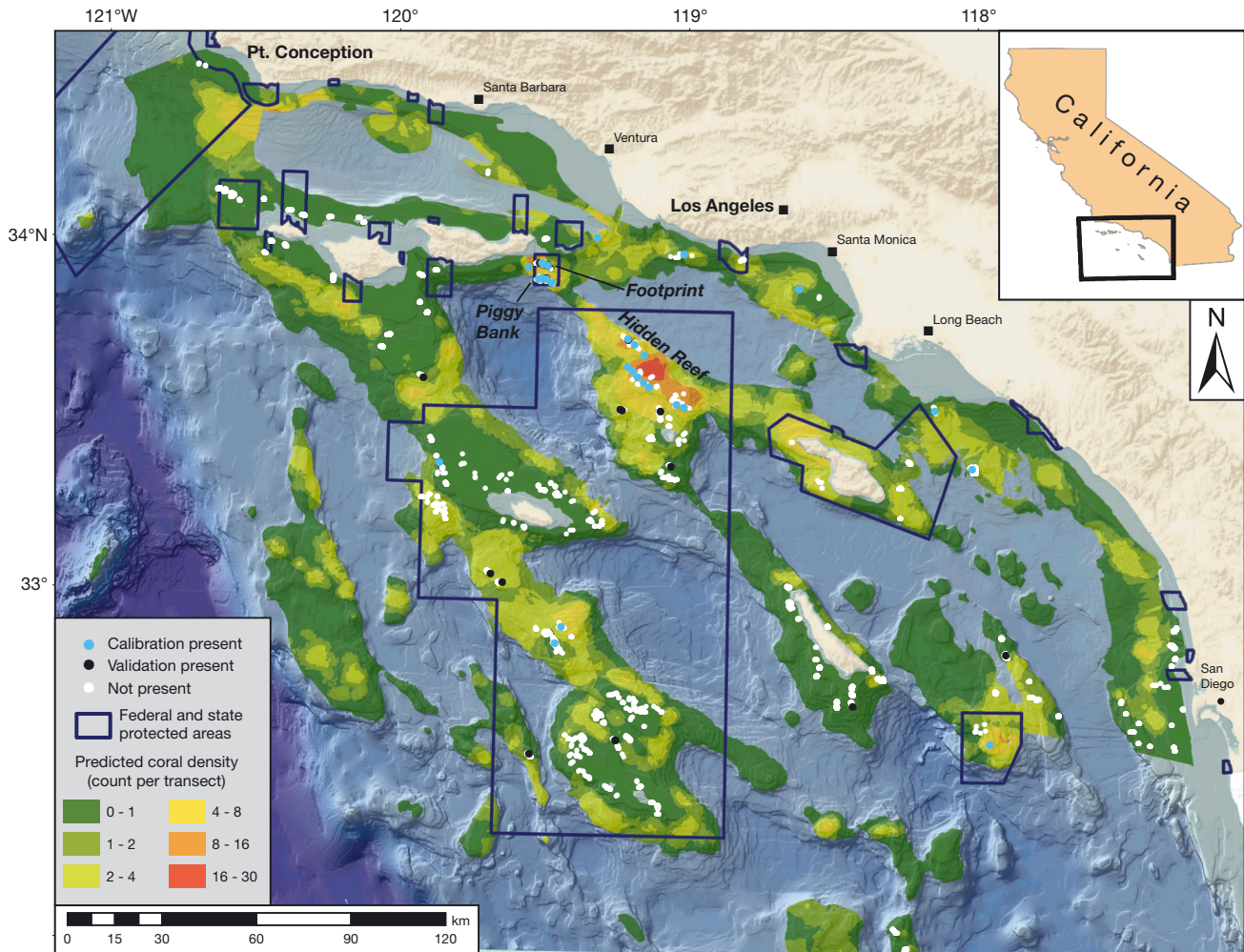
Fig. 2. Study area in the Southern California Bight. Density (coral colonies per transect group) predicted from a generalized additive model, presence and absence from our calibration data set and from a National Ocean Service/National Marine Fisheries Service independent data set of Christmas tree corals, along with boundaries of areas closed to fishing also shown. Mean transect area = 740 m^2

'Delta' and 'Kraken 2' video transect. Transect lengths ranged from 75 to 2334 m, with a mean ± SD transect length of 370 ± 75 m. The proportion of hard substratum type (i.e. isolated high-relief rock pinnacle, rocky outcrop with 30 to 80° relief, flat rock, boulder [>25.5 cm], and cobble [6.5–25.5 cm]) was estimated for each transect. When Christmas tree corals were present and the video frame height and quality were adequate (n = 117 transects), we measured the height of individual Christmas tree coral colonies.

We generated oceanographic potential covariates at seafloor depth for temperature, salinity, dissolved oxygen saturation, and northward (meridional) and eastward (zonal) current velocities from oceanographic models originally developed for the northern Pacific Ocean. The physical model covariates are based on the ROMS (Xiu et al. 2010, Xiu & Chai 2011), and the biogeochemical covariate (oxygen) is based on the Carbon, Si(OH)$_4$, Nitrogen Ecosystem model (CoSiNE; Chai et al. 2002); both models have a horizontal resolution of 0.125° (~14 km). This coupled ROMS-CoSiNE model configuration has been evaluated repeatedly with independent observations throughout the North Pacific (Polovina et al. 2008, Bidigare et al. 2009, Chai et al. 2009, Liu & Chai 2009, Xiu et al. 2012). With the exception of current velocity, oceanographic data were averaged values for 2004 to 2006; for current velocities, we used monthly averaged values for 2004 to 2006. We developed a climatology over a recent 3 yr period for temperature, salinity, and dissolved oxygen for several reasons. First, Christmas tree corals are long-lived and sessile; their size and distribution integrates a complex suite of conditions over the course of their existence (Love

et al. 2007). Therefore, we argue that averaged values for these variables represented the coral colonies' experience more realistically than a snapshot when the sample was taken. Second, conditions near the ocean floor within the California Bight have relatively low variability over time with regard to salinity, temperature, and dissolved oxygen; preliminary analyses indicated that most of the variation in these values occurred spatially. Finally, we chose a recent 3 yr period because it overlaps the data collection time period, encompasses much of the temporal variation, and represents recent conditions that are more relevant to potential management decisions. Alternatively, preliminary analyses indicated that current velocity data varied substantially on a monthly basis. Furthermore, we wished to examine whether the current velocity at a particular time of year would yield an informative covariate for our models, in addition to potentially indicating larval release timing that we may investigate in future studies. ROMS current velocities were not intended to represent fine-scale effects; rather, these values were intended to represent a more general description of current velocity direction and magnitude broadly across a given transect region.

We also examined a metric of surface productivity intended to coarsely represent organic material available to benthic organisms, the chlorophyll persistence index (CPI). CPI data, which quantify chlorophyll *a* variance in terms of the frequency of anomalies that exceed 1 SD from the mean relative to a spatial model for the ecosystem, were obtained from Suryan et al. (2012). Depth and corresponding slope and profile (curvature in the direction of maximum slope) values (using Spatial Analyst; ESRI™ ArcMAP® v.10) were derived from a 90 m resolution digital elevation model downloaded from the NOAA National Geophysical Data Center (Eakins 2003). Spatial data manipulation, tabulation, and interpolation were implemented using ESRI™ ArcMAP® v.10.

