

Getting to the bottom of fishery interactions with living habitats: spatiotemporal trends in disturbance of corals and sponges on the US west coast

Lewis A. K. Barnett^{1,*}, Shannon M. Hennessey², Timothy E. Essington², Andrew O. Shelton³, Blake E. Feist³, Trevor A. Branch², Michelle M. McClure⁴

¹School of Aquatic & Fishery Sciences, University of Washington, Seattle, WA 98195, USA; under contract to Fishery Resource Analysis and Monitoring Division, Northwest Fisheries Science Center, National Marine Fisheries Service, NOAA, Seattle, WA 98112, USA

²School of Aquatic and Fishery Sciences, University of Washington, Seattle, WA 98195, USA

³Conservation Biology Division, Northwest Fisheries Science Center, National Marine Fisheries Service, NOAA, Seattle, WA 98112, USA

⁴Fishery Resource Analysis and Monitoring Division, Northwest Fisheries Science Center, National Marine Fisheries Service, NOAA, Seattle, WA 98112, USA

ABSTRACT: Despite evidence that mobile bottom fishing gear causes physical damage to habitat-forming organisms on the seafloor, likely indirectly affecting associated fishes, it is difficult to determine how conservation and management policies influence such effects because researchers do not typically systematically quantify the extent and intensity of gear–habitat interactions. Here, we estimated spatiotemporal trends in bottom trawling in areas containing biogenic habitat (sponges and corals) on the US west coast to evaluate the effect of spatial closures, catch shares, and vessel buybacks. We predicted highest probabilities of biogenic habitat occurrence in moderate to deep depths north of Cape Mendocino and off southern California, and highest gear–habitat interaction frequencies in moderate depths off Oregon and Washington. Temporal trends in total biogenic habitat contacts tracked changes in fishing effort, mostly declining between 2003 and 2014 (declines between start and end year ranged from 51–55% across taxa). However, the predicted frequency of contacts per unit effort increased by 17–56% across taxa from 2003–2009, coinciding with implementation of spatial closures, and our results indicate this was due to effort displacement and shifting spatial distribution of fishing. These relative interaction rates then declined by 10–34% after implementation of catch shares. Thus, although spatial closures may protect habitat within protected areas, without complementary policies, spatial closures may increase gear–habitat interactions in adjacent areas due to changes in fisher behavior and fishing effort displacement.

KEY WORDS: Bottom trawling · Biogenic habitat · Catch shares · Spatial closures

Resale or republication not permitted without written consent of the publisher

INTRODUCTION

Habitat loss is likely the greatest threat to global biodiversity (Valiela et al. 2001, Brooks et al. 2002, Lotze et al. 2006, Sala & Knowlton 2006); therefore, habitat protection is a key tool in conservation biology (Rosenberg et al. 2000, Groom et al. 2006), because it provides an umbrella approach to managing ecologi-

cal communities. Researchers have increasingly emphasized habitat protection in marine conservation and fisheries as part of a movement towards ecosystem-based management (Rosenberg et al. 2000, Garcia et al. 2003, Babcock et al. 2005). Nearshore habitats face direct threats from land use and eutrophication (Hunte & Wittenberg 1992), along with fisheries and aquaculture (Claudet & Fraschetti 2010), whereas the greatest

direct threat to offshore habitat is likely physical damage from mobile bottom-contact fishing gear, particularly dredges and trawls (Watling & Norse 1998, Kaiser et al. 2002, Clark et al. 2016). The causes and consequences of nearshore habitat degradation are well documented (Pandolfi et al. 2003, Lotze et al. 2006), whereas quantitative documentation of offshore habitat damage and how this is affected by fishery management policies is limited (but see for example Collie et al. 2000, Kaiser et al. 2006, Pitcher et al. 2016, 2017). This inequality of information is concerning because offshore waters are fished with larger trawl gear and contain deep-water organisms that have slower life histories than those in the nearshore, indicating more severe and long-lasting consequences (Clark et al. 2016).

Biogenic habitats, i.e. those created by structure-forming living organisms, provide important nursery, refuge, and foraging zones for marine fauna (Ewel et al. 1998, Steneck et al. 2002, Graham 2004, Mumby et al. 2004, Aburto-Oropeza et al. 2008), and protect coastlines from storms and sea-level rise (Arkema et al. 2013). Offshore biogenic habitats are also important for many demersal fishes (e.g. Brodeur 2001, Heifetz 2002, Auster 2005, Stone 2006, Du Preez & Tunnicliffe 2011). Although it is difficult to directly demonstrate the value of these deep-water biogenic habitats for fishes (Tissot et al. 2006, Thorson & Barnett 2017), research suggests that they increase food abundance and provide shelter and nursery functions (Heifetz 2002, Freese & Wing 2003, Auster 2005, 2007, Stone 2006, Baillon et al. 2012). The ecological services that biogenic habitat provides are threatened by anthropogenic pressures, including ocean acidification, eutrophication, sedimentation, pollution, and physical disturbance (Valiela et al. 2001, Kleypas et al. 2006, Duke et al. 2007, Mangialajo et al. 2008, Foster & Schiel 2010).

Biogenic habitats, particularly those created by erect structure-forming invertebrates such as corals and sponges, are susceptible to direct physical damage by bottom-contact fishing gear (e.g. bottom trawls) (Clark et al. 2016). In addition to direct damage causing death and reduced cover and biomass of such organisms, trawling can reduce species richness of corals, sponges, and associated invertebrates (Koslow et al. 2001, Kaiser et al. 2002, Hermsen et al. 2003, Hiddink et al. 2006a, Althaus et al. 2009). Given the fragility of these communities, even limited fishing effort can significantly diminish cover of large structure-forming invertebrates. For example, each haul causes reductions (usually measured as changes in density of undamaged units or areal cov-

erage) of epibenthic invertebrates averaging 16%, but ranging from 4–90% (Pham et al. 2014), with typical reductions of 10–20% for biogenic habitats on tropical coral reefs that are trawled with light gear (e.g. Pitcher et al. 2000, BurrIDGE et al. 2003) and an average of 45% for sponges and sea whips in some deeper, temperate rocky reefs that are trawled with large gear (Freese et al. 1999). The influence of trawling on biogenic habitat over soft substrates (primarily sea pens and sea whips, Order Pennatulacea) may be lower than that on hard substrates. For example, Lindholm et al. (2015) found no difference in overall density of such taxa between trawled treatments and untrawled control areas; however, heterogeneity of trawl effort has been suggested as a cause of observed patterns of erect (undisturbed) sea whip density (Brodeur 2001, Lindholm et al. 2008), and these organisms have limited capacity to recover from physical damage (Malecha & Stone 2009).

Fragile, erect, sessile organisms like many corals and sponges are moderately to highly sensitive to perturbation, suggesting that within a disturbed area either all or many colonies may die (Hewitt et al. 2011, Clark et al. 2016). Once damaged, recovery takes up to 10s to 100s of years, based on the slow life history of many deep-water taxa (Rooper et al. 2011, Clark et al. 2016). These species may grow radially as slowly as 0.005 mm yr^{-1} (Carreiro-Silva et al. 2013) and can live for more than 4000 yr (Roark et al. 2009), but species residing nearer to coastal margins are estimated to live closer to 100–300 yr and grow at rates of $0.009\text{--}0.580 \text{ mm yr}^{-1}$ (Andrews et al. 2002, Andrews et al. 2005, Hill et al. 2011, Aranha et al. 2014). For example, deep seamount habitats off Australia and New Zealand have shown a lack of recovery on ecological timescales (10 yr; Williams et al. 2010), whereas 20–75% of species analyzed in the Great Barrier Reef fully recovered after only 5 yr (Pitcher et al. 2016). In addition, lack of larval supply and realized connectivity may reduce the likelihood of recolonization and metapopulation persistence in the deep sea (Lacharité & Metaxas 2013). Given the potential for these severe and long-lasting impacts, understanding the magnitude and extent of interactions between fishing gear and biogenic habitats is important for informing policy.

Mapping structure-forming invertebrates to determine their exposure to fishing or other potentially damaging human activities is an essential element of risk analysis, and researchers have identified this task as the top priority for determining the effect of trawling on seafloor habitat (Kaiser et al. 2016). To assess the realized influence of fishing on biogenic

habitat and help make marine spatial planning decisions, one needs to know the distribution of the organisms that create habitat and the extent and intensity of the trawl effort (Johnson 2002, Bellman et al. 2005, Kaiser et al. 2016). Finally, one needs knowledge of how the overlap of these 2 variables has changed in space and time to assess how management policies have influenced the scale of interaction between trawling and biogenic habitat. Although many studies have predicted the distribution of biogenic habitat (e.g. Tittensor et al. 2009) or trawling effort (e.g. Bellman et al. 2005) separately, and some have summarized the degree of overlap between them for a given period of time (e.g. National Research Council 2002, Penney & Guinotte 2013, Grabowski et al. 2014), few have quantified concurrent spatial and temporal changes in the interaction between trawling and biogenic habitat. Here, we estimated the interaction (magnitude and extent) between bottom-trawl activity and areas where corals and sponges (hereafter biogenic habitat) are exposed to trawling along the US west coast during a 13 yr period. We then used this information to assess how management efforts and fisher behavior may have changed this interaction in time and space.

MATERIALS AND METHODS

System

The US west coast groundfish fishery may be the dominant driver of direct anthropogenic change affecting structure-forming invertebrates along the US Pacific coast (Bellman et al. 2005). This fishery's catch includes 2 of the top 3 deep-sea species groups in terms of landings worldwide: Pacific rockfishes and thornyheads (*Sebastes* and *Sebastolobus* spp.), and sablefish (*Anoplopoma fimbria*) (Clark et al. 2016). Most bottom trawling off the US west coast is attributable to the bottom trawl sector of the groundfish fishery, and other fisheries using bottom-contact gear on the US west coast (fixed-gear fisheries such as pot and longline) are assumed to have lower impacts on benthic habitats (Bellman et al. 2013, Pham et al. 2014).

Management changes in the US west coast groundfish bottom-trawl fishery over the last 20 yr provide an opportunity to understand the effect of fisheries policies on biogenic habitats. In the 1990s,

many species became overfished and catch limits were greatly reduced (Hilborn et al. 2012). In 2000, regulations limited the maximum size of trawl footropes for fishing on the continental shelf, banning the large 'rockhopper' gear, which likely led to a vast reduction in trawling over rocky seafloor (Bellman et al. 2005). A system of closed areas (Rockfish Conservation Areas) was implemented beginning in 2002, which prohibited trawling at temporally varying depths (generally between 175 and 450 m) along the continental shelf, where most fishing had previously occurred. A vessel buyback program began in late 2003 to reduce fleet capacity. To protect Essential Fish Habitat, roughly 25% (34 million acres [~ 13.8 million ha]) of the area historically fished was closed to trawling in 2006 (PFMC 2008). Finally, policymakers implemented catch shares in 2011. The annual quota of allowable catch was divided among individuals, based on historical catches, and could be traded or leased. Given these policy changes, we split the 13 yr time period into 3 'management regimes': 2002–2005, 2006–2010, and 2011–2014 (hereafter 'early,' 'middle,' and 'late'). In the early period, fishery effort followed a continued decline from a high level in response to stricter catch limits implemented just prior (Hilborn et al. 2012); in the middle period, effort rose again before a sudden drop in the final year; and in the late period, fishing effort continued to decline to its current long-term low (Fig. 1).

