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CONTRIBUTED PAPER

Convergence of fishers' knowledge with a species distribution model in a Peruvian shark fishery

Julia G. Mason[1] | Joanna Alfaro-Shigueto[2] | Jeffrey C. Mangel[3] | Stephanie Brodie[4] | Steven J. Bograd[4] | Larry B. Crowder[1] | Elliott L. Hazen[4]

[1]Department of Biology, Hopkins Marine Station of Stanford University, Pacific Grove, California

[2]ProDelphinus, Universidad Cientifica del Sur, Miraflores, Peru

[3]ProDelphinus, University of Exeter, Miraflores, Peru

[4]Environmental Research Division, NOAA Southwest Fisheries Science Center, Institute of Marine Science, University of California Santa Cruz, Monterey, California

Correspondence
Julia G. Mason, Hopkins Marine Station of Stanford University, 120 Ocean View Boulevard, Pacific Grove, CA 93950.
Email: jgmason@stanford.edu

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Limited data on the spatial, environmental, and human dimensions of small-scale fisheries hinder conservation planning, so the incorporation of fishers' local ecological knowledge may be a valuable way to fill data gaps while legitimizing management decisions. In Peru, vulnerable and poorly assessed juvenile smooth hammerhead sharks (*Sphyrna zygaena*) are the most commonly caught shark species in a small-scale drift gillnet fishery. We conducted semistructured interviews with 87 hammerhead fishers in three major Peruvian ports to elucidate the spatiotemporal niche of the hammerhead fishery and environmental drivers of juvenile hammerhead catch. We also built a biophysical model of hammerhead distribution that correlated remotely sensed environmental variables with a spatially explicit fishery observer dataset. Overall, we found a consensus between fishers' knowledge and species distribution modeling. Sea surface temperature and chlorophyll-a emerged as important environmental drivers of juvenile hammerhead catch, with both fishers' knowledge and the biophysical model identifying similar habitat preferences (~20–23°C and log chl-a >−1.6 mg/m^3). Participatory mapping of fishing grounds also corresponded to the spatiotemporal patterns of predicted hammerhead distribution. This study points to the utility of combining fishers' knowledge and biophysical modeling for spatial, temporal, and/or dynamic management of these sharks in Peru and in other data-poor fisheries globally.

KEYWORDS
conservation planning, epistemological pluralism, generalized additive model, juvenile shark habitat, local ecological knowledge, small-scale fisheries, *Sphyrna zygaena*

1 | INTRODUCTION

Shark species, considered the most threatened marine vertebrate taxa globally (Dulvy, Carlson, et al., 2014), are also among the most data deficient (Hoffmann et al., 2018). In particular, limited data regarding exploitation in small-scale fisheries represents a challenge to conserving shark species worldwide (Worm et al., 2013). In Peru, sharks are targeted for human consumption and comprise approximately one third of small-scale fisheries landings (Gonzalez-Pestana, Kouri, & Velez-Zuazo, 2014). High catch of juvenile smooth hammerhead sharks (*Sphyrna zygaena*), in particular, presents a conservation concern. Evaluated as vulnerable by the International Union for the Conservation of Nature (IUCN), smooth hammerheads are poorly assessed and lack data on their distribution and life history (Simpfendorfer, 2005), especially for the eastern Pacific. Smooth hammerheads are

Combining biophysical models and fishers' local ecological knowledge holds promise for conservation planning in data-poor fisheries.