Data analysis

Many of the video transects overlapped spatially, and examination of Moran's 'I' plots indicated a highly clumped spatial distribution of Christmas tree corals. Therefore, we combined transects and averaged coral density [count/(transect width × transect length)] and substratum values based on horizontal spatial proximity and depth. We calculated Euclidian distances among transects based on latitude, longitude, and depth ('vegdist' function in R; Oksanen

2004). We grouped transects with hierarchical cluster analysis using Ward's method and cut the tree at 60 groups ('hclust' function in R; Maechler et al. 2012) based on visual examination of the spatial arrangements of the groups and global Moran's test for spatial autocorrelation of both transect locations and coral density simultaneously ('moran.test' function in R; Bivand et al. 2012). We chose the largest number of transect groups (n = 60) which did not exhibit a significantly clustered spatial pattern as our sample units. Of these transect groups, 25 had corresponding coral size data.

We developed predictive models based on the hypothesis that the distribution of Christmas tree corals was largely controlled by environmental factors (Guisan & Zimmermann 2000). Our measured response variables were the density (mean count per transect group area) and size (mean individual colony height per transect group) of Christmas tree corals. We described the relationship of coral density with environmental covariates using GAMs (Hastie & Tibshirani 1990, Wood 2000) because we had an adequate quantity of coral density data for this technique and because GAMs are more flexible and can capture the expected non-linear response of organisms to environmental gradients better than strictly linear methods (Hastie & Tibshirani 1990, Austin 2002). We constructed GAMs ('mgcv' package; Wood 2004) with a quasi-Poisson error distribution to allow for over-dispersion in inferences based on density data and a log link (Godambe & Heyde 1987, Ver Hoef & Boveng 2007).

We developed GLMs (Chambers & Hastie 1993) to describe size–environment relationships because we had fewer size data and because this method is a linear technique that may use fewer data than its nonparametric, data-hungry extension, the GAM. GLMs were developed with a Gaussian error distribution and a log link. We completed both modeling exercises using R software (Version 2.15.1; Ihaka & Gentleman 1996). We selected models based on the lowest values of Akaike's information criterion (AIC) using the 'MuMIn' package (Bartoń 2011). We used *k*-fold cross-validation in which we split the data into equal-sized parts and then iteratively used part of the data to fit the model and a different part to test it (Hastie et al. 2009). We repeated each *k*-fold cross validation process 500 times and examined the distribution of the coefficient of determination and other model evaluation values. We also evaluated the results of our coral density model with an independent presence–absence dataset for the Southern California Bight (P. Etnoyer & K. Stierhoff unpublished data).

We identified groups of covariates that were collinear (|r|< 0.7; Dormann et al. 2013) and then selected the single covariate from each group that had the strongest relationship with the response variable (Christmas tree coral density or size) as determined by non-parametric regression; we chose the single covariates with the greatest leave-one-out jack-knifed coefficient of determination (R^2). We chose candidate covariates from among 3 groups, in addition to CPI, which represented primary productivity at the ocean's surface. The first highly correlated covariate group comprised temperature, oxygen, and salinity. The second covariate group included monthly current components that exhibited a substantial relationship ($R^2 > 0.1$) to the response variable. The third group represented the benthic physical setting and included depth, slope, and profile. Finally, we included an interaction between depth and our productivity covariate (CPI), by which we examined the potential effect of organic particle flux over depth on the response variable (coral size or density). Because each of the candidate covariates had a biologically realistic basis for being considered, we constructed all subsets of the models with 4 or fewer covariates and included the main effects when an interaction was considered. We conducted data exploration by visualizing various characteristics of the datasets approximately following Zuur et al. (2007).

No region-wide datasets of seafloor substratum types were available at the appropriate scale and resolution. We therefore constructed a map of predicted coral density only for areas identified as either 'ridge,' 'shelf,' or 'flank' megahabitat features (Greene et al. 2007). These categories represent physiography and depth on a spatial scale of a few to 10s of kilometers. Ridge habitats are characterized as crests (including seamounts) that are 200 to 2500 m deep, continental and island shelf habitats are 0 to 200 m deep, and flanks are continental slope or basin/island margins that are 200 to 3000 m deep. Christmas tree corals in our database only occurred within these 3 megahabitat categories. We further constrained our model predictions to the depth range (50 to 860 m) of dives in our dataset, and only interpolated predictions within the ranges of the model covariates as determined by standard error estimates (SE = 10) of the predictions.

We described the biotic co-occurrences of Christmas tree corals, in the context of our final model covariates, by constructing NMS plots (Kruskal 1964, Mather 1976) implemented with PC-ORD software (McCune & Mefford 2006) and overlaid with environmental gradient contours. We positioned individual samples by average Bray-Curtis dissimilarity dis-

tances (Bray & Curtis 1957) according to covariation and association among fish and invertebrate taxa. We began with a random initial starting configuration and determined the appropriate number of dimensions for the best ordination by examining stress versus dimension plots. We determined the best solution when the standard deviation in stress over the preceding 10 iterations reached 1×10^{-5}. Individual taxa were plotted in ordination space by calculating a weighted average for each taxon across all of the sites' scores. We performed an indirect gradient analysis of the relationship among taxa and model covariates, representing each habitat variable as a contour gradient overlaid on top of the previously constructed NMS ordination plot (Virtanen et al. 2006, Salemaa et al. 2008, Huff et al. 2011) using R software (Ihaka & Gentleman 1996, Oksanen 2004). We constructed habitat variable contours with non-parametrically smoothed surfaces that were fitted from GAMs (Gaussian error distribution with identity link) with thin plate splines (Wood 2000). The degree of smoothing was determined using cross-validated R^2 to determine goodness-of-fit. We tested the significance of each environmental gradient contour surface with an ANOVA.

RESULTS

Coral observations

Christmas tree corals were present at 27 of 60 transect groups. We observed corals at depths that ranged from 58 to 914 m and at densities from 1 colony per 10 transects (0.003 colonies m^{-2}) to 24 colonies per transect (0.446 colonies m^{-2}). Coral colonies were always attached to some hard substrate. Transect groups ranged from 1 to 100% hard substrate, and the median value for our observations was 63%. Summary statistics for Christmas tree coral observations and model covariates for transects where corals were present are displayed in Table 1.

Predicting coral density: GAM

We examined boxplots of median and quartile monthly modeled velocities of bottom currents (both eastward and northward components) at locations where Christmas tree corals were present or absent and corresponding bar plots that indicate the strength of the current–coral relationship (Fig. 3). Bottom currents were weaker at locations where corals were

Table 1. *Antipathes dendrochristos.* Summary statistics for Christmas tree coral observations and model covariates for transects where corals were present