We addressed whether the substantial changes in policies affecting the US west coast groundfish bottom-trawl fishery during our study period altered interaction frequencies between gear and biogenic habitat. *A priori*, we expected interactions with bio-

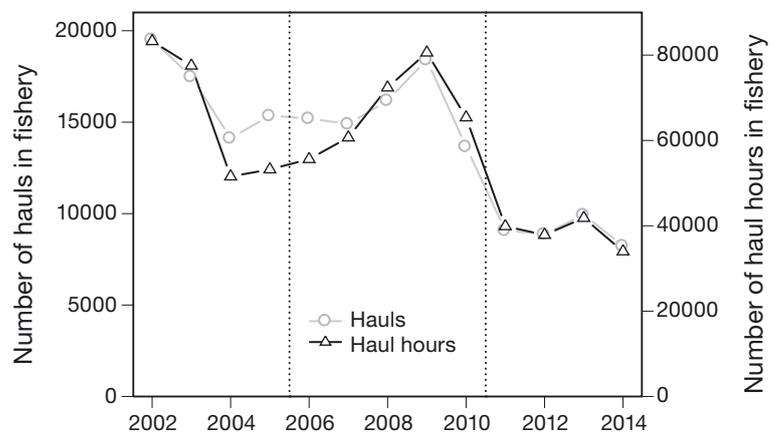


Fig. 1. US west coast bottom-trawl fishery effort during the period of interest, as defined from a combination of at-sea observer data and fishery log-book data. The vertical dotted lines indicate the timing of major policy changes: implementation of large spatial closures in 2006 and catch shares in 2011

genic habitat to covary positively with changes in fishing effort. We expected spatial closures, and perhaps catch shares, would contribute to reducing effects of fishing on habitat based on first principles; however, it is unclear whether catch shares have empirically altered the effect of fishing on habitat in other systems (Branch 2009).

Approach

We created a habitat exposure map by predicting the probability of trawl gear encountering and retaining corals and sponges (hereafter all references to interactions between gear and biogenic habitat will imply retention). Note that our usage of ‘exposure’ differs from other definitions that invoke the potential effect of stressors on an element of interest. We predicted the intensity and spatial distribution of interactions between biogenic habitat and trawl gear by intersecting this habitat exposure map with trawl towlines. To verify these predictions, we compared the predicted interactions to those observed directly with at-sea observer data. We describe these processes in turn below.

Habitat exposure model data preparation

We analyzed the occurrence of biogenic habitat in fishery-independent trawl samples (thus ‘occurrence’ implies that the habitat was present and detected) to identify where bottom trawlers are likely to encounter structure-forming invertebrates in a given haul. Note that this is potentially different from a map of organismal distribution based on direct observation or habitat suitability, but, for consistency with the species distribution modeling literature, we refer to the chance of observing biogenic habitat in a single trawl sample as the probability of occurrence. Thus, instead of using submersible observations to produce a habitat distribution map, we produce a habitat exposure map using fishery-independent trawl surveys, which provide large-scale systematic sampling that is unavailable with other methods. Although trawl gear does not retain all biogenic habitat species, the same gear and methods are used throughout the study region. Thus, recoveries of biogenic habitat in trawl surveys can be used to document biogenic habitat occurrence on a relative scale; the detailed information about the probability of detecting biogenic habitat in trawl nets needed to scale observations to true

probabilities of occurrence are unavailable. Furthermore, these relative probabilities of occurrence are apt for predicting where commercial trawlers are likely to come into contact with biogenic habitat given the physical limitations of trawl gear (i.e. within trawlable grounds), particularly if survey and commercial gear are similar. Specifically, we analyzed data from the NOAA US West Coast Groundfish Bottom Trawl Survey (Bradburn et al. 2011) which uses trawl gear that is similar to that used in the commercial fishery since 2002. This annual survey occurs from May to October at depths from 55 to 1280 m, spanning from Cape Flattery, Washington (US–Canada border), south to the US–Mexico border. We analyzed the 2003–2012 surveys, which consisted of 7232 hauls, where locations were selected randomly on trawlable seafloor habitat (i.e. areas without extensive rocks or boulders; Fig. 2b,c) stratified by depth and latitude. Each haul included data on taxon detection, haul midpoint coordinates, and depth.

To create a predictive map of biogenic habitat probability of occurrence throughout the study area, we compiled depth and substrate data layers to use as candidate environmental predictor variables. We used an existing gridded bathymetry data layer (3-arcsecond resolution, ~90 m) for depth (NOAA 2003; Fig. 2a). We obtained substrate type polygons from the Pacific Coast Ocean Observing System (PaCOOS) West Coast Habitat Server data layers (<http://pacoos.coas.oregonstate.edu/datasets.html>; Surficial Geologic Habitat Version 3 [WA, OR, CA]), which were summarized by category (rock, boulder, sand, and soft sediment; Fig. 2b). We extracted depth and substrate values on a regular grid (at 2 × 2 km cell centroids) using the Point Sampling Tool plugin (Jurgiel 2013) in QGIS (version 2.8.1-1; QGIS Development Team 2015) to construct a spatial dataset for extending our predictions across the entire study area.

We aggregated invertebrate taxa to higher taxonomic levels because of varying taxonomic resolution in the records. This also ensured there were sufficient presence data for each taxonomic group, as finer-scale groupings provided sparse data and poor model fits. We present results for 3 major groups: subclass Hexacorallia, excluding anemones and dominated by black corals (hereafter hexacorals); subclass Octocorallia, primarily sea pens (hereafter octocorals); and phylum Porifera (sponges) (see Table S1 in the Supplement at www.int-res.com/articles/suppl/m574p029_supp.pdf for number of occurrences by taxon). Approximately 40% of hauls recorded at least 1 of these invertebrate groups.

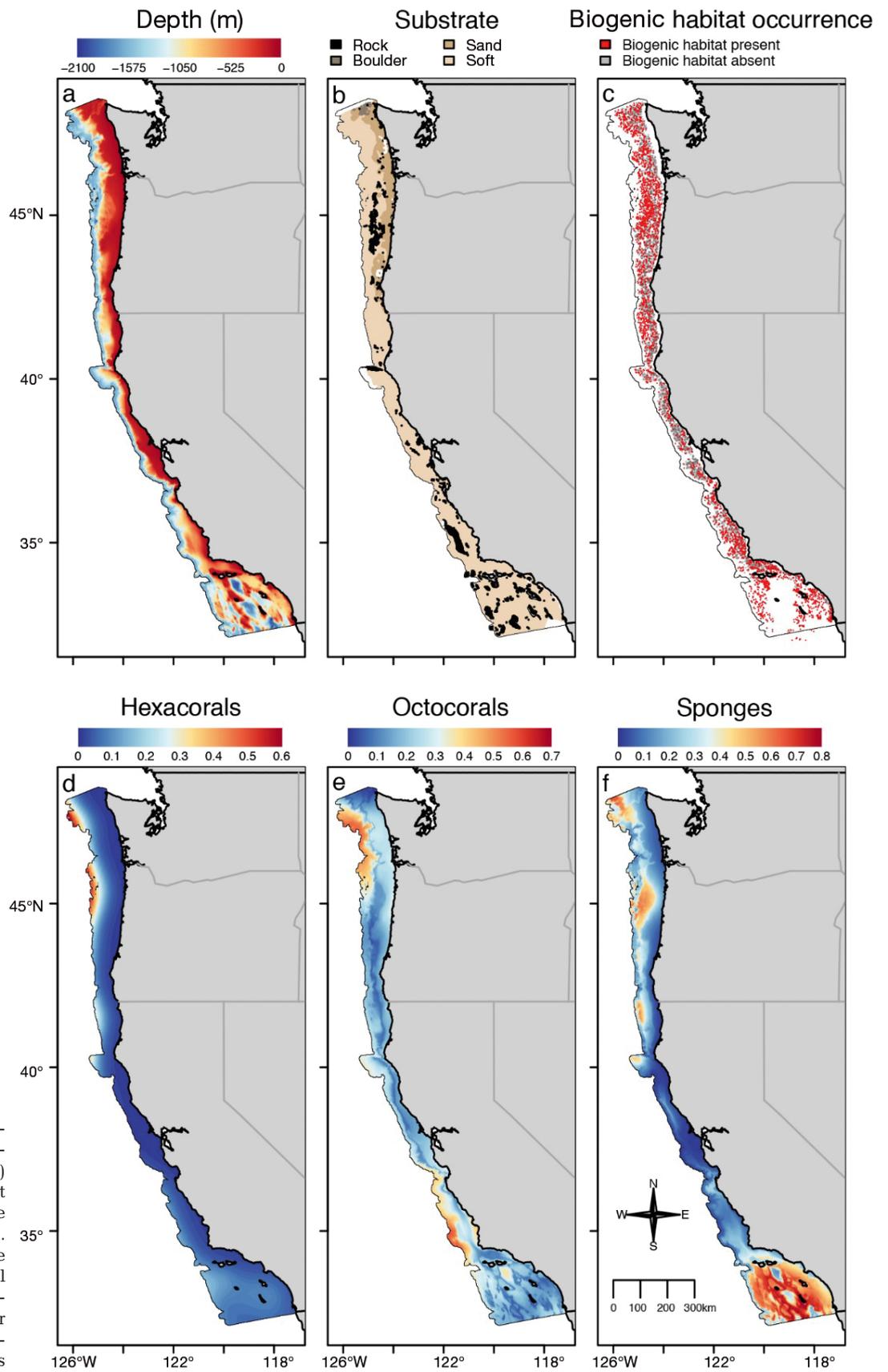


Fig. 2. Spatial distribution of (a) depth, (b) substrate categories, and (c) actual biogenic habitat occurrence across the model prediction area. Lower panels show the best-supported model predictions of the probability of occurrence for (d) hexacorals, (e) octocorals, and (f) sponges

Habitat exposure model construction

We estimated the probability of occurrence of structure-forming invertebrates by spatial location, to identify areas where trawls are more likely to disturb these biogenic habitats. To evaluate the probability of biogenic habitat occurrence in trawl samples at a given location i , θ_i , we constructed binomial (*logit* link) general additive models (GAMs) using the *mgcv* package (Wood 2007) in R (version 3.2.3; R Development Core Team 2015). We used GAMs because they allow us to model space explicitly as a bivariate smoother of depth and location, allowing for non-linear relationships between predictor and response variables. Data were first randomly assigned into model training (2/3 of data) and testing (1/3 of data) datasets. We used the training dataset to construct GAMs for hexacorals, octocorals, and sponges, using the covariates of northings and eastings, depth, and substrate category. Location and depth were smoothed using a tensor-product smoothing spline s . Smooth knots were constrained for the depth term to prevent overfitting (knots = 4, 4, and 7 for hexacorals, octocorals, and sponges, respectively). Thus, we aimed to model the presence or absence of biogenic habitat at each location y_i based on an estimated probability of occurrence θ_i , where $\mathbf{Y} \sim \text{Bernoulli}(\boldsymbol{\theta})$ such that $y_i = 1$ with probability θ_i and $y_i = 0$ with probability $1 - \theta_i$, where $0 \leq \theta_i \leq 1$. The full model for estimating the probability of occurrence is then:

$$\text{Logit}(\boldsymbol{\theta}) = s(\text{Northing, Easting}) + s(\text{Depth}) + \text{Substrate} \quad (1)$$

Habitat exposure model validation and prediction

To select a best-supported model for each biogenic habitat taxon, we made predictions with environmental data from the training dataset for each of 7 fitted models: taxon presence predicted by (1) intercept, (2) smoothed northing and easting (location), (3) smoothed depth, (4) substrate, (5) smoothed depth and substrate, (6) smoothed location and smoothed depth, and (7) smoothed location, smoothed depth, and substrate (see Table 1). We compared these predictions to observations in the testing dataset and cross-validated. The models best supported by the data were taken as those that have the highest out-of-bag predictive ability (i.e. those that best predict values from the testing dataset, using the training dataset), given consideration of model complexity to

avoid overfitting (i.e. a balance between fit and parsimony). Thus for out-of-bag observation x_i with $i = 1, 2, \dots, I$ (where $x_i = 1$ if present and $x_i = 0$ if absent), a measure of the predictive accuracy of model m is

$$L_m = \sum_{i=1}^I \{x_i \log[\hat{p}(x_i)] + (1 - x_i) \log[1 - \hat{p}(x_i)]\} \quad (2)$$

where $\hat{p}(x_i)$ is the predicted value of that observation from the GAM. Thus, L_m represents the logarithmic score (Gneiting & Raftery 2007) for predictive accuracy across all out-of-bag observations. The model with maximum log-score L_m provides the best predictive performance; however, to avoid overfitting, we defined the best-supported model as the most parsimonious model with the highest or nearly highest log score. We compared models based on their exponentiated log-score per observation $\exp(L_m/I)$, which indicates how well on average the model predictions match the observations. Once the preferred model was selected, we made a complete map of predicted probability of occurrence across the entire region for each biogenic habitat taxon, providing predictions for each 2×2 km grid using the extracted location, depth, and substrate layers (where applicable) as model covariates.