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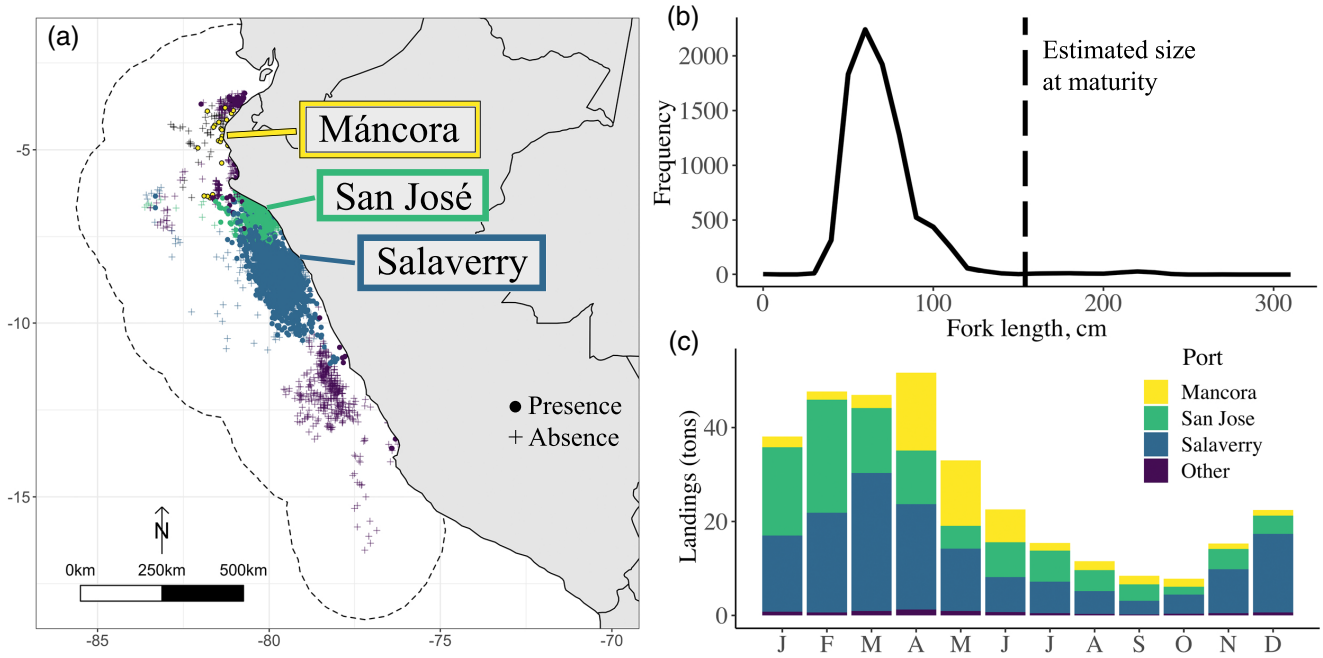


FIGURE 1 (a) Location of 1,644 gillnet sets with hammerheads present (circles) and 2,207 gillnet sets with hammerheads absent (plusses) used to build the generalized additive model. Interview locations are indicated, and sets from the corresponding points shaded accordingly (darkest points indicate sets from ports not interviewed). Dashed line indicates fishing grounds defined by a 2° buffer around all presence and absence points. (b) Distribution of fork length of 9,086 observed smooth hammerheads in gillnet sets between 2004 and 2016. Dashed line indicates estimated size at maturity. (c) Recorded mean monthly landings (tons) recorded of smooth hammerhead sharks from January 1997, when Peru started recording disaggregated shark species landings, until September 2013 (Adapted from de la Puente Jeri, 2013)

the third most commonly caught shark species in Peru and the most commonly caught in the drift gillnet fishery that operates out of northern ports (Figure 1a) (Gonzalez-Pestana et al., 2014), with total annual landings of approximately 500 tons (de la Puente Jeri, 2013). While legally defined as "small-scale" based on vessel size and operation with manual labor, these fisheries operate on a scale comparable to industrial fisheries, with over 100,000 km of nets in the water annually and fishing trips lasting up to 3 weeks (Alfaro-Shigueto et al., 2010). Nearly 18,000 small-scale vessels reportedly operate along the 2,400 km coast, employing over 67,000 fishers (Guevara-Carrasco & Bertrand, 2017).

Landings of smooth hammerheads in Peru are almost entirely juveniles (Figure 1b), theorized to be due to overlap between fishing grounds and coastal nursery areas (Castañeda, 2001; Gonzalez-Pestana, 2014). Seasonal patterns in official landings data (Figure 1c) suggest that female sharks approach coastal areas for parturition in the early austral summer (November and December), and juveniles aggregate along the coast for several months before migrating out for an oceanic adulthood (Compagno, 1984; Simpfendorfer, 2005). These landings data do not precisely reflect where sharks are caught given fishers' highly mobile behavior, but currently inform management decisions, including a seasonal fishing ban implemented in 2016 to protect juvenile hammerheads (IMARPE, 2014; PRODUCE, 2016) following the 2013 listing of three hammerhead species under Appendix II of the Convention on the International Trade of Endangered Species (CITES). Better understanding of the distribution and environmental niche of juvenile hammerhead sharks would contribute to regional knowledge of this species and inform fisheries management.

Species distribution models, which correlate documented presences and, if available, absences of species with environmental predictor variables, have been suggested as a valuable tool for conservation decision-making (Guisan et al., 2013). For smooth hammerheads in Peru, identifying environmental characteristics of nursery areas and spatial zones of high catch might inform management at finer spatial and/or temporal scales than landings data. However, species distribution models are data-intensive, especially when integrating multiple models as ensembles as is sometimes recommended (Araújo & New, 2007; Scales et al., 2017). The costs of collecting spatially explicit species data may be prohibitive for poorly studied species in remote areas.