| Statistic	Mean	SD	Minimum	Median	Maximum	Resolution
Colonies per transect	4.9	7.4	0.1	1.6	24.0	Transect
Coral colony height (cm)	47	52	10	30	262	Transect
Colonies m^{-2}	0.061	0.081	0.003	0.026	0.446	Transect
Percent hard substrate	57	30	1	63	100	Transect
Depth (m)	228	153	58	183	914	90 m
Temperature (°C)	8.0	1.2	4.9	8.4	9.6	0.125°
Chlorophyll persistence index	17	2	13	17	20	0.125°
Northward current (m s^{-1})	0.001	0.006	−0.005	0.000	0.014	0.125°
Eastward current (m s^{-1})	−0.001	0.012	−0.024	0.000	0.013	0.125°
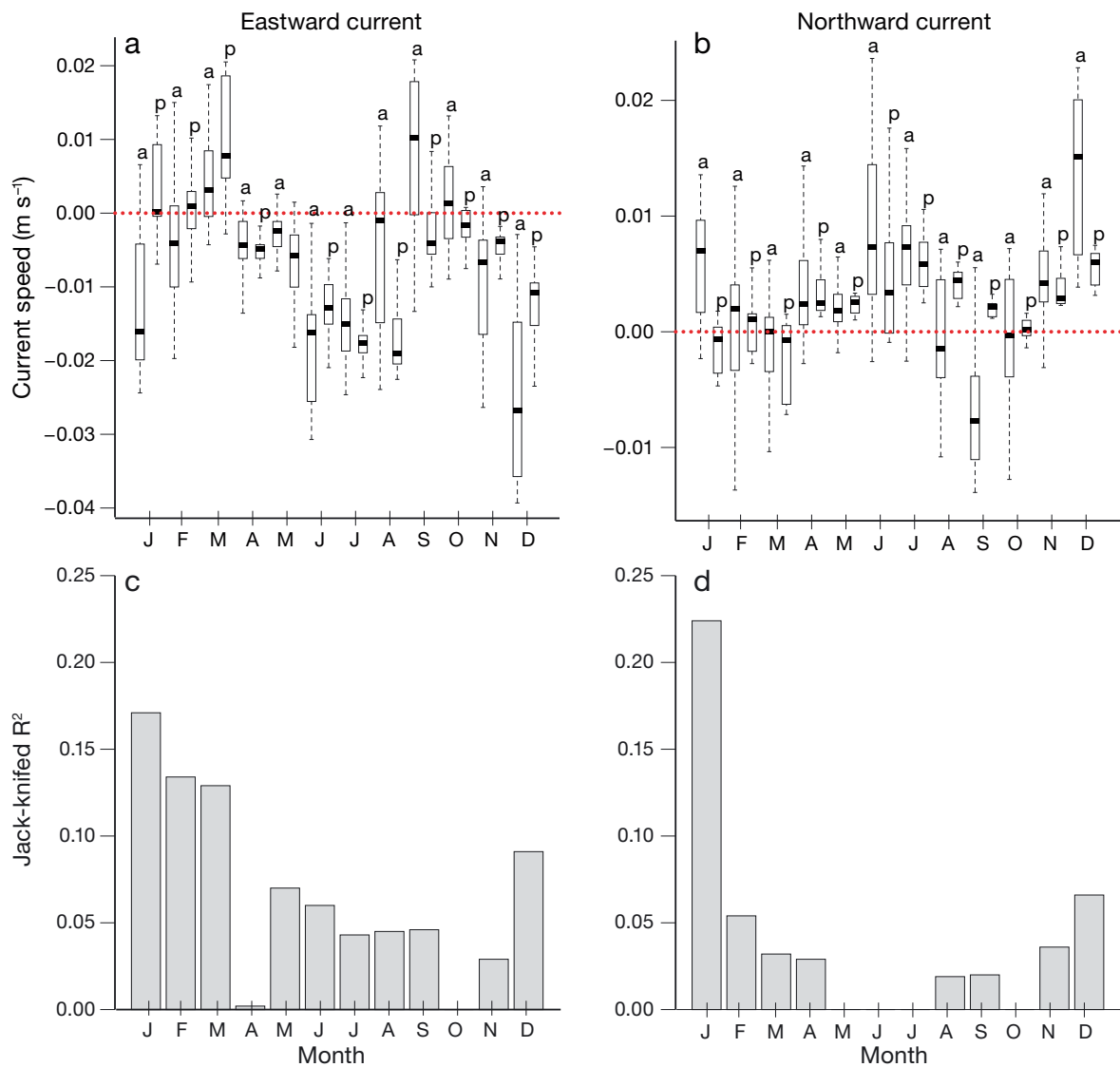
Fig. 3. Monthly (a) eastward and (b) northward bottom current velocities. Each monthly pair is labeled 'a,' indicating samples (n = 33) in the dataset where Christmas tree corals were absent and 'p,' indicating samples (n = 27) where Christmas tree corals were present each month. Black bar = median, box = quartiles, whiskers = range. (c,d) Bar-plots represent leave-one-out jack-knifed R^2 values for the non-parametric regressions between Christmas tree coral quantity and current velocities for each month

present than at locations where corals were absent. For both eastward and northward current components, the current–coral relationship was strongest in January ($R^2 = 0.17$ and 0.23, respectively), and median northward current velocity in January was near 0 m s^{-1} at locations where corals were present and 0.007 m s^{-1} where corals were absent. Modeled water temperatures at the seafloor were warmest during January (mean ± SE = 7.7 ± 0.19°C) when the coral–current relationship was strongest.

After we removed collinear covariates from the analysis, temperature, January northward current velocity (Jan North), CPI, and depth remained as candidates in the selection process for our model to predict coral density. A GAM that included Depth, Jan North, CPI, Temperature, and the interaction Depth × CPI ranked highest ($w_i = 0.69$) out of the 20 models that were constructed from all possible subsets of the candidate variables that included both main effects with an interaction present (Table 2). The final model accounted for 88.4% of the deviance in coral density and had a mean $R^2 = 0.51$ for 500 runs of 10-fold cross-validation.

The Depth response curves (Fig. 4a) indicated that there was a greater density (coral colonies per transect group area) of Christmas tree corals at higher (third quartile) CPI values across the same depth range than at lower (first quartile) CPI values. Mid-range depths (300–500 m) had the highest modeled coral density. There was a deeper optimum depth range and greater coral density at high CPI values over the same depth values (Fig. 4a). The CPI

response curve indicated generally increasing coral quantity with greater values of CPI (Fig 4b). The Jan North velocity response curve was unimodal (Fig. 4c), centered around 0 m s^{-1} (northward), and was consistent with the coral–current relationships identified in Fig. 3. The Temperature response curve was unimodal with the greatest density of corals centered about 8.5°C.

Predicting coral size: GLM

After we removed collinear covariates from the analysis, Temperature, January eastward current velocity (Jan East), August eastward current velocity (Aug East), CPI, and Depth remained as candidates in the selection process for a model to predict coral size. A GLM that included Depth, CPI, Jan East, Temperature, and the interaction Depth × CPI ranked highest ($w_i = 0.40$) out of the 40 models that were constructed from all possible subsets of the candidate variables (Table 1). The final model accounted for 89.8% of the deviance in the coral size dataset, with the greatest deviance reduction attributed to CPI and Depth (Table 3). The final GLM had a mean $R^2 = 0.40$ for 500 runs of 5-fold cross-validation.

The largest coral colonies were predicted at shallower depths (Fig. 5a), and coral size increased with increasing CPI values (Fig. 5b). The Jan East response curve exhibited decreasing coral size as the eastward component of the current velocity in January increased (Fig. 5c), and coral size decreased with increasing mean temperatures (Fig. 5d). There was an increasing trend in coral size with increasing CPI over similar depths (Fig. 5a) and greater coral sizes at shallower depths (first quartile of depth) versus deeper depths (third quartile of depth) over similar CPI values (Fig. 5b).