Gear-habitat interaction prediction

To estimate spatiotemporal trends in the overlap between the bottom-trawl activity and biogenic habitat, we calculated an index of the expected number of contacts between commercial groundfish bottom-trawl gear and biogenic habitat. We derived the contact index by intersecting the habitat exposure prediction maps with the locations of the hauls conducted by the fishery, implicitly conditioned on an unknown retention probability that is assumed to be constant. We assumed that hauls were linear transects between the start and end points recorded in logbook data provided by the Pacific Fisheries Information Network (representing self-reported data for each haul from all groundfish bottom-trawl vessels operating off the US west coast between 2002 and 2014: 180 984 total hauls, comprising the majority of all hauls notwithstanding some incomplete reporting). To filter out hauls with erroneous locations, we only included hauls where the distance and duration towed implied a speed of less than 11 km h^{-1} . We also ran the analyses excluding hauls that were inferred to be too slow ($< 1.5 \text{ km h}^{-1}$), indicating that they may have followed a circuitous path, but excluding these tows did not change the conclusions of our research

so they were retained. Assuming that each intersection of a haul transect and a spatial cell of the habitat exposure map represents an independent Bernoulli trial with a probability of occurrence in a given cell, the number of contacts between trawl gear and biogenic habitat during a haul follows a Poisson-binomial distribution (an extension of the binomial distribution allowing for variation in probability of success among trials; Wang 1993) where the expected number of contacts is the sum of the occurrence probabilities over all j spatial cells and all k hauls $\Sigma \hat{p}_{j,k}$, with variance $\Sigma[\hat{p}_{j,k}(1 - \hat{p}_{j,k})]$. To assure the robustness of this approach, we compared these results with those acquired when the occurrence probabilities were weighted by the distance towed through each cell. In this weighted probability approach, we redefined the number of trials as the result of dividing the computed distance each haul traveled through each cell $d_{j,k}$ by the average distance of a haul in the fishery-independent survey \bar{d} (~ 1 km) used to predict occurrence probabilities. Thus, the expected number of contacts in the weighted case was $\Sigma(\hat{p}_{j,k} d_{j,k} \bar{d}^{-1})$. To visualize the predicted temporal and spatial trends in the interactions between biogenic habitat and fishing gear, we summarized the predicted number of contacts by year and by spatial cell.

Observed gear–habitat interactions

We compared the temporal trends in predicted contacts between biogenic habitat and fishing gear to relative encounter frequencies (encounters per haul) reported by at-sea observations of discarded catch provided by the West Coast Groundfish Observer Program at the Northwest Fisheries Science Center (hereafter these measures will be termed ‘observed’ interactions). Note that an encounter is a different measure than a contact, where we define the latter to indicate an instance of contact during a haul (of which there may be >1), and the former indicates the presence of biogenic habitat in a trawl sample (which does not exceed 1, regardless of whether there was >1 contact). Thus, we distinguish these terms when necessary, but also use ‘interaction’ as a broad term that refers more generally to either contacts or encounters.

Observers were present on approximately 20% of trips between 2002 and 2010 and 100% of trips since 2011. We scaled up the encounters with biogenic habitat in the early period (to account for lower observer coverage) by multiplying the number of total hours of trawl effort in the fishery by the number of

encounters per hour of trawl effort on observed hauls. Although this scaling does not account for the spatial extent of observer coverage, qualitative comparisons between locations of observed and unobserved hauls indicate that observed hauls adequately approximate the spatial distribution of trawling during this period (see Fig. 1 in the annual reports of the NWFSC Observer Program Data Products Limited Entry Bottom Trawl: www.nwfsc.noaa.gov/research/divisions/fram/observation/data_products/bottom_trawl.cfm).

RESULTS

Spatial patterns of habitat exposure

We evaluated model performance by comparing the observed and predicted occurrences of biogenic habitat from the fishery-independent survey. Performance was similar across models of intermediate to full complexity, and there was no strong evidence to make inferences about particular predictor variables. However, this does not significantly affect our analysis, which was focused on the quality of the predictions themselves. In general, the best-supported models included location and often depth (Table 1), which explained a reasonable amount of deviance in occupancy of hexacorals and sponges, but were less predictive of octocoral distribution.

Hexacorals had the fewest observations, 280 in total, and were predicted to have low probability of occurrence throughout the region (Fig. 2d). The best-supported model for hexacorals included the smoothed location (northing, easting) and had a much higher log-score than the other models evaluated (Table 1; deviance explained = 12.8%). The difference in predictive accuracy between the best-supported model and other candidate models ranged from 0.004 to 0.019 (or 0.04 to 1.9%; Table 1; also see comparison in Fig. S1 in the Supplement). Predicted probability of hexacoral occurrence was highest along the westernmost edges of the prediction area off Washington and Oregon (Fig. 2d). This model performed well compared to the test data observations, especially at low predicted values (Fig. S2a). There was a slight tendency to overestimate at high probability of occurrence, likely due to the paucity of observations in this range.

Octocorals occurred more commonly than hexacorals throughout the prediction area. Areas with particularly high probability of occurrence (above the 75th percentile; termed ‘hotspots’) generally occur-

Table 1. Comparison of constructed models predicting the probability of biogenic habitat taxa presence over the US west coast prediction area. The exponentiated log-score per observation $\exp(L_m/I)$ provides an indication of how well on average (per observation) the model predictions match the observations (model fit: the higher the number, the better the fit). The difference in this metric between the candidate models $\Delta \exp(L_m/I)$ indicates the percentage difference in predictive probability per observation. The deviance explained gives a measure of how much of the variability in the data the model explains. The selected models are shown in **bold**, and were chosen to balance fit and parsimony (i.e. the simplest model with the highest log-score, or with a log-score that is only marginally lower than the highest log-score)

Models	$\exp(L_m/I)$	$\Delta \exp(L_m/I)$	Deviance explained (%)
Hexacorallia (hexacorals)			
Intercept + $s(\text{Northing}, \text{Easting}) + s(\text{Depth}) + \text{Substrate}$	0.866	-0.005	15.2
Intercept + $s(\text{Northing}, \text{Easting}) + s(\text{Depth})$	0.867	-0.004	15.0
Intercept + $s(\text{Northing}, \text{Easting})$	0.871	0.000	12.8
Intercept + $s(\text{Depth}) + \text{Substrate}$	0.861	-0.010	11.4
Intercept + $s(\text{Depth})$	0.861	-0.010	10.0
Intercept + Substrate	0.856	-0.015	1.6
Intercept	0.853	-0.019	0.0
Octocorallia (octocorals)			
Intercept + $s(\text{Northing}, \text{Easting}) + s(\text{Depth}) + \text{Substrate}$	0.627	-0.001	5.4
Intercept + $s(\text{Northing}, \text{Easting}) + s(\text{Depth})$	0.628	0.000	4.9
Intercept + $s(\text{Northing}, \text{Easting})$	0.626	-0.002	3.5
Intercept + $s(\text{Depth}) + \text{Substrate}$	0.623	-0.004	1.7
Intercept + $s(\text{Depth})$	0.623	-0.004	1.4
Intercept + Substrate	0.620	-0.007	0.4
Intercept	0.621	-0.007	0.0
Porifera (sponges)			
Intercept + $s(\text{Northing}, \text{Easting}) + s(\text{Depth}) + \text{Substrate}$	0.643	0.002	18.8
Intercept + $s(\text{Northing}, \text{Easting}) + s(\text{Depth})$	0.641	0.000	17.6
Intercept + $s(\text{Northing}, \text{Easting})$	0.638	-0.003	16.8
Intercept + $s(\text{Depth}) + \text{Substrate}$	0.602	-0.039	7.5
Intercept + $s(\text{Depth})$	0.602	-0.039	5.6
Intercept + Substrate	0.587	-0.054	2.3
Intercept	0.583	-0.058	0.0

red in deeper waters (Fig. 2e). The best-supported model for octocorals included smoothed location and smoothed depth (Table 1; deviance explained = 4.9%). This model had the highest log-score of the candidate models, and was therefore selected as the best-supported model despite the better visual fit of the model with smoothed location as the only covariate (Fig. S3). Predictive accuracies of the candidate models were all within 0.007 of the best-supported model, indicating relatively comparable performance. The best-supported model had more variable performance over the range of occurrence probability than that for hexacorals, but still remained within a reasonable range of performance (Fig. S2b). Like the hexacoral models, the best-supported model for octocorals tended to over-predict occurrence, especially at higher probabilities of occurrence (>0.4). The model predicted increased probability of catch with depth, indicating a (local) minimum probability of occurrence at 400 m, and a (global) maximum probability of occurrence around 1000 m (Fig. S4a). Two major hotspots were near the 1280 m isobath—off

the coast of Washington, and from Point Sur to Point Conception off central California.

Sponges were frequently observed in the survey hauls (Fig. 2f), and their occurrence showed strong relationships with depth and location, although with different patterns than the octocorals. The best-supported model for sponges also included smoothed location and depth covariates (Table 1; deviance explained = 17.6%). While the full model had a slightly higher log-score, the visual fit of the selected best-supported model appeared to be more consistent in not under- or over-predicting the probability of occurrence and was therefore selected over the full model (Fig. S5).

Predictive accuracy ranged widely for candidate models predicting sponge occurrence, with differences up to 0.058 relative to the best-supported model. This model had a consistently strong relationship between the probabilities of sponge occurrence and test training data (Fig. S5e). Probability of sponge occurrence had an intermediate optimum with respect to depth, occurring most commonly near

the 500 m isobath (Fig. S4b). Hotspots occurred at intermediate depths off Washington, Oregon, and southern California (Fig. 2f).

Summarized over the entire region, the predicted distribution of biogenic habitat occurrence probabilities was fairly constrained for hexacorals and octocorals, yet quite broad for sponges (Fig. 3a–c). We predicted that most locations have low to no probability of hexacoral occurrence, but all areas have a non-zero probability of octocoral occurrence. The spatial distribution of sponge exposure was broader than that of corals, such that trawl locations spanned a wide range of occurrence probabilities.

Predicted spatial distribution of gear–habitat interactions

The distribution of trawling effort in the fishery, with respect to biogenic habitat, was quite similar to the complete distribution of biogenic habitat occurrence probabilities available over the entire region (Fig. 3; compare rows). However, the distribution of occurrence probabilities within fished areas was

slightly skewed toward lower occurrence probabilities and did not contain the highest values observed over the entire region. Thus, we expect that there were fewer contacts between gear and biogenic habitat in the fishery than if fishers were choosing haul locations at random.