Mapping coral distribution and environmental covariates

Areas within the Southern California Bight that have the highest predicted densities of Christmas tree corals also have relatively weak modeled current velocities during January (Fig. 6a). CPI values (Fig. 6b)
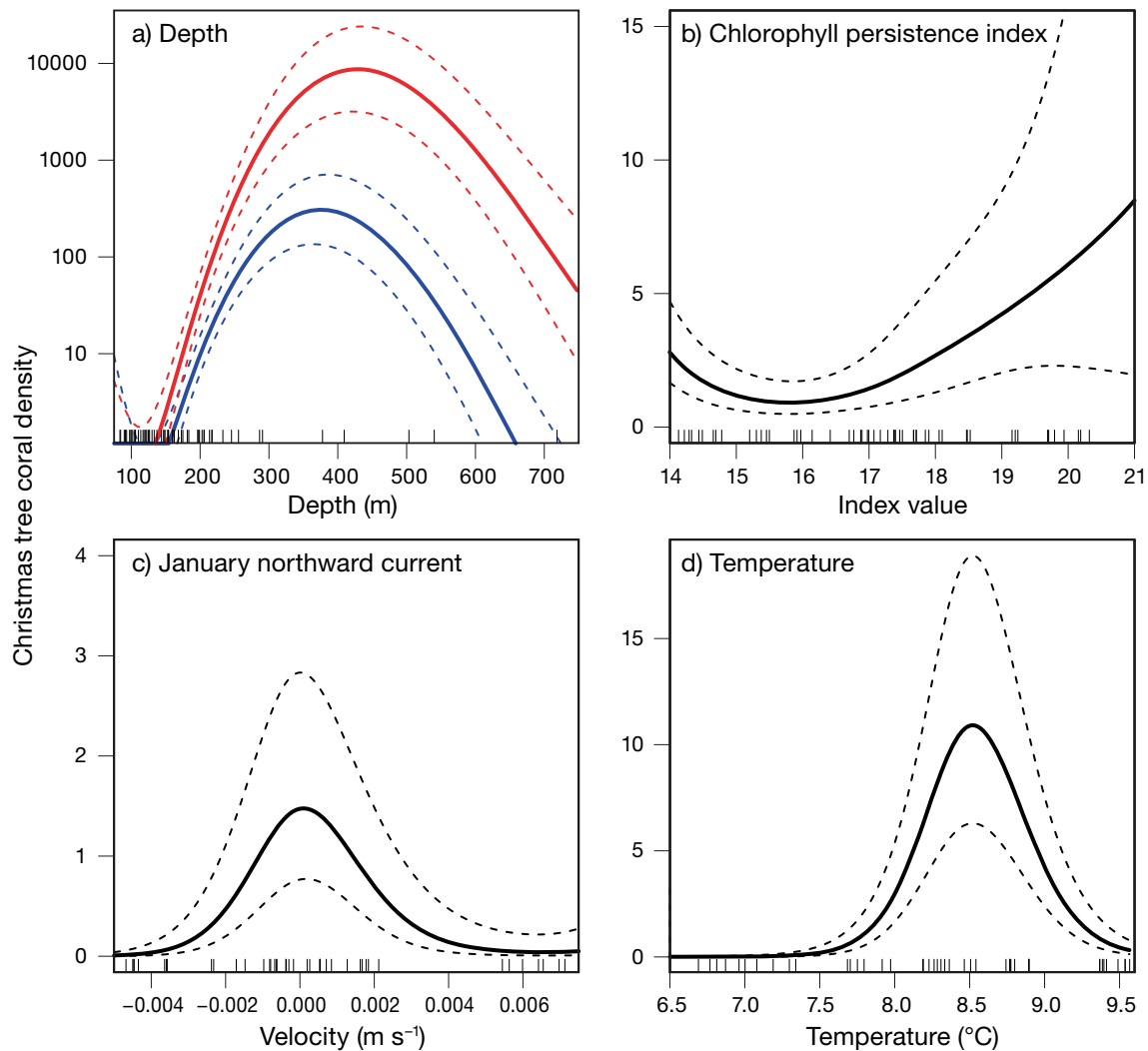
Table 2. *Antipathes dendrochristos*. Results of model selection examining environmental features that influence the density and size of Christmas tree corals in the Southern California Bight. Models are ranked by Akaike's information criterion (AIC) and Akaike weights (w_i) with either quasi-AIC (coral density models; ΔQAIC) or corrected for small sample size (coral size models; ΔAIC$_c$). Only the top sequential models representing nearly all of the weight for each response are included. Coral density was predicted with generalized additive models (GAMs) using a quasi-Poisson error distribution and a log link. Coral size was predicted with general linear models (GLMs) using a Gaussian error distribution and log link. CPI: chlorophyll persistence index

Model effects	w_i	ΔQAIC or ΔAIC$_C$
Coral density (GAMs)		
Depth + CPI + Depth×CPI + Jan North Current + Temperature	0.69	0
Depth + CPI + Jan North Current + Temperature	0.26	1.9
Depth + CPI + Depth×CPI + Temperature	0.05	5.4
Coral size (GLMs)		
Depth + CPI + Depth×CPI + Jan East Current + Temperature	0.40	0
Depth + CPI + Depth×CPI + Temperature	0.22	1.2
Depth + CPI + Jan East Current + Temperature	0.15	2.0

Fig. 4. *Antipathes dendrochristos.* Response curves for the generalized additive model-predicted density (coral colonies per transect group) of Christmas tree corals versus (a) depth, (b) chlorophyll persistence index (CPI), (c) January northward current, and (d) temperature. Solid lines represent the mean and dashed lines represent 1 SE from the mean. For (a) depth plots, velocity and temperature were held at the median value and curves are displayed for the first and third quartiles of CPI (15.3 [blue] and 17.9 [red], respectively). For the (b) CPI, (c) January northward current, and (d) temperature plots, all other covariates were held at median values. Rug plots along the *x*-axis indicate observed data points

Table 3. *Antipathes dendrochristos.* Analysis of deviance for the generalized linear model for size response of Christmas tree corals. Terms added sequentially in the order they occur in the table. CPI: chlorophyll persistence index; Jan East: January eastward current

Model	Deviance reduction	Residual df	Residual deviance
Null		24	64 097
CPI	23 633	23	40 464
Depth	20 907	22	19 558
Jan East	3587	21	15 971
Temperature	7720	20	8251
Depth×CPI	1734	19	6517

were greatest in the northwest portion of the study area and decreased along a southward-inshore gradient throughout the Bight. There was a relatively uniform gradient of high-to-low seafloor temperature from inshore to offshore throughout the Bight (Fig. 6c). Relatively high densities (hotspots) of Christmas tree corals were predicted to occur on various banks throughout the Bight, but were more concentrated in the north and in several near-shore areas from Point Conception to San Diego. The most substantial predicted hotspots of coral density occurred on Piggy Bank and Footprint Seamounts and near Hidden Reef (Fig. 2).
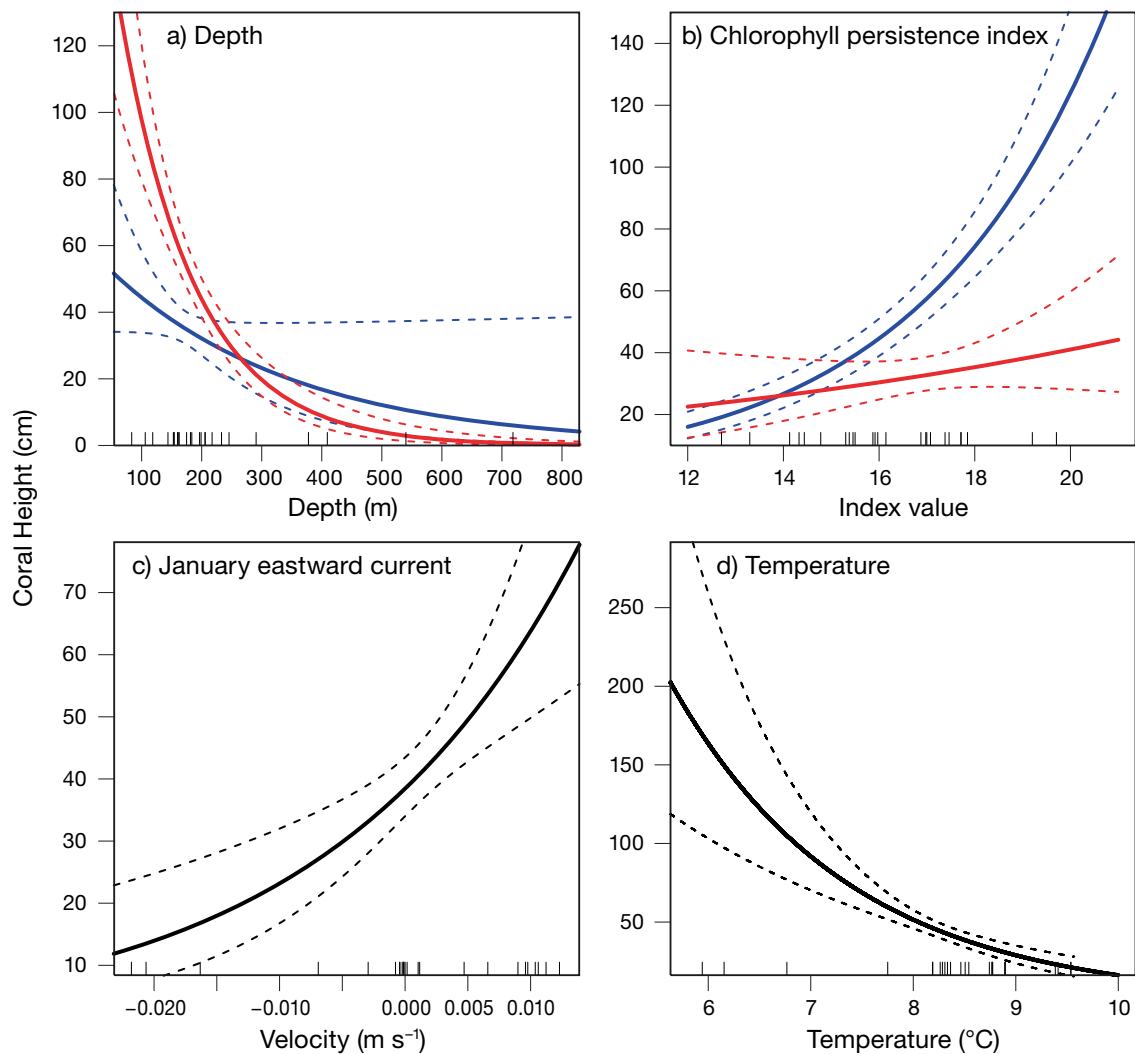
Fig. 5. *Antipathes dendrochristos.* Response curves for the generalized linear model-predicted size of Christmas tree corals versus (a) depth, (b) chlorophyll persistence index (CPI), (c) January eastward current, and (d) temperature. Solid lines represent the mean and dashed lines represent 1 SE from the mean. For (a) depth and (b) CPI plots, velocity and temperature were set at median values and curves are displayed for the first and third quartiles of CPI (15.3 [blue] and 17.9 [red], respectively) for the depth response curve, and depth (112 m [blue] and 204 m [red], respectively) for the CPI response curve. For (c) January eastward current and (d) temperature, all other covariates were set at median values. Rug plots along the *x*-axis indicate calibration data points

An independent data set (from the National Ocean Service and the National Marine Fisheries Service Southwest Fisheries Science Center) of the presence and absence of Christmas tree corals validated the major coral hotspots predicted by the coral density model. We grouped independent validation data into 15 samples by location and depth, in the same way that our model calibration data were grouped, and made predictions for the sample locations. Thirteen out of 15 of the presence records in the validation dataset coincided with model predictions >1 coral colony per transect (740 m^2). The predictive capabil-

ity of our model declined in the southern offshore areas where we did not survey. In the independent validation data set, 2 Christmas tree corals occurred in the southern offshore areas but were predicted to occur at <1 coral colony per 740 m^2.

Biotic associations

Based on the results from our NMS analysis, the relationship of Christmas tree coral colonies to 85 fish and other invertebrate taxa from 47 transect groups
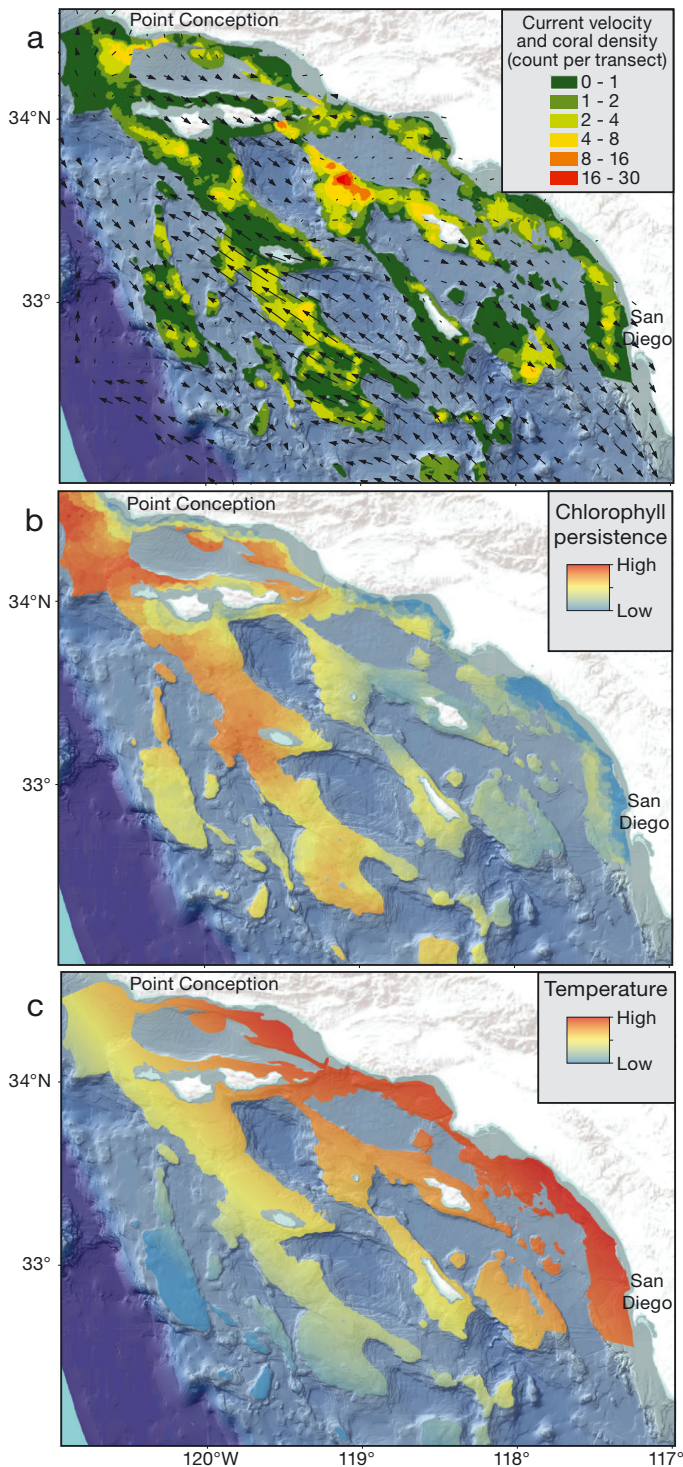
Fig. 6. *Antipathes dendrochristos.* Spatial distribution of model covariates and the predicted density (coral count per transect) of Christmas tree corals throughout the Southern California Bight. (a) Arrows represent the magnitude and direction of modeled current velocity near the seafloor in January (min. = 0 m s^{-1}, max. = 0.3 m s^{-1}), (b) predicted chlorophyll persistence index (min. = 2.4, max. = 24.4), (c) predicted seafloor temperature (min. = 1.9°C, max. = 10.0°C)

was described in the context of the final GAM covariates and the proportion of hard substratum per sample unit (Appendix 1). We chose a 2-dimensional solution for the NMS plot by examining scree plots, and Monte Carlo runs resulted in a p-value of 0.004, suggesting that the final stress value had a low probability of random occurrence (McCune et al. 2002). Stress for the final solution was 14 (after 83 iterations). The proportion of variance represented by 2 axes between the original distance matrix and the ordination distances was $R^2 = 0.75$, and the orthogonality $[100(1 - R^2$ of axis pair)] of axes 1 and 2 was 99.2%.