We predicted that most of the interactions between trawls and biogenic habitat occurred north of Cape Mendocino, primarily off Oregon and Washington near spatial closures designed to protect habitat (Fig. 4, compare a–c with location of closures in d). Areas of highest interaction frequency for all species included the deep seafloor off the northern Washington coast near the ‘Biogenic 1’ bottom-trawl closure and off northern Oregon, just inshore of the Astoria Canyon closure. For octocorals (and for sponges to a limited extent), there was an area of high interaction frequency just north of Cape Mendocino and near the ‘Grays Canyon’ bottom-trawl closure north of Astoria Canyon, near the continental shelf break off southern Washington (Fig. 4b–d). We predicted that all taxa have incurred moderate trawl disturbance off northern Oregon between the inshore side of the Astoria Canyon closure and the Heceta Bank closure,

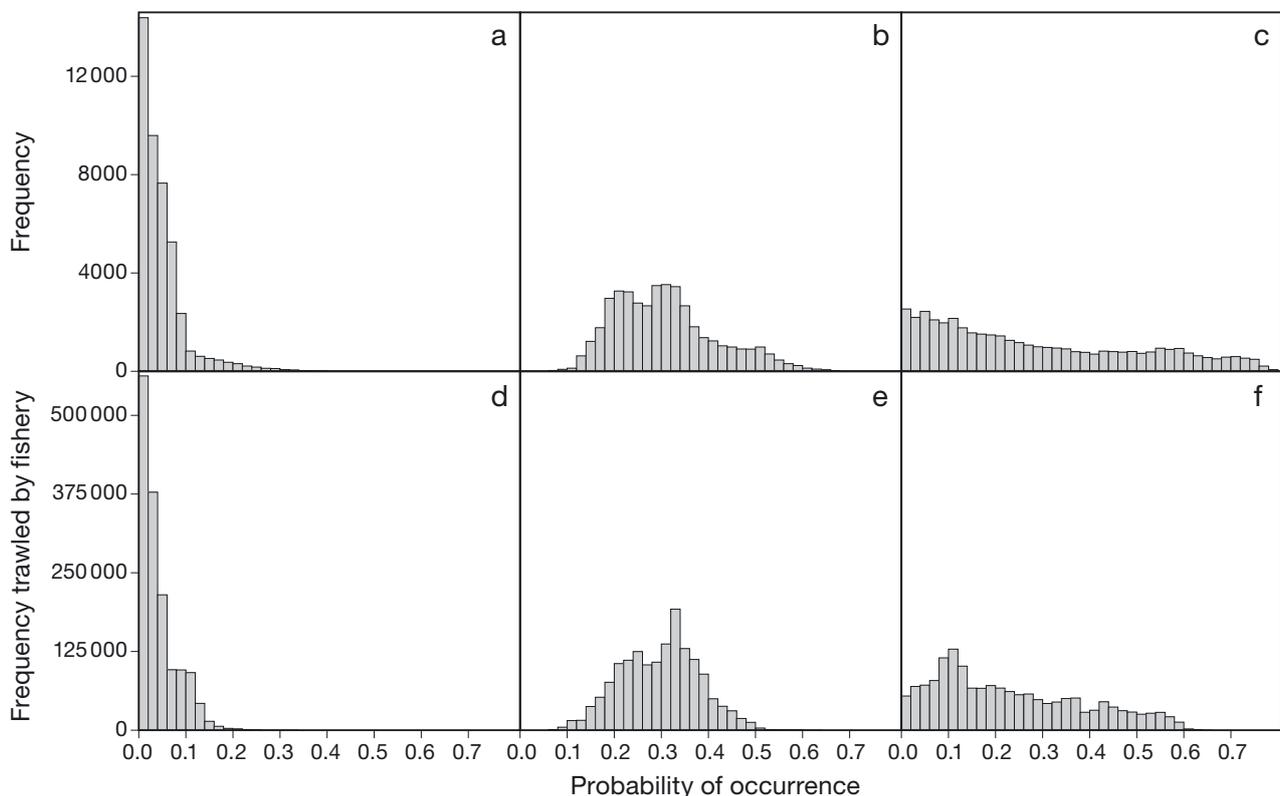


Fig. 3. Biogenic habitat exposure to trawl gear, summarized (a–c) for all areas across the region (distribution of spatial cells by probability of occurrence) and (d–f) by the distribution of fishing effort (cumulative number of times spatial cells with a specific occurrence probability were inferred to be intersected by fishery hauls) for (a,d) hexacorals, (b,e) octocorals, and (c,f) sponges

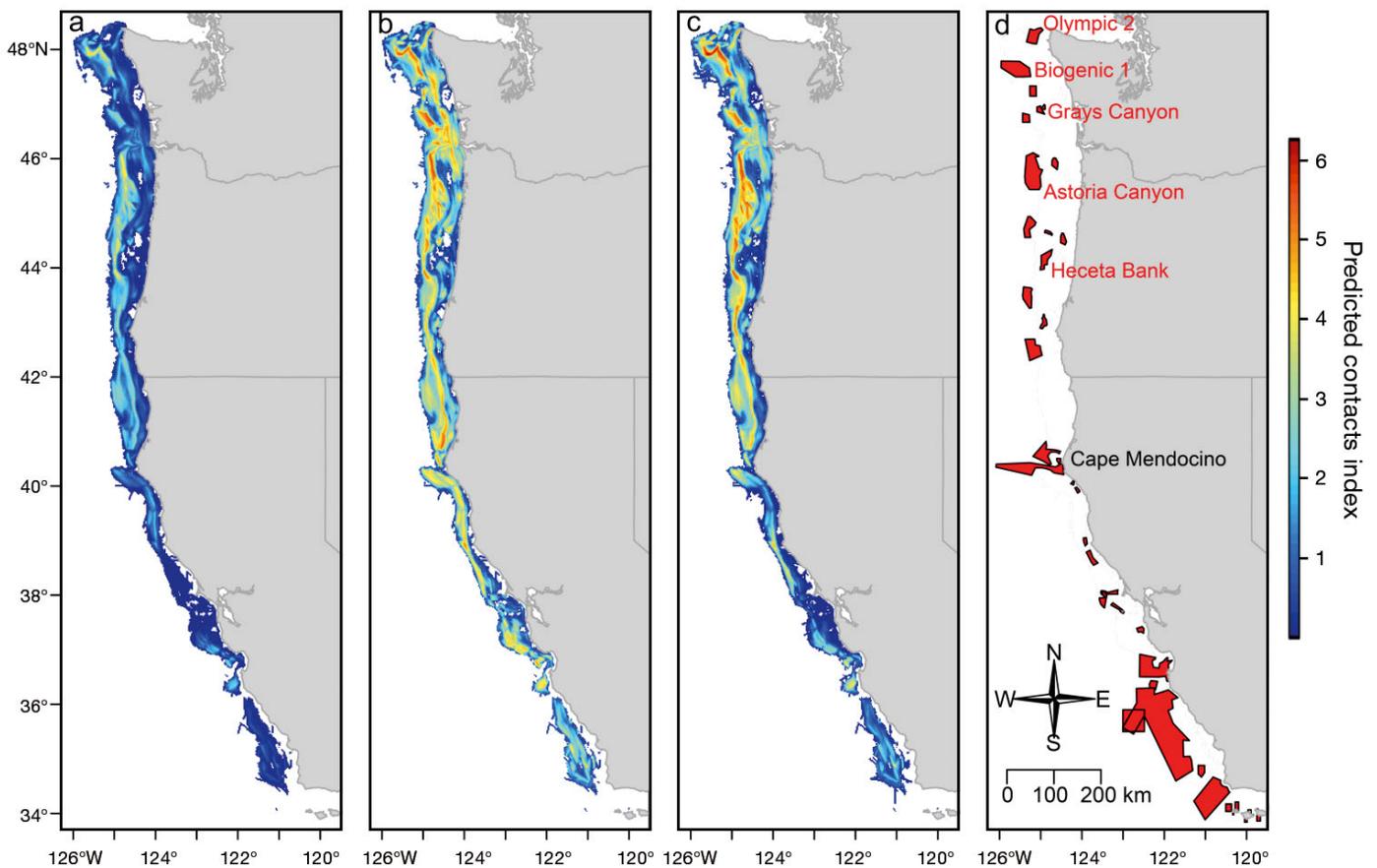


Fig. 4. Predicted groundfish bottom-trawl interactions with US west coast biogenic habitat summarized across all years (2002–2014) for (a) hexacorals, (b) octocorals, and (c) sponges, with (d) a map of landmarks and areas closed to bottom-trawling highlighted in red (note that this does not show the boundaries of the coast-wide trawl Rockfish Conservation Area, which are dynamic). The predicted contacts index is plotted on a log + 1 scale to ease visualization of large-scale patterns

with hexacorals being particularly affected just south of Heceta Bank. We predicted moderate-to-low trawl influences on the mid-shelf off northern Washington near the edge of the ‘Olympic 2’ bottom-trawl closure, particularly for octocorals.

Predicted change in spatial distribution of gear–habitat interactions with time

By mapping the intersection between haul locations in the fishery during each of the 3 time periods and the distribution of biogenic habitat exposure (which is assumed to be constant), we revealed substantive changes in the pattern of interaction between biogenic habitat and trawl gear. In general, trawl interactions with biogenic habitat were distributed somewhat diffusely along the US west coast early (2002–2005; Figs. 5a, S6a, S7a), became con-

centrated within a narrower band of coastal waters during the middle years (2006–2010; Figs. 5b, S6b, S7b), and moved deeper and more northerly in later years (2011–2014; Figs. 5c, S6c, S7c). For sponges, for example, early interactions on the continental shelf in far northern Washington were not realized in subsequent periods, as trawling was banned around much of the area near the Biogenic 1 and Olympic 2 closures (Fig. 5). Conversely, interactions in deeper waters off northern Washington and central and northern Oregon peaked in the middle period before moderating because of reduced fishing effort in very deep and very shallow waters (Somers et al. 2015).

Over time, per unit of effort, the groundfish bottom-trawl fishery changed in terms of where hauls have occurred relative to biogenic habitat occurrence probabilities (Fig. 6, compare modes among years; Kruskal-Wallis $p < 0.001$, $df = 2$ for all taxa; hexacoral $\chi^2 = 16374$, octocoral $\chi^2 = 4720$,

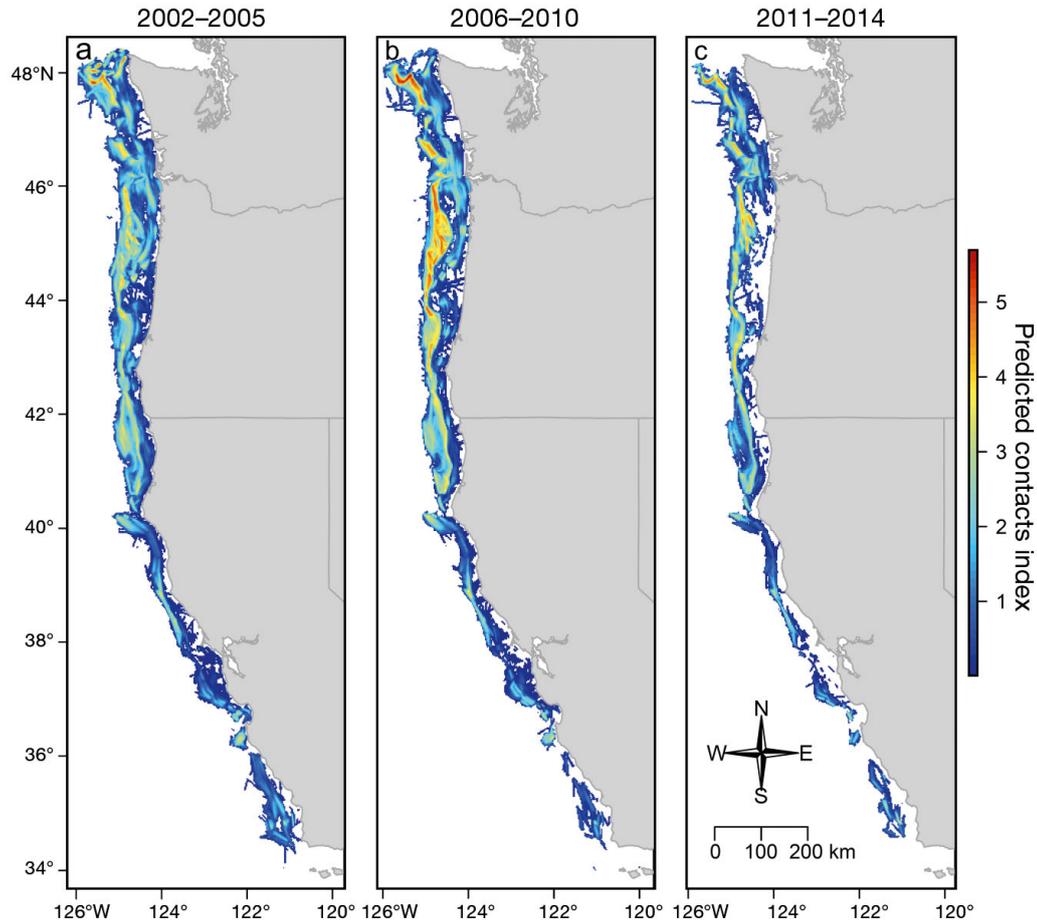


Fig. 5. Predicted groundfish bottom-trawl interactions with US west coast sponges summarized by management period. The predicted contacts index is plotted on a log + 1 scale. Similar patterns were found for hexacorals and octocorals (see Figs. S6 & S7 in the Supplement)

sponge $\chi^2 = 20\,557$). There was a spatial shift of effort towards areas containing higher occurrence probabilities of biogenic habitat over time (see Figs. S5–S7 for maps of predicted encounters by year). This relative increase in overlap between trawl distribution and areas of high probability of occurrence with biogenic habitat peaked in the middle to late periods, particularly for hexacorals and sponges (Fig. 6a,c).