Benthic assemblage structure varied extensively over the environmental gradients. Weighted-average NMS scores for 47 representative taxa (out of 85) were plotted in the original sample ordination space (Fig. 7). Christmas tree corals were positioned centrally in the NMS plots relative to the other taxa and occurred at the approximate median of the environmental gradients. In general, fish and invertebrate taxa separated along the horizontal axis in each covariate plot. The distribution of Christmas tree corals was centered at 250 m depth (Fig. 7a), along with a variety of rockfishes (e.g. greenblotched and bronzespotted) and sponges (e.g. barrel and branching). Christmas tree corals were associated with relatively high proportions of hard substratum (70−80%; Fig. 7b), but not as strongly as many sponge taxa were (e.g. foliose, shelf, and branching sponges occurred in samples with 90% hard substratum). Fewer taxa occurred in samples with relatively low proportions of hard substratum. The CPI gradient (Fig. 7c) was approximately orthogonal with the depth gradient (Fig. 7a), and greater CPI values were associated with benthic invertebrates rather than fish taxa (particularly at deeper depths). Christmas tree corals were situated near the 0 velocity of the northward seafloor current in January (Fig. 7d), in accordance with results from the best coral density GAM.

DISCUSSION

Our analysis revealed that ocean currents and regions of relatively high surface primary productivity, especially in combination with depth, are important predictors of Christmas tree coral density. We included the CPI covariate to represent a coarse proxy for the amount of food (organic material) available to benthic organisms over a large temporal scale because the abundance and size of these long-lived corals may reflect climate-driven patterns in their
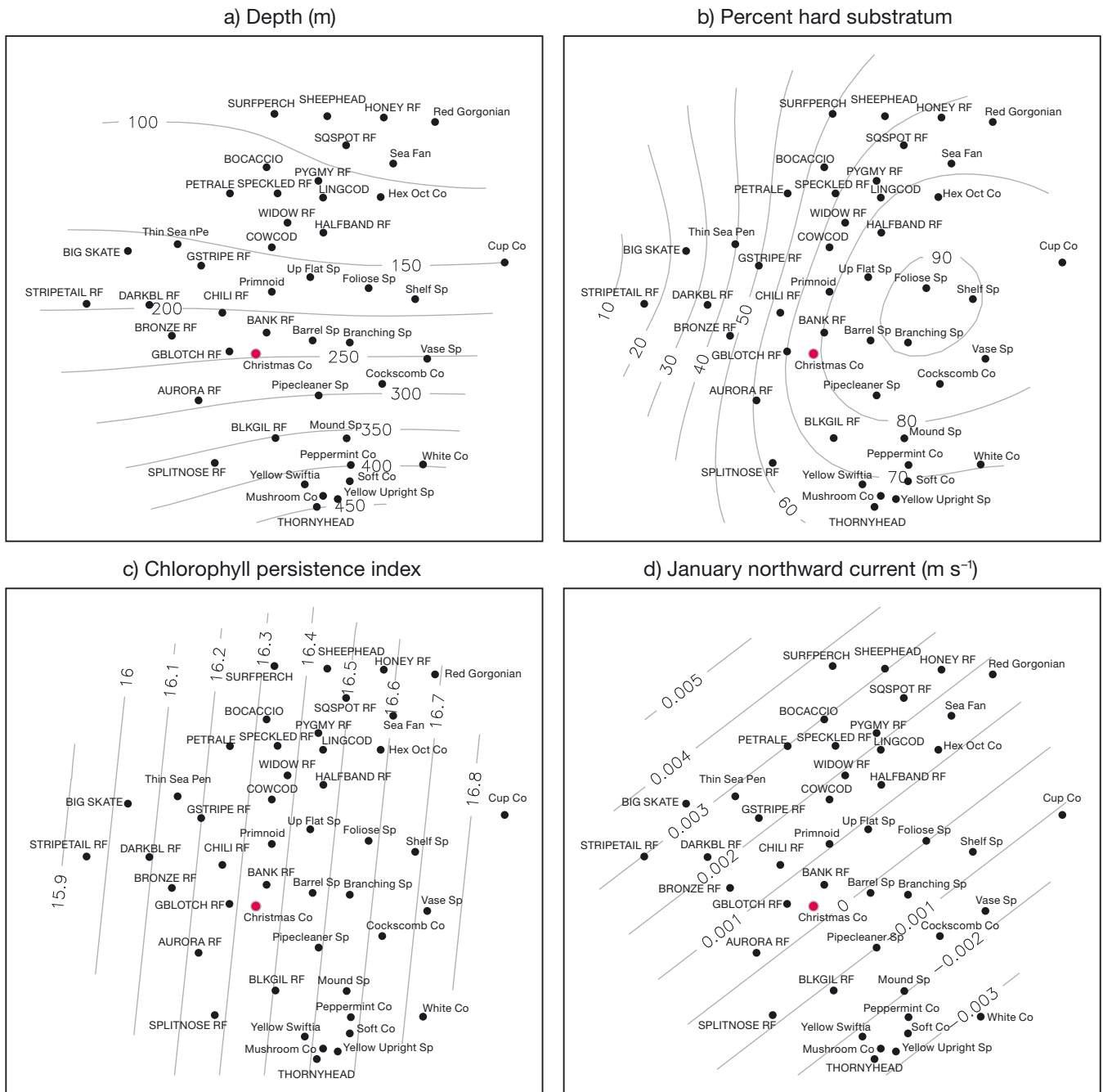
Fig. 7. Non-metric multidimensional scaling plots based on the Bray-Curtis distances among sample transects. Each panel contains the identical taxon constellation (Christmas tree coral depicted in red) with a different fitted contour surface for covariates in the coral density GAM: (a) depth, (b) percent hard substratum (rock, pinnacle, flat rock, boulder, and cobble) per transect, (c) chlorophyll persistence index, and (d) January northward current. Only 47 of 85 taxa are displayed to improve the readability of the plots; the complete list of taxa is available in Appendix 1

food supply (Smith et al. 1994, Ruhl & Smith 2004, Suryan et al. 2012). The cold-water coral *Lophelia pertusa* subsists on phytoplankton delivered from primary productivity near the surface (Duineveld et al. 2004, 2007, 2012), and phytoplankton and detritus may be consumed by antipatharians as well (Wagner

et al. 2012). The modeled interaction of CPI with depth supports our hypothesis that areas with persistent levels of surface productivity have a more tenuous connection to benthic organisms (e.g. Christmas tree corals) at greater depths than those closer to the surface. Depth, by itself, may act as a surrogate for

any number of other correlated factors that have physiological consequences, such as temperature, oxygen, salinity, and aragonite or calcite saturation. However, depth is easily measured, and such data may be more reliably accurate and available than those of other modeled habitat features. Finally, seafloor currents at the scale of our oceanographic model were hypothesized to affect corals by 2 general mechanisms that we discuss in detail below: food transport and larval dispersal.

Seafloor currents may be important for supplying food to cold-water corals (Frederiksen et al. 1992, Druffel et al. 1995, Davies et al. 2009). Topographic relief can accelerate currents, thereby improving particle supply to corals (Genin et al. 1986, Thiem et al. 2006). This mechanism would deliver organic particles that are re-suspended by turbulence and then transported by advection. However, particles near the seafloor may contain fewer usable labile organic compounds as a result of microbial activity in the benthic boundary (Ritzrau et al. 1997). An alternative explanation to the particle supply hypothesis for fine-scale positioning of cold-water corals lies in the requirement of most corals for a hard substrate attachment; following larval settlement, suspended sediments and organic particles may settle and smother small, developing corals (White et al. 2005). There is evidence that breaking internal waves may deliver food to cold-water corals either by redistributing particles in the bottom mixed layer or by increasing vertical nutrient flux, which promotes surface productivity (Frederiksen et al. 1992). Davies et al. (2009) suggested that the food supply for the cold-water coral *Lophelia pertusa* in the North Atlantic Ocean originated outside the reef area through an interaction among tides, rapidly down-welled surface water, and topography. Our oceanographic circulation model may reflect current patterns that are correlated with a food supply arriving more directly from surface layers. It also is feasible that our CPI values are associated with complex food delivery mechanisms, and that coarse covariate resolution (0.125°) benefits the coral model function because there may be significant lateral advection of organic particles from the surface to the benthos (Smith & Kaufmann 1999).

Although Christmas tree coral reproductive traits have not been documented, black corals tend to be gonochoric and fertilization likely occurs externally (Wagner et al. 2011, 2012). Studies also suggest that spawning is synchronous and tied to seasonal cycles in food input, although tidal or annual temperature cycles may be more important in less seasonal areas (Gooday 2002, Gori et al. 2007, Roberts et al. 2009). For relatively shallow black corals, the reproductive cycle appears to be periodic, and gamete maturity coincides with periods of higher water temperatures (Parker et al. 1997, Wagner et al. 2011). Very little is known about the larval biology of black corals; currently larval behavior has been observed only in laboratory cultures of *Antipathella fiordensis* (Miller 1996). These larvae were weak swimmers, negatively buoyant, and lived a maximum of 10 d. In another study of this species, fine-scale patterns of relatedness suggested that dispersal of black coral larvae is highly philopatric with settlement very close to parental colonies (Miller 1998). The scale of larval dispersal may be highly variable and is likely to be associated with bottom current velocity (Richards et al. 1995, Miller 1998) and micro-scale flow, which may affect larval supply to high-relief, rugose areas (Willis & Oliver 1990, Graham & Sebens 1996). The importance of the January bottom currents in our models is consistent with the hypothesis that restricted larval dispersal is an adaptation to deep-sea environments in which Christmas tree corals live on isolated, rocky outcrops. Modeled January water temperatures from our study were the warmest temperatures of the year. If spawning occurs during the warmest months, as previous research on closely related species indicates, then locations with weak bottom currents would be more likely to retain larvae and decrease the likelihood of larvae being dispersed away from suitable habitat or becoming isolated from conspecifics. Our finding that areas within the Bight that are associated with weak bottom currents in January are predicted to have the greatest density of coral colonies provides support for this hypothesized mechanism.

Models that incorporate both the growth and survival of individuals may provide a more accurate determination of suitable coral habitat (Stoner 2003). Our GLM of predicted coral size incorporated CPI, January eastward current, depth, the interaction of depth and CPI, and temperature. This finding, using an alternative response and a subset of the data, was in accord with the results of our GAM of predicted coral densities and adds credence to our inference that modeled oceanographic factors associated with growth and reproduction may explain a substantial portion of the variance in coral distribution. Greater CPI values were associated with larger coral, which supports the inference that greater surface productivity improves coral habitat suitability in the Southern California Bight. Because there are fewer size data, the nature of the depth–CPI interaction in the

GLM model is less clear than in the GAM results. There was a trend of larger corals across similar shallow depths with increasing CPI, but there were few data on size of colonies at deep water depths and low CPI values, so an analogous relationship to coral density and CPI is more difficult to discern. Temperature has been shown to be an important determinant of coral distribution (Roberts et al. 2009), and mean temperatures in our GLM indicated smaller coral colonies in warmer water, despite the trend of larger coral colonies occurring in shallower water. It may be that larger, shallow corals benefit from localized upwelling which may result in both colder temperatures and increased primary productivity. In contrast, predicted coral density was greatest at relatively warmer temperatures in our data set. Because temperature is strongly collinear with salinity and dissolved oxygen, the interpretation of this response is ambiguous since it may be affected by the other collinear covariates as well.

Modeled oceanographic data have shown promise for predicting the distribution of marine species by characterizing important habitat features across broad regions (Huff et al. 2012). We chose to focus on specific mechanisms of interest and considered relevant covariates based on our knowledge of ocean conditions in the Southern California Bight and the availability of consistent oceanographic model output. We felt that Christmas tree corals at our study scale were less likely to be affected by minimum calcite saturation state or aragonite saturation horizon, which were important in large-scale or global coral models, because Christmas tree corals are non-calcified corals that occur at relatively shallow depths (Guinotte et al. 2006, Davies et al. 2008, Yesson et al. 2012).

Predictive modeling holds great potential to improve our understanding of the ecological niche occupied by cold-water corals, although our ability to predict suitable habitat is limited by the resolution and availability of relevant environmental data and by a lack of knowledge regarding their life histories. A significant limitation in developing models to predict the distribution and abundance of cold-water corals is the lack of high-resolution spatial data on seafloor depth and substrate type. Fine-scale physical features and topographical characteristics are important determinants of deep-water coral distributions (Stone 2006, Woodby et al. 2009). Globally, only 5 to 10 % of the seafloor is currently mapped at a useful resolution to study the importance of detailed landscape configuration for the distribution of cold-water corals (Wright & Heyman 2008). High-resolu-

tion mapping of about 75 000 km^2 of the seafloor to a depth of 1300 m is still needed off California. Cold-water coral habitats incorporate a complex set of interactions among oceanography, food supply, and suitable substrata. Broad-scale geographic information on substratum types in our study was limited to megahabitat features on a spatial scale of 100 to 1000 m. Given the unconditional necessity of rocky substrata for the presence of Christmas tree corals, the acquisition of Bight-wide high-resolution spatial data on substratum types is required in order to improve the predictive performance of habitat-based coral models.

Both the GAM and GLM described a high proportion of the variance in the data using penalized log-likelihood methods and generalized cross-validation to avoid model over-fitting. Nonetheless, model predictions may function quite well with training data (or a subset of it), but then perform poorly with data from an independent set of validation sites. By using validation data from the same samples as our calibration dataset, our *k*-fold cross-validation process was moderately rigorous. Our models provided realistic estimates of predictive performance; our GAM accounted for 51 % of the variance in coral density, and our GLM accounted for 40 % of the variance in coral colony size. The independent dataset contained presence records that were obtained using a different survey methodology and that have covariates outside the range of our modeled calibration data. However, these independent data provided a qualitative assessment of the strengths and weaknesses in the predictive power of our density model, including agreement with model predictions comparable to our cross-validation results. As expected, model performance was poorest in areas with no calibration data (primarily in the southern portion of the Bight). Collecting information on coral densities and size composition in these areas remains a priority.

Christmas tree corals could indicate habitat potential for the broader associated community and could be a useful proxy for worthwhile habitats to protect. From our NMS plots, the relative position of Christmas tree corals in the community was defined in the context of factors that were included in our selected GAM and GLM models (e.g. productivity, depth, current strength) or known to be important to these corals (i.e. available rocky substrata). Gradient maps such as these may be used to compare habitat requirements of different taxa, and to identify patterns for future ecological investigations or conservation planning. In our dataset, Christmas tree corals occupy a relatively central position in the community

and are widely distributed across the gradients. The complex 3-dimensional architecture of Christmas tree corals and conditions in which they occur provide a variety of niches for many members of this benthic community. Mobile organisms, such as fish, may hide among their branches but not be obligate associates with black corals (Tissot et al. 2006). Many organisms, such as crinoids, basket stars, and brittle stars, occupy the dead branches and trunks of these corals (Love et al. 2007). Although there may not be clear evidence that fish and invertebrates depend on Christmas tree corals, these species co-occur in areas with similar habitat features (Tissot et al. 2006).