Although the typical location of a haul in the fishery shifted to areas with greater probability of biogenic habitat occurrence, the overall spatial extent of fishery overlap with exposed biogenic habitat (particularly octocorals and sponges) largely declined (Fig. 7, solid lines; declines between start and end year ranged from 52–53% across taxa), following trends in total fishing effort. When broken down specifically by time period, the extent of overlap decreased in the early period (by 29–48% across taxa), increased during the middle period (by 2–170%), and decreased during the later period (by 13–15%). This pattern remains largely the same when analyzing

the extent of area with moderate to high frequency of interactions between gear and habitat (Fig. 7, broken lines), yet the overall declining trend is no longer evident.

Predicted and observed change in frequency of gear–habitat interactions with time

Although fishing effort shifted toward more exposed areas, the predicted index of total contacts between trawl gear and biogenic habitat generally followed the trend of total fishing effort (Fig. 1), mostly declining over the study period with the particular exception of 2008–2010 (Fig. 8a–c; declines between start and end year ranged from 51–55% across taxa). Observed encounters (those from the fishery-dependent at-sea observer program) followed a similar trend but were lower at the beginning of the time period (Fig. 8e,f). Across all years, octocorals and sponges were the taxa with the most

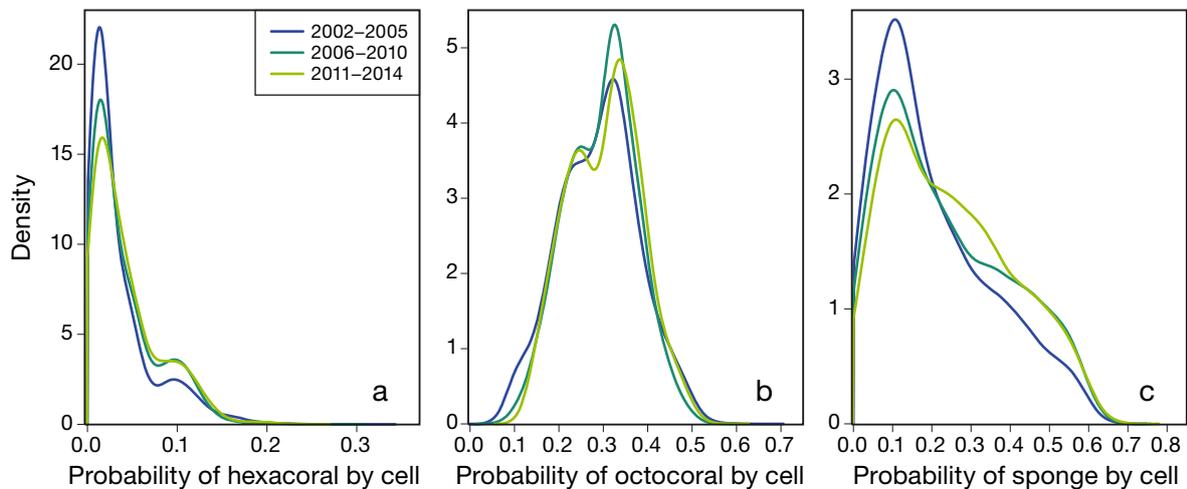


Fig. 6. Depiction of how fishing effort shifted over time as demonstrated by the distribution of habitat exposure of fished areas by management period for (a) hexacorals, (b) octocorals, and (c) sponges. These are represented by kernel density estimates of the distribution of the general additive model output (i.e. the plots can be thought of as smoothed histograms)

frequent gear interactions (Fig. 8; compare line heights among columns). Qualitative trends in the predicted number of contacts index were largely unchanged by weighting the occurrence probabilities by the distance towed through each cell (Fig. S8), so we used the unweighted approach throughout.

In contrast to trends in total gear–habitat interactions, the overall trend in the relative frequency of predicted contacts (contacts per haul) was an increase with time until 2009 (ranging from 17–56% across taxa), after which there was a moderate

decline (10–34%; Fig. 9a–c). Observed relative frequencies of encounter also increased over time for octocorals (132%), but the response was parabolic for sponges (743% increase between 2002 and 2008; 87% decrease between 2008 and 2014) and no trend was evident for hexacorals (Fig. 9d–f). Notably, the observed relative frequencies of encounter were lower than predicted relative frequencies of encounter by up to an order of magnitude (compare modes in Fig. 3d–f to values in Fig. 9d–f). This discrepancy is even more dramatic considering that

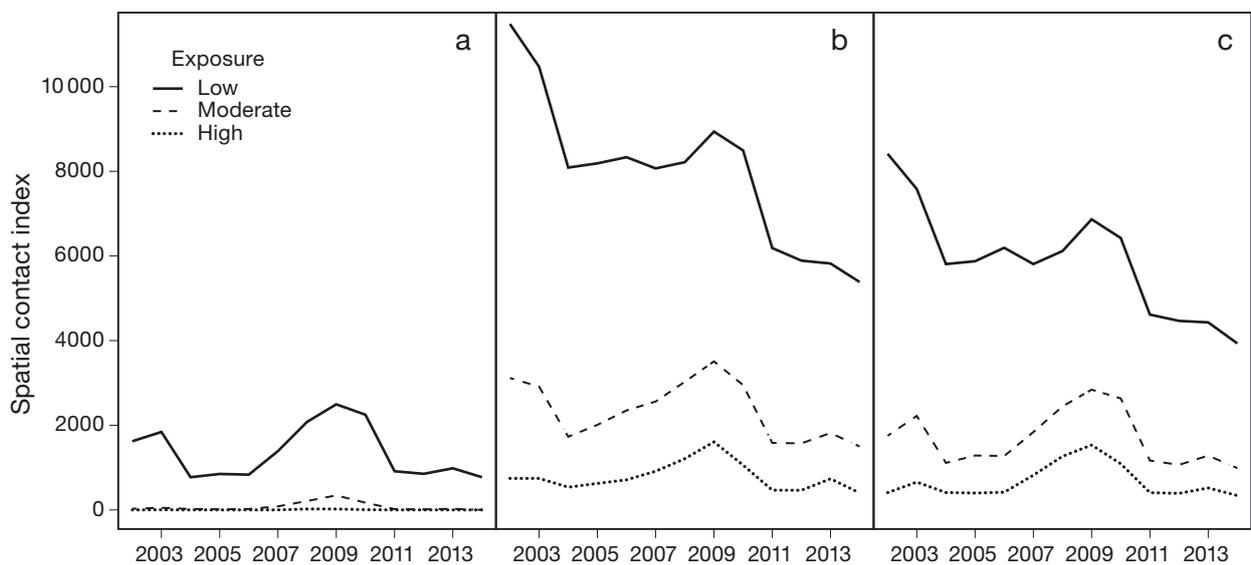


Fig. 7. Predicted temporal changes in spatial extent of contacts between groundfish bottom-trawls and US west coast biogenic habitat, including (a) hexacorals, (b) octocorals, and (c) sponges. The spatial contact index represents the number of spatial cells (2×2 km) each year with a number of expected interactions ≥ 1 (low intensity), 5 (moderate intensity), or 10 (high intensity)

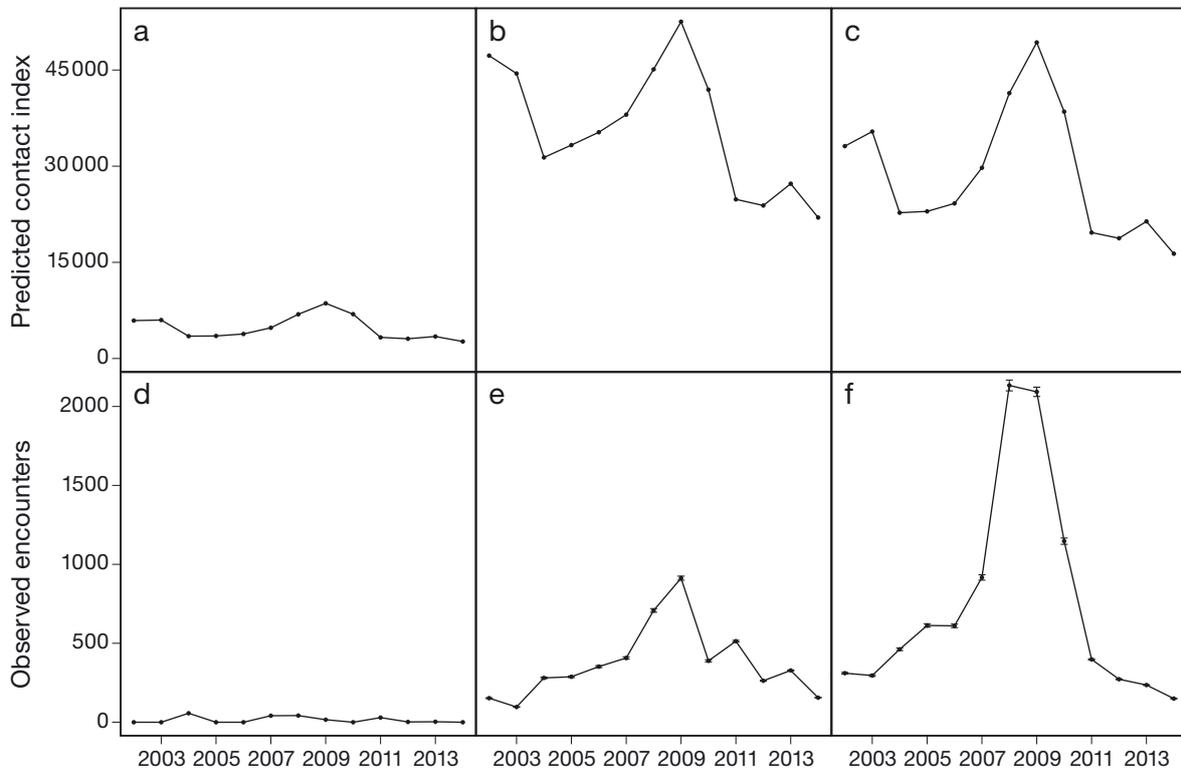


Fig. 8. (a–c) Predicted and (d–f) observed temporal trends in total groundfish bottom-trawl interactions with US west coast biogenic habitat, including (a,d) hexacorals, (b,e) octocorals, and (c,f) sponges. Error bars represent 2 SE

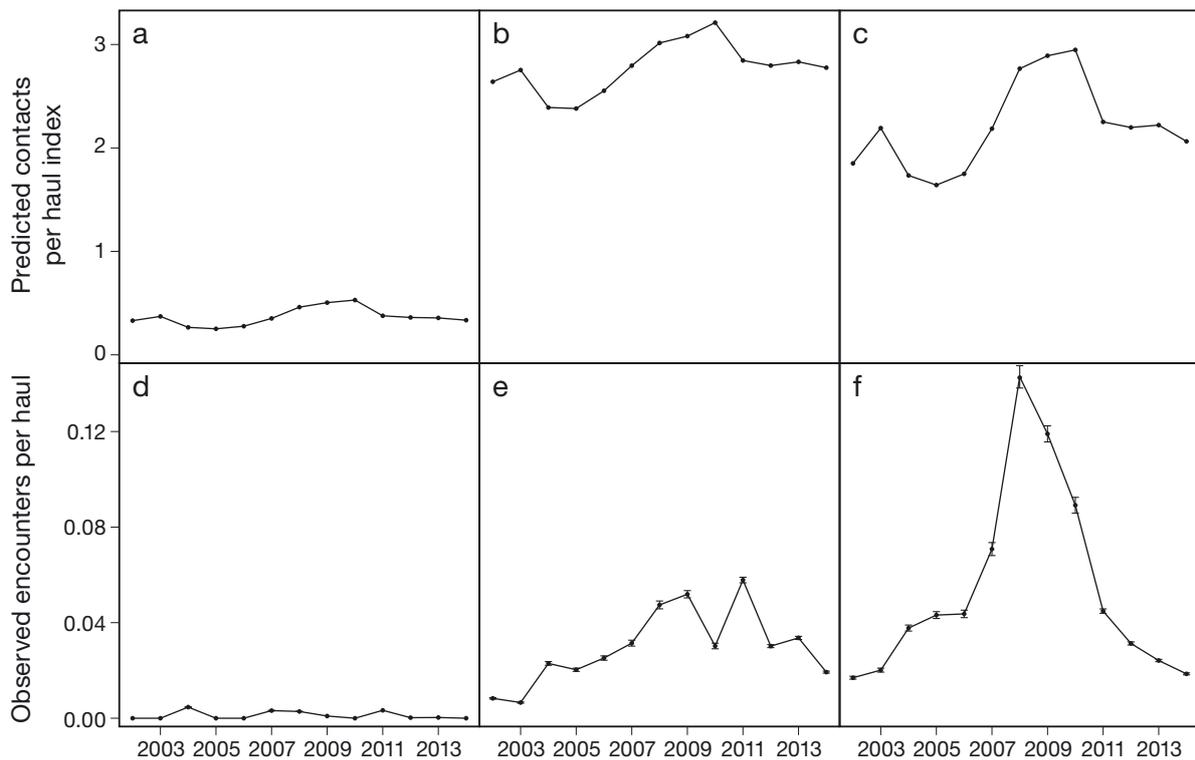


Fig. 9. (a–c) Predicted and (d–f) observed temporal trends in relative frequency of groundfish bottom-trawl interactions with US west coast biogenic habitat, including (a,d) hexacorals, (b,e) octocorals, and (c,f) sponges. Error bars represent 2 SE

haul durations in the fishery are far longer (interquartile range: 2.2–5.8 h) than those in the survey (interquartile range: 0.27–0.32 h). We emphasize that our prediction method provides an index of the number of contacts, not an absolute estimate, where the latter would be of greater magnitude given that we only detected contacts if the gear retained the biogenic habitat.

DISCUSSION

Here, we analyzed spatiotemporal patterns of anthropogenic disturbance of biogenic habitat at a regional scale, providing insight into how policies may have influenced such patterns. We quantified the intensity and extent of interactions between mobile commercial fishing gear and deep-water structure-forming invertebrates, which may contribute to fish productivity (e.g. Freese & Wing 2003, Auster 2005, 2007, Baillon et al. 2012). We found substantial spatial differences in exposure among taxa that led to contrasts in the spatial distribution of predicted interactions between trawl gear and biogenic habitat. While the overall spatial extent of gear–habitat interactions contracted over time, there was significant variation in the distribution of fishing effort that caused an increase in frequency of interactions per unit effort, which coincided with implementation of spatial closures. Subsequent implementation of catch shares did not significantly affect the distribution of fishing effort relative to the distribution of biogenic habitat exposure, yet there was a coincident decline in our index of the number of gear–habitat interactions, consistent with a large decrease in total fleetwide trawling effort. Throughout the study period, changes in total fleetwide effort had a greater effect on the gear–habitat interaction index than did changes in the distribution of fleetwide effort.

The interaction between bottom trawling and US west coast biogenic habitat varied among taxa. In general, biogenic habitat was most affected by bottom trawling in deep waters off Oregon and Washington, where much of the region's fishing effort occurs (Somers et al. 2015), and we predict that octocorals and sponges are quite abundant in these offshore waters. Octocorals and sponges had the highest frequency of interaction with trawl gear, yet both groups were also found in regions of southern California where little or no trawling occurs. Hexacorals were rarely recorded in either the survey or the fishery, and consequently their distribution was not well predicted. However, the relative intensity and extent

of gear interactions is expected to be low for hexacorals, particularly in the context of the presumed overall distribution of black corals (the taxon with the greatest representation within our hexacoral group) across the broader region (Guinotte & Davies 2014). For example, our predicted spatial distribution of hexacoral exposure and trawl interactions was somewhat consistent with predictions from Guinotte & Davies (2014) based on a habitat suitability model, in particular, indicating that most black corals are located deeper than bottom trawling.

The overall effect of bottom trawling on US west coast biogenic habitat remains highly uncertain, in part because of the discrepancy between observed and predicted relative interaction frequencies. This discrepancy has at least 4 plausible explanations: (1) the predicted contact index is biased because the survey gear used to predict habitat exposure is too different from that used in the fishery; (2) fishers are actively and successfully avoiding areas with high habitat exposure, given knowledge of the small-scale variation in the distribution of biogenic habitat; (3) fishers tend to trawl along known tracks (Branch et al. 2005), leading to low encounter rates due to local depletion or flattening of biogenic habitat caused by repeated trawling of the same areas; (4) observed encounter rates are biased low because of detection and reporting issues. Explanation 1 is unlikely, given that the index is accurately capturing most of the broader temporal trends and the fact that the trawl gear used in the survey and fishery are very similar with the exception of a slightly larger midsection of footrope and smaller mesh size in the codend liner of the survey gear (Bradburn et al. 2011). Explanation 2 is the most convincing, given that the low amount of deviance explained by our habitat exposure models indicates there is much fine-scale variation in the distribution of biogenic habitat. It is also possible that the survey is accessing small, isolated (i.e. surrounded by rough substrate) patches of soft-bottom habitat that fishers typically avoid given their preference for longer hauls over continuous soft-bottom habitat (Bellman et al. 2005), providing limited indirect support for explanation 3, which is plausible yet lacks any direct evidence. Finally, explanation 4 is highly unlikely given the extensive training of at-sea observers and the fact that the magnitude of difference between observed and predicted interactions is too large to be accounted for by an occasional lack of detection or identification of small quantities of biogenic habitat in the catch. In summary, the available evidence indicates that perhaps the most likely cause of the discrepancy in magnitude of the frequency of

interactions between trawl gear and biogenic habitat is the tendency for fishers to avoid known patches of rough seafloor (where rocks or biogenic habitat may interfere with fishing activities).

Spatiotemporal trends in overall frequency of interactions with biogenic habitat were largely—but not exclusively—explained by fleetwide fishing effort, which is consistent with predictions and observed correlation of responses to effort changes in other systems (Hiddink et al. 2006b, Pears et al. 2012, Pitcher 2013, Pitcher et al. 2016). Although fishing effort has typically decreased since 2008, the fishery has been more concentrated on areas with high probability of biogenic habitat occurrence, and the relative biogenic habitat interaction frequencies (interactions per haul) have remained high. This spatial shift is likely due to fishing becoming more concentrated in the north and focusing on a narrower range of depths over the years (Somers et al. 2015), which may have been driven by spatial fishery closures implemented in 2006. One might expect that such closures of rocky areas would lead to a decrease in the number of hauls through locations with exposed biogenic habitat, but many of these areas may have been already inaccessible given the restrictions on footrope size implemented in 2002 (Bellman et al. 2005).

The implementation of the catch-share program does not appear to have reduced disturbance of biogenic habitat beyond its role in effort reduction. Catch shares reduced trawl effort through restricted allocation (Kuriyama et al. 2016), and potentially by fishers responding to changing incentives and switching to fixed gear (Kroetz & Sanchirico 2010, E. Steiner & D. Holland unpubl.). The one possible exception is sponges, for which the decrease in observed relative frequency of interaction since 2010 has been much more dramatic than that of the predicted relative interaction frequency. Perhaps fishers attempt to avoid sponges because of potential damage to gear or nuisance of removing them from the net, and therefore catch shares—by negating a race to fish—have made fishers more precautionary in how or where they fish. Other evidence supports the presence of such precautions, as fishers are not utilizing their entire quota for many species (Kuriyama et al. 2016). However, the potential for damaging or losing gear on high-relief rocky habitat, or the risk of incidentally catching species for which the quota is low and thus costly to obtain (e.g. yelloweye rockfish *Sebastes ruberrimus*) are the most likely drivers of decreased interactions with sponges. Across systems, there are limited data to assess how catch shares for

targeted finfishes affect habitat disturbance (Branch 2009), but our results indicate that such policies can facilitate reductions in seafloor disturbance, albeit indirectly by modifying effort. Generally, catch shares are only likely to have a substantial direct effect on habitat disturbance if there are individual bycatch quotas for structure-forming invertebrates, as implemented for corals and sponges in British Columbia, Canada (Wallace et al. 2015). Theory also supports the potential effectiveness of individual habitat quotas for conservation of biogenic habitat, with indications that this approach is more likely to be effective and efficient than implementation of no-take areas (Holland & Schnier 2006).

The efficacy of spatial closures for habitat protection is not as clear as that of effort reduction (Duplisea et al. 2002, Dinmore et al. 2003, Hiddink et al. 2006b). While spatial closures may be the best tool for habitat protection in regions where sensitive habitats are highly concentrated, such as seamounts in the deep ocean (Clark & Dunn 2012), without complementary policies to reduce effort, the effect on biogenic habitat may intensify in unprotected areas. Although our results indicate that this form of effort displacement may have led to increasing disturbance frequency for some forms of US west coast biogenic habitat following spatial closures designed to protect fish habitat, we caution that this interpretation is clouded by the fact that high-relief rocky habitats (which often contain large populations of biogenic habitat) are not included in our analysis. In addition, given that cumulative habitat damage is often an asymptotic function of the number of hauls conducted in the same area (e.g. Poiner et al. 1998), it is plausible that spatial closures may have increased the overall population viability of biogenic habitat by constraining the spatial extent of fishing effects on biogenic habitat while preserving source populations for resettlement. Indeed, spatial heterogeneity in trawling is predicted to facilitate population persistence and increase recovery time, but this may have negligible or negative consequences unless the spatial distribution of trawling is relatively constant (Duplisea et al. 2002, Dinmore et al. 2003) and concentrated on areas with the fastest recovery rates (Lambert et al. 2014), i.e. permanent, stationary no-trawl or no-take zones placed on slow-recovering biogenic habitats (Hiddink et al. 2006b). Thus, long-term benefits to US west coast biogenic habitat may be more likely to arise from the stationary closures rather than the dynamic, coast-wide Rockfish Conservation Area. However, the results of this study and several others indicate that reducing the risk of

gear–habitat interactions is better accomplished with uniform effort reduction than with additional spatial closures (Ellis & Pantus 2001, Pitcher et al. 2007, 2016, Ellis et al. 2008). Given the complex socio-economic dynamics of fisheries, if policymakers decide to increase protections for biogenic habitat they should consider a combination of effort reduction along with other policies such as spatial closures, move-on rules, gear modifications, and individual bycatch quotas for structure-forming invertebrates.