Some areas of predicted high densities of Christmas tree corals in the Southern California Bight are located inside marine protected areas where bottom-fishing gear has been prohibited (Fig. 2). However, there are several predicted hotspots of these corals that remain unprotected from fishing activities, particularly in areas adjacent to Point Conception and the most populated portions of the Bight near the ports of Los Angeles, Long Beach, and San Diego. Relatively little is known about the occurrence of Christmas tree corals and other coral species in these unprotected rocky areas, and yet numerous potential stressors (e.g. water pollution, marine debris, sustained fishing) have prevailed for decades in coastal waters within 20 km of the greater Los Angeles–San Diego metropolitan area. A great deal could be learned about the resiliency of these cold-water corals by assessing their abundance, diversity, and health in unprotected areas and making comparisons with those afforded protection from fishing and other impacts.

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Appendix 1. Taxa (code and scientific and common names) used in the non-metric multidimensional scaling ordination (ordered by ascending depth). **Bold** names indicate taxa plotted in Fig. 7. Frequency of occurrence is the number of transect groups (out of 47) in which a given taxon occurred. Depth is the abundance-weighted average depth

Code	Scientific name	Common name	Frequency of occurrence	Depth (m)
Red Gorgonian	*Leptogorgia chilensis*	Red gorgonian	5	62
HONEY RF	*Sebastes umbrosus*	Honeycomb rockfish	10	81
SHEEPHEAD	*Semicossyphus pulcher*	California sheephead	5	82
YTAIL	*Sebastes flavidus*	Yellowtail rockfish	6	97
CRYPTO	*Cryptotrema corallinum*	Deepwater blenny	15	99
ROSY RK	*Sebastes rosaceus*	Rosy rockfish	18	101
OLIVE	*Sebastes serranoides*	Olive rockfish	7	102
Z.ROSA	*Zalembius rosaceus*	Pink surfperch	9	105
BGOBY	*Rhinogobiops nicholsii*	Blackeye goby	28	106
SURFPERCH	**Embiotocidae**	Unidentified surfperch	5	107
VERM RK	*Sebastes miniatus*	Vermilion rockfish	23	108
SQSPOT RF	*Sebastes hopkinsi*	Squarespot rockfish	32	116
MOSER	*Sebastes moseri*	Whitespotted rockfish	15	117
STARRY	*Sebastes constellatus*	Starry rockfish	31	118
RONQUL	*Rathbunella* spp.	Unidentified ronquil	11	121
HALFBAND RF	*Sebastes semicinctus*	Halfbanded rockfish	29	123
GSPOT RK	*Sebastes chlorostictus*	Greenspotted rockfish	34	126
YOY	*Sebastes* spp. young-of-year	Juvenile rockfish	38	126
PETRALE	*Eopsetta jordani*	Petrale sole	5	127
PYGMY RF	*Sebastes wilsoni*	Pygmy rockfish	32	128
SPECKLED RF	*Sebastes ovalis*	Speckled rockfish	26	131
FLAG	*Sebastes rubrivinctus*	Flag rockfish	28	131
YEYE RK	*Sebastes ruberrimus*	Yelloweye rockfish	5	131
LINGCOD	*Ophiodon elongatus*	Lingcod	30	133
BOCACCIO	*Sebastes paucispinis*	Bocaccio	35	135
WIDOW RF	*Sebastes entomelas*	Widow rockfish	21	142
Acanthogorgia	*Acanthogorgia* spp.	Gold coral	11	146
Hex Oct Co	**Hexacorallia/Octocorallia**	Unidentified coral	18	158
COWCOD	*Sebastes levis*	Cowcod	32	158
P.VETU	*Parophrys vetulus*	English sole	9	160
GSTRIPE RF	*Sebastes elongatus*	Greenstriped rockfish	33	161
CUSK	Ophidiidae	Unidentified cuskeel	18	164
R.INOR	*Raja inornata*	California skate	5	167
SBELLY RK	*Sebastes jordani*	Shortbelly rockfish	29	175
Primnoid	*Plumarella longispina*	Primnoid coral	25	179
Sea Fan	**Gorgonacea**	Unidentified sea fan	21	179
R.RHIN	*Raja rhina*	Longnose skate	7	180
BIG SKATE	*Raja binoculata*	Big skate	6	181
EOS	*Sebastes eos*	Pink rockfish	6	184
CHILI RF	*Sebastes goodei*	Chilipepper rockfish	9	184
Up Flat Sp	**Porifera no. 2**	Upright flat sponges	44	186
Thin Sea Pen	**Pennatulacea**	Thin sea pen coral	29	187
SHARP RK	*Sebastes zacentrus*	Sharpchin rockfish	6	188
H.COLL	*Hydrolagus colliei*	Spotted ratfish	32	191
Styloco	*Stylocordyla* spp.	Stalked sponge	6	197
DARKBL RF	*Sebastes crameri*	Darkblotched rockfish	11	197
SCULP	Cottidae	Unidentified sculpin	32	198
GBLOTCH RF	*Sebastes rosenblatti*	Greenblotched rockfish	28	198
Foliose Sp	**Porifera no. 1**	Foliose sponge	42	198
STRIPETAIL RF	*Sebastes saxicola*	Stripetail rockfish	14	202
PRICKLE	Stichaeidae	Unidentified prickleback	13	204
Porife12	Porifera no. 12	Unidentified sponge	15	205
BANK RF	*Sebastes rufus*	Bank rockfish	33	214
Porife5	Porifera no. 5	Vase sponge	43	218
Barrel Sp	**Porifera no. 3**	Barrel sponge	42	221
Cup Co	**Scleractinia**	Cup coral	10	221

Appendix 1 (continued)

Code	Scientific name	Common name	Frequency of occurrence	Depth (m)
Shelf Sp	**Porifera no. 4**	Shelf sponge	33	224
BRONZE RF	***Sebastes gilli***	Bronzespotted rockfish	7	228
White Co	***Lophelia pertusa***	White coral	13	233
POACHER	Agonidae	Unidentified poacher	29	240
Branching Sp	**Porifera no. 7**	Branching sponge	18	243
Christmas Co	***Antipathes dendrochristos***	Christmas tree coral	26	243
Cockscomb Co	***Desmophyllum dianthus***	Cockscomb coral	8	246
Zoantha	Zoantharia	Zoanthid coral	15	257
Pipecleaner Sp	***Asbestopluma* spp.**	Pipecleaner sponge	12	284
M.PACI	*Microstomus pacificus*	Dover sole	17	289
Mound Sp	**Porifera no. 6**	Mound sponge	18	300
Vase Sp	***Heterochone calyx***	Fingered goblet vase sponge	11	309
SPLITNOSE RF	***Sebastes diploproa***	Splitnose rockfish	9	312
AURORA RF	***Sebastes aurora***	Aurora rockfish	6	344
Porife8	Porifera no. 8	Tube sponge	9	348
BLKGIL RF	***Sebastes melanostomus***	Blackgill rockfish	5	364
Polymas	*Polymastia* spp.	Nipple foliose sponge	5	377
Porife9	Porifera no. 9	Puffball mound sponge	9	387
Farrea	*Farrea occa*	Lace foliose sponge	8	392
Paragora	*Paragorgia arborea*	Bubblegum coral	8	403
Stauroc	*Staurocalyptus* spp.	Picasso sponge	8	412
HAGFSH	*Eptatretus* spp.	Unidentified hagfish	12	422
Yellow Upright Sp	***Mycale* spp.**	Yellow upright flat sponge	9	426
Thenea	*Thenea muricata*	Clear foliose sponge	5	430
Peppermint Co	***Paragorgia* spp.**	Peppermint coral	7	434
Soft Co	***Clavularia* spp.**	Soft coral	5	438
Mushroom Co	***Anthomastus ritteri***	Mushroom coral	6	458
THORNYHEAD	***Sebastolobus* spp.**	Unidentified thornyhead	6	466
Yellow Swiftia	**Plexauridae**	*Swiftia*-type coral, red with yellow polyps	5	481