There are several major sources of uncertainty in our analysis. The primary source of uncertainty arises from the use of trawl sampling, which is a coarse—but the only available—method for directly estimating the exposure of biogenic habitat at large spatial scales and fine resolution. Given the low magnitude of deviance explained by our models of spatial biogenic habitat exposure to trawls, it is clear that our ability to map exposed biogenic habitat is somewhat limited by, for example, the presence of much fine-scale variation in the distribution of structure-forming taxa. The deviance explained by our best-supported models (5–18%) is similar to that of another study from the northeast Pacific that also used a GAM fit to trawl survey data, but with more environmental predictor variables (8–19%; Rooper et al. 2014). Thus, it is more likely that the low explanatory power of our models is due to the mismatch between scales of trawl sampling and habitat heterogeneity in this region than the lack of additional environmental predictors. Another source of uncertainty arises because we are not accounting for biogenic habitat that is present in untrawlable habitat, and the fact that structure-forming invertebrates can be damaged and pass through the net, and therefore go undetected. The variation in retention by taxon observed in some regions (Auster et al. 2011 and references therein) could introduce additional uncertainty in the magnitude of gear–habitat interactions overall and bias our comparison across taxa, but this would not affect the results on relative spatiotemporal trends in interactions. Furthermore, bottom-trawl samples are good predictors of biogenic habitat distribution in other areas of the northeast Pacific, such as the eastern Bering Sea, based on validation using camera surveys (Rooper et al. 2016). In an effort to mitigate some of the uncertainty associated with our sampling methods, we focused on occurrence rather than the biomass of biogenic habitat retained in the gear, so each observation could indicate the presence of a dense aggregation of invertebrates that is creating substantial habitat or a few sparse organisms providing little structure. There are likely factors not in-

cluded in our analysis that are changing through time and could theoretically confound our interpretation of the influence of management policies on habitat. However, it is unlikely that the changes in the spatial distribution of fishing effort were driven by shifts in the distribution of fishes targeted by bottom trawling in this region (Thorson et al. 2016).

We demonstrate that the magnitude of gear–habitat interactions is largely driven by fleetwide trawl effort, based on an evaluation of spatiotemporal patterns at a coast-wide scale that would be unobtainable with existing alternative methods. Future research on this topic would benefit from incorporating fine-scale vessel tracking information to increase precision of trawl path estimates. *In situ* observations would also be particularly useful to determine the relationship between the magnitude of damage done by trawl gear and the quantity of biogenic habitat retained in the net.

Acknowledgements. We thank the NWFSC observer analyst team for facilitating data access (particularly Jon McVeigh, Jason Jannot, and Kayleigh Somers); NWFSC FRAM Fisheries Research Survey Team (Keith Bosley, John Buchanan, Mark Bradburn, Doug Draper, Melissa Head, John Harms, Aimee Keller, Dan Kamikawa, Victor Simon, and Vanessa Tuttle) and fishermen crew on the US West Coast Groundfish Bottom Trawl Survey; Jordan Watson and Allan Hicks for technical assistance; Waldo Wakefield, Curt Whitmire, and Joseph Bizzarro for helpful discussions; and Will Satterthwaite and 4 anonymous reviewers for comments that helped improve the manuscript. Funding was provided by the Gordon and Betty Moore Foundation and the Joint Institute for the Study of the Atmosphere and Ocean (JISAO) under NOAA Cooperative Agreement No. NA15OAR 4320063, Contribution No. 2016-01-24. T.A.B. was supported in part by the Richard C. and Lois M. Worthington Endowed Professor in Fisheries Management.

LITERATURE CITED

- ✦ Aburto-Oropeza O, Ezcurra E, Danemann G, Valdez V, Murray J, Sala E (2008) Mangroves in the Gulf of California increase fishery yields. *Proc Natl Acad Sci USA* 105: 10456–10459
- ✦ Althaus F, Williams A, Schlacher TA, Kloser RJ and others (2009) Impacts of bottom trawling on deep-coral ecosystems of seamounts are long-lasting. *Mar Ecol Prog Ser* 397:279–294
- ✦ Andrews A, Cordes EE, Mahoney MM, Munk K, Coale KH, Cailliet GM, Heifetz J (2002) Age, growth and radiometric age validation of a deep-sea, habit-forming gorgonian (*Primnoa resedaeformis*) from the Gulf of Alaska. *Hydrobiologia* 471:101–110
- Andrews AH, Cailliet GM, Kerr LA, Coale KH, Lundstrom C, DeVogelaere AP (2005) Investigations of age and growth for three deep-sea corals from the Davidson Seamount off central California. In: Freiwald A, Roberts JM (eds) *Cold-water corals and ecosystems*. Springer, Berlin, p 1021–1038

- Aranha R, Edinger E, Layne G, Piercey G (2014) Growth rate variation and potential paleoceanographic proxies in *Primnoa pacifica*: insights from high-resolution trace element microanalysis. *Deep Sea Res II* 99:213–226
- Arkema KK, Guannel G, Verutes G, Wood SA and others (2013) Coastal habitats shield people and property from sea-level rise and storms. *Nat Clim Chang* 3:913–918
- Auster PJ (2005) Are deep-water corals important habitats for fishes? In: Freiwald A, Roberts JM (eds) *Cold-water corals and ecosystems*. Springer, Berlin, p 747–760
- Auster PJ (2007) Linking deep-water corals and fish populations. *Bull Mar Sci* 81:93–99
- Auster PJ, Cjerde K, Heupel E, Watling L, Grehan A, Rogers AD (2011) Definition and detection of vulnerable marine ecosystems on the high seas: problems with the 'move-on' rule. *ICES J Mar Sci* 68:254–264
- Babcock EA, Pikitch EK, McAllister MK, Apostolaki P, Santora C (2005) A perspective on the use of spatialized indicators for ecosystem-based fishery management through spatial zoning. *ICES J Mar Sci* 62:469–476
- Baillon S, Hamel JF, Wareham VE, Mercier A (2012) Deep cold-water corals as nurseries for fish larvae. *Front Ecol Environ* 10:351–356
- Bellman MA, Heppell SA, Goldfinger C (2005) Evaluation of a US West Coast groundfish habitat conservation regulation via analysis of spatial and temporal patterns of trawl fishing effort. *Can J Fish Aquat Sci* 62:2886–2900
- Bellman MA, Wakefield W, Whitmire CE, Feist B (2013) Methods for examining stressors to EFH. In: *Groundfish essential fish habitat synthesis report appendices*. Supplemental NMFS Synthesis Report 2. NMFS, Seattle, WA, p 151–338
- Bradburn MJ, Keller AA, Horness BH (2011) The 2003 to 2008 US West Coast bottom trawl surveys of groundfish resources off Washington, Oregon, and California: estimates of distribution, abundance, length, and age composition. *Tech Memo NMFS-NWFSC-114*. US Department of Commerce, NOAA, Seattle, WA
- Branch TA (2009) How do individual transferable quotas affect marine ecosystems? *Fish Fish* 10:39–57
- Branch TA, Hilborn R, Bogazzi E (2005) Escaping the tyranny of the grid: a more realistic way of defining fishing opportunities. *Can J Fish Aquat Sci* 62:631–642
- Brodeur RD (2001) Habitat-specific distribution of Pacific ocean perch (*Sebastes alutus*) in Pribilof Canyon, Bering Sea. *Cont Shelf Res* 21:207–224
- Brooks TM, Mittermeier RA, Mittermeier CG, Da Fonseca GA and others (2002) Habitat loss and extinction in the hotspots of biodiversity. *Conserv Biol* 16:909–923
- Burrige C, Pitcher C, Wassenberg T, Poiner I, Hill B (2003) Measurement of the rate of depletion of benthic fauna by prawn (shrimp) otter trawls: an experiment in the Great Barrier Reef, Australia. *Fish Res* 60:237–253
- Carreiro-Silva M, Andrews AH, Braga-Henriques A, de Matos V, Porteiro FM, Santos RS (2013) Variability in growth rates of long-lived black coral *Leiopathes* sp. from the Azores. *Mar Ecol Prog Ser* 473:189–199
- Clark MR, Dunn MR (2012) Spatial management of deep-sea seamount fisheries: balancing sustainable exploitation and habitat conservation. *Environ Conserv* 39:204–214
- Clark MR, Althaus F, Schlacher TA, Williams A, Bowden DA, Rowden AA (2016) The impacts of deep-sea fisheries on benthic communities: a review. *ICES J Mar Sci* 73(Suppl 1):i51–i69
- Claudet J, Fraschetti S (2010) Human-driven impacts on marine habitats: a regional meta-analysis in the Mediterranean Sea. *Biol Conserv* 143:2195–2206
- Collie JS, Hall SJ, Kaiser MJ, Poiner IR (2000) A quantitative analysis of fishing impacts on shelf-sea benthos. *J Anim Ecol* 69:785–798
- Dinmore TA, Duplisea DE, Rackham BD, Maxwell DL, Jennings S (2003) Impact of a large-scale area closure on patterns of fishing disturbance and the consequences for benthic communities. *ICES J Mar Sci* 60:371–380
- Du Preez C, Tunnicliffe V (2011) Shortspine thornyhead and rockfish (Scorpaenidae) distribution in response to substratum, biogenic structures and trawling. *Mar Ecol Prog Ser* 425:217–231
- Duke NC, Meynecke JO, Dittmann S, Ellison AM and others (2007) A world without mangroves? *Science* 317:41–42
- Duplisea DE, Jennings S, Warr KJ, Dinmore TA (2002) A size-based model of the impacts of bottom trawling on benthic community structure. *Can J Fish Aquat Sci* 59:1785–1795
- Ellis N, Pantus F (2001) Management strategy modelling: tools to evaluate trawl management strategies with respect to impacts on benthic biota within the Great Barrier Reef Marine Park area. *CSIRO Marine Research*, Cleveland
- Ellis N, Pantus F, Welna A, Butler A (2008) Evaluating ecosystem-based management options: effects of trawling in Torres Strait, Australia. *Cont Shelf Res* 28:2324–2338
- Ewel KC, Twilley RR, Ong JE (1998) Different kinds of mangrove forests provide different goods and services. *Glob Ecol Biogeogr Lett* 7:83–94
- Foster MS, Schiel DR (2010) Loss of predators and the collapse of southern California kelp forests (?): alternatives, explanations and generalizations. *J Exp Mar Biol Ecol* 393:59–70
- Freese JL, Wing BL (2003) Juvenile red rockfish, *Sebastes* sp., associations with sponges in the Gulf of Alaska. *Mar Fish Rev* 65:38–42
- Freese L, Auster PJ, Heifetz J, Wing BL (1999) Effects of trawling on seafloor habitat and associated invertebrate taxa in the Gulf of Alaska. *Mar Ecol Prog Ser* 182:119–126
- Garcia SM, Zerbi A, Aliaume C, Do Chi T, Lasserre G (2003) The ecosystem approach to fisheries: issues, terminology, principles, institutional foundations, implementation and outlook. *Fish Tech Pap* 443. Food and Agriculture Organization, Rome
- Gneiting T, Raftery AE (2007) Strictly proper scoring rules, prediction, and estimation. *J Am Stat Assoc* 102:359–378
- Grabowski JH, Bachman M, Demarest C, Eayrs S and others (2014) Assessing the vulnerability of marine benthos to fishing gear impacts. *Rev Fish Sci Aquacult* 22:142–155
- Graham MH (2004) Effects of local deforestation on the diversity and structure of southern California giant kelp forest food webs. *Ecosystems* 7:341–357
- Groom MJ, Meffe GK, Carroll CR (2006) *Principles of conservation biology*. Sinauer Associates, Sunderland, MA
- Guinotte JM, Davies AJ (2014) Predicted deep-sea coral habitat suitability for the US West Coast. *PLOS ONE* 9:e93918
- Heifetz J (2002) Coral in Alaska: distribution, abundance, and species associations. *Hydrobiologia* 471:19–28
- Hermesen JM, Collie JS, Valentine PC (2003) Mobile fishing gear reduces benthic megafaunal production on Georges Bank. *Mar Ecol Prog Ser* 260:97–108
- Hewitt JE, Julian KA, Bone E (2011) Chatham-Challenger Ocean Survey 20/20 post-voyage analyses: Objective 10,

- biotic habitats and their sensitivity to physical disturbance. New Zealand Aquatic Environment and Biodiversity Report No. 81. Ministry of Fisheries, Wellington
- Hiddink J, Jennings S, Kaiser M, Queirós A, Duplisea D, Piet G (2006a) Cumulative impacts of seabed trawl disturbance on benthic biomass, production, and species richness in different habitats. *Can J Fish Aquat Sci* 63:721–736
- ✦ Hiddink J, Hutton T, Jennings S, Kaiser M (2006b) Predicting the effects of area closures and fishing effort restrictions on the production, biomass, and species richness of benthic invertebrate communities. *ICES J Mar Sci* 63:822–830
- ✦ Hilborn R, Stewart IJ, Branch TA, Jensen OP (2012) Defining trade-offs among conservation, profitability, and food security in the California Current bottom-trawl fishery. *Conserv Biol* 26:257–266
- Hill T, Spero H, Guilderson T, LaVigne M, Clague D, Macalello S, Jang N (2011) Temperature and vital effect controls on bamboo coral (*Isididae*) isotope geochemistry: a test of the 'lines method'. *Geochem Geophys Geosyst* 12:Q04008
- ✦ Holland DS, Schnier KE (2006) Protecting marine biodiversity: a comparison of individual habitat quotas and marine protected areas. *Can J Fish Aquat Sci* 63:1481–1495
- ✦ Hunte W, Wittenberg M (1992) Effects of eutrophication and sedimentation on juvenile corals. II. Settlement. *Mar Biol* 114:625–632
- Johnson KA (2002) A review of national and international literature on the effects of fishing on benthic habitats. Tech Memo NMFS-F/SPO-57. US Department of Commerce, NOAA, National Marine Fisheries Service, Silver Spring, MD
- ✦ Jurgiel B (2013) Point sampling tool. QGIS plugin. plugins.qgis.org/plugins/pointssamplingtool/
- ✦ Kaiser MJ, Collie JS, Hall SJ, Jennings S, Poiner IR (2002) Modification of marine habitats by trawling activities: prognosis and solutions. *Fish Fish* 3:114–136
- ✦ Kaiser MJ, Clarke KR, Hinz H, Austen MCV, Somerfield PJ, Karakassis I (2006) Global analysis of response and recovery of benthic biota to fishing. *Mar Ecol Prog Ser* 311:1–14
- ✦ Kaiser MJ, Hilborn R, Jennings S, Amaroso R and others (2016) Prioritization of knowledge-needs to achieve best practices for bottom trawling in relation to seabed habitats. *Fish Fish* 17:637–663
- Kleypas JA, Feely RA, Fabry VJ, Langdon C, Sabine CL, Robbins LL (2006) Impacts of ocean acidification on coral reefs and other marine calcifiers: a guide for future research. Report of a workshop held 18–20 April 2005, St. Petersburg, FL, sponsored by NSF, NOAA, USGS www.isse.ucar.edu/florida/report/Ocean_acidification_res_guide_compressed.pdf
- ✦ Koslow JA, Gowlett-Holmes K, Lowry JK, O'Hara T, Poore GCB, Williams A (2001) Seamount benthic macrofauna off southern Tasmania: community structure and impacts of trawling. *Mar Ecol Prog Ser* 213:111–125
- Kroetz K, Sanchirico JN (2010) Economic insights into the costs of design restrictions in ITQ programs. Resources for the Future, Washington, DC
- ✦ Kuriyama PT, Branch TA, Bellman MA, Rutherford K (2016) Catch shares have not led to catch-quota balancing in two North American multispecies trawl fisheries. *Mar Policy* 71:60–70
- ✦ Lacharité M, Metaxas A (2013) Early life history of deep-water gorgonian corals may limit their abundance. *PLOS ONE* 8:e65394
- Lambert GI, Jennings S, Kaiser MJ, Davies TW, Hiddink JG (2014) Quantifying recovery rates and resilience of seabed habitats impacted by bottom fishing. *J Appl Ecol* 51:1326–1336
- ✦ Lindholm J, Kelly M, Kline D, de Marignac J (2008) Patterns in the local distribution of the sea whip, *Halipterus willemoesi*, in an area impacted by mobile fishing gear. *Mar Technol Soc J* 42:64–68
- ✦ Lindholm J, Gleason M, Kline D, Clary L, Rienecke S, Cramer A, Los Huertos M (2015) Ecological effects of bottom trawling on the structural attributes of fish habitat in unconsolidated sediments along the central California outer continental shelf. *Fish Bull* 113:82–97
- ✦ Lotze HK, Lenihan HS, Bourque BJ, Bradbury RH and others (2006) Depletion, degradation, and recovery potential of estuaries and coastal seas. *Science* 312:1806–1809
- ✦ Malecha PW, Stone RP (2009) Response of the sea whip *Halipterus willemoesi* to simulated trawl disturbance and its vulnerability to subsequent predation. *Mar Ecol Prog Ser* 388:197–206
- ✦ Mangialajo L, Chiantore M, Cattaneo-Vietti R (2008) Loss of fucoid algae along a gradient of urbanisation, and structure of benthic assemblages. *Mar Ecol Prog Ser* 358:63–74
- ✦ Mumby PJ, Edwards AJ, Arias-Gonzalez JE, Lindeman KC and others (2004) Mangroves enhance the biomass of coral reef fish communities in the Caribbean. *Nature* 427:533–536
- National Research Council (2002) Effects of trawling and dredging on seafloor habitat. National Academies Press, Washington, DC
- NOAA (2003) U.S. Coastal Relief Model - Northwest Pacific. National Geophysical Data Center, NESDIS, NOAA, US Department of Commerce. www.ngdc.noaa.gov/mgg/coastal/crm.html
- ✦ Pandolfi JM, Bradbury RH, Sala E, Hughes TP and others (2003) Global trajectories of the long-term decline of coral reef ecosystems. *Science* 301:955–958
- Pears R, Morison A, Jebreen E, Dunning MC and others (2012) Ecological risk assessment of the east coast otter trawl fishery in the Great Barrier Reef Marine Park: Tech Rep. Great Barrier Reef Marine Park Authority, Townsville
- ✦ Penney AJ, Guinotte JM (2013) Evaluation of New Zealand's high-seas bottom trawl closures using predictive habitat models and quantitative risk assessment. *PLOS ONE* 8:e82273
- PFMC (Pacific Fishery Management Council) (2008) Pacific Coast Groundfish Fishery Management Plan for the California, Oregon, and Washington groundfish fishery as amended through Amendment 19 (including Amendment 15). Pacific Fishery Management Council, Portland, OR
- ✦ Pham CK, Diogo H, Menezes G, Porteiro F, Braga-Henriques A, Vandepierre F, Morato T (2014) Deep-water longline fishing has reduced impact on Vulnerable Marine Ecosystems. *Sci Rep* 4:4837
- ✦ Pitcher CR (2013) Environmental sustainability assessment update for habitats, assemblages and bycatch species in the Torres Strait Prawn Fishery. Sci Tech Rep. CSIRO. <http://pzja.gov.au/wp-content/uploads/2013/07/Pitcher-Torres-Strait-trawl-sustainability-assessment-update-Final.pdf>
- ✦ Pitcher C, Poiner I, Hill B, Burrige C (2000) Implications of the effects of trawling on sessile megazoobenthos on a tropical shelf in northeastern Australia. *ICES J Mar Sci* 57:1359–1368
- Pitcher R, Doherty P, Arnold P, Hooper J and others (2007)

- Seabed biodiversity on the continental shelf of the Great Barrier Reef World Heritage Area. AIMS/CSIRO/QM/QDPI CRC Reef Research Task Final Report. CSIRO Marine and Atmospheric Research, Cleveland
- Pitcher CR, Ellis N, Venables WN, Wassenberg TJ and others (2016) Effects of trawling on sessile megabenthos in the Great Barrier Reef and evaluation of the efficacy of management strategies. *ICES J Mar Sci* 73:i115–i126
- Pitcher CR, Ellis N, Jennings S, Hiddink JG and others (2017) Estimating the sustainability of towed fishing-gear impacts on seabed habitats: a simple quantitative risk assessment method applicable to data-limited fisheries. *Methods Ecol Evol* 8:472–480
- Poiner I, Glaister J, Pitcher R, Burrige C and others (1998) Environmental effects of prawn trawling in the far northern section of the Great Barrier Reef Marine Park: 1991–1996. Final Report to the Great Barrier Reef Marine Park Authority and Fisheries Research and Development Corporation, Collingwood
- QGIS Development Team (2015) QGIS Geographic Information System. Open Source Geospatial Foundation Project. <http://qgis.osgeo.org>
- R Development Core Team (2015) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna
- Roark EB, Guilderson TP, Dunbar RB, Fallon SJ, Mucciarone DA (2009) Extreme longevity in proteinaceous deep-sea corals. *Proc Natl Acad Sci USA* 106:5204–5208
- Rooper CN, Wilkins ME, Rose CS, Coon C (2011) Modeling the impacts of bottom trawling and the subsequent recovery rates of sponges and corals in the Aleutian Islands, Alaska. *Cont Shelf Res* 31:1827–1834
- Rooper CN, Zimmermann M, Prescott MM, Hermann AJ (2014) Predictive models of coral and sponge distribution, abundance and diversity in bottom trawl surveys of the Aleutian Islands, Alaska. *Mar Ecol Prog Ser* 503: 157–176
- Rooper CN, Sigler MF, Goddard P, Malecha P and others (2016) Validation and improvement of species distribution models for structure-forming invertebrates in the eastern Bering Sea with an independent survey. *Mar Ecol Prog Ser* 551:117–130
- Rosenberg A, Bigford TE, Leathery S, Hill RL, Bickers K (2000) Ecosystem approaches to fishery management through essential fish habitat. *Bull Mar Sci* 66:535–542
- Sala E, Knowlton N (2006) Global marine biodiversity trends. *Annu Rev Environ Resour* 31:93–122
- Somers KA, Jannot JE, Hastie J, Lee YW, McVeigh J, Whitmire CE (2015) Fishing effort in the 2002–2013 U.S. Pacific Coast groundfish fisheries. West Coast Groundfish Observer Program, NMFS, NWFSC, Seattle, WA
- Steneck RS, Graham MH, Bourque BJ, Corbett D, Erlandson JM, Estes JA, Tegner MJ (2002) Kelp forest ecosystems: biodiversity, stability, resilience and future. *Environ Conserv* 29:436–459
- Stone R (2006) Coral habitat in the Aleutian Islands of Alaska: depth distribution, fine-scale species associations, and fisheries interactions. *Coral Reefs* 25:229–238
- Thorson JT, Barnett LAK (2017) Comparing estimates of abundance trends and distribution shifts using single- and multi-species models of fishes and biogenic habitat. *ICES J Mar Sci* 74:1311–1321
- Thorson JT, Pinsky ML, Ward EJ (2016) Model-based inference for estimating shifts in species distribution, area occupied and centre of gravity. *Methods Ecol Evol* 7: 990–1002
- Tissot BN, Yoklavich MM, Love MS, York K, Amend M (2006) Benthic invertebrates that form habitat on deep banks off southern California, with special reference to deep sea coral. *Fish Bull* 104:167–181
- Tittensor DP, Baco AR, Brewin PE, Clark MR and others (2009) Predicting global habitat suitability for stony corals on seamounts. *J Biogeogr* 36:1111–1128
- Valiela I, Bowen JL, York JK (2001) Mangrove forests: one of the world's threatened major tropical environments. *Bio-science* 51:807–815
- Wallace S, Turris B, Driscoll J, Bodtger K, Mose B, Munro G (2015) Canada's Pacific groundfish trawl habitat agreement: a global first in an ecosystem approach to bottom trawl impacts. *Mar Policy* 60:240–248
- Wang YH (1993) On the number of successes in independent trials. *Stat Sin* 3:295–312
- Watling L, Norse EA (1998) Disturbance of the seabed by mobile fishing gear: a comparison to forest clearcutting. *Conserv Biol* 12:1180–1197
- Williams A, Schlacher TA, Rowden AA, Althaus F and others (2010) Seamount megabenthic assemblages fail to recover from trawling impacts. *Mar Ecol* 31:183–199
- Wood S (2007) The mgcv package. <http://cran.r-project.org/web/packages/mgcv/index.html>

Editorial responsibility: Tim McClanahan, Mombasa, Kenya

*Submitted: October 31, 2016; Accepted: May 16, 2017
Proofs received from author(s): June 22, 2017*