One potential solution is incorporating local ecological knowledge throughout the planning process (Anadón, Giménez, Ballestar, & Pérez, 2009; Bélisle, Asselin, Leblanc, & Gauthier, 2018; Folke, 2004). In addition to filling data gaps, incorporating local knowledge in ecological models can legitimize management decisions and empower communities in resource management (Bélisle et al., 2018). Local ecological knowledge has been variously defined (Davis & Ruddle, 2010); here we take the more experiential version of "place-based empirical knowledge" (Bélisle et al., 2018). Increasingly called for in fisheries research and management, fishers' local ecological knowledge has been used to extend

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scientific time-series, refine stock assessments, design marine protected areas, and provide valuable social insight for informing management (Aswani, 2018; Hind, 2014; Johannes, Freeman, & Hamilton, 2000; Neis, 1992; Sáenz-Arroyo, Roberts, Torre, Cariño-Olvera, & Enríquez-Andrade, 2005). Ecological modeling and studies of fishers' knowledge often examine similar spatial questions, yet rarely are the results compared or integrated. While a few studies have incorporated local knowledge with ecological models, applications to marine environments and fisheries are limited (Bélisle et al., 2018; Grant & Berkes, 2007; Zhang & Vincent, 2017). In particular, studies with both spatially explicit biophysical models and fishers' ecological knowledge have not been conducted for fisheries applications. Examining fishers' knowledge alongside ecological models could be a valuable way to understand and manage data-poor small-scale fisheries, and holds potential for elasmobranch conservation globally.

Peru's hammerhead shark fishery provides a unique opportunity to incorporate fishers' knowledge with a spatially explicit onboard observer dataset spanning over a decade. Collected by trained observers at a Peruvian conservation nonprofit, these may be the only spatially explicit data on this species for this region. Furthermore, the high mobility and broad spatial scale of this fishery make the coarse spatiotemporal resolution of local knowledge studies more appropriate (Zhang & Vincent, 2017). The goal of our study is to examine the distribution of juvenile smooth hammerhead shark habitat along the Peruvian coast. We use two approaches: a statistical biophysical model and semistructured interviews eliciting fishers' ecological knowledge.

2 | METHODS

2.1 | Fisheries data

Onboard fishery observers recorded drift gillnet catch composition and fishing location from 2000 to 2016 across 13° of latitude (16.53°–3.37°S). Observers used Global Positioning System (GPS) devices to record the location of each net set at the onset of net deploy, end of net deploy, start of net retrieval, and end of net retrieval; we used the coordinates at the onset of net deploy in this study. Observers also recorded the main objective species for each fishing trip, port of departure and entry, and net dimensions. Observers identified animals to the species level with onboard guides and, conditions permitting, recorded sex, maturity (clasper state), and length (fork length or total length) of elasmobranchs. Observers more frequently recorded fork length than total length, so we converted all lengths to fork lengths (cm) with the conversion total length/1.28 for males and (total length + 0.616)/2.18 for females, which was derived from larger hammerheads (>1 m) in the Atlantic Ocean (Mas, Forselledo, & Domingo, 2014). Fork length at maturity is 151.33 cm for males and 156.73 cm for females based on estimates for smooth hammerheads in the Gulf of California (Nava & Márquez-Farías, 2014). We classified each net set by the presence or absence of juvenile hammerhead sharks. We omitted any sets for which latitude, longitude, or date data were missing, and sets from 38 trips for which observers did not measure hammerheads in any sets but reported hammerhead capture for the trip.

2.2 | Biophysical model

To determine juvenile hammerhead shark distribution and probability of presence, we built generalized additive models (GAMs) with a binomial distribution with the package mgcv (version 1.8.22) in R (version 3.4.2). We tested 17 predictor variables based on previously published studies of juvenile shark habitat (Alfaro-Shigueto, 2014; Campos, 2014; Cartamil et al., 2010; Oh, Sequeira, Meekan, Ruppert, & Meeuwig, 2017). These predictors included spatial variables: latitude, longitude, distance to coast (m), distance to protected coastal islands (m), distance to river mouths (m) (distances calculated with the R package geosphere version 1.5.7), and depth (m; from GEBCO bathymetry data); temporal variables as factors: year and month; variables regarding fishing behavior: port of departure ($n = 13$), whether the trip explicitly targeted sharks (binomial yes or no), and net mesh size (cm); satellite-derived environmental variables downloaded from Southwest Fisheries Science Center Environmental Research Division's ERDDAP (Simons, 2017): log-transformed chlorophyll-a concentration (chl-a, mg/m^3, 8 day composites from SeaWifs, MODIS, and VIIRS), sea surface temperature (SST) mean and *SD* (°C, from Pathfinder, MUR, and GHRSST); and mesoscale environmental variables downloaded from Aviso+ and the Copernicus Marine Environment Monitoring Service: sea level anomaly (SLA, m), finite-size Lyapunov exponents (FSLE, per day), and FSLE direction (theta, °). Log chl-a outliers less than −10 mg/m^3 were removed. We used a correlogram correlation matrix to evaluate collinearity between variables and in cases where correlation >0.6 we built models for each correlated variable and dropped the variable that yielded a poorer Akaike's Information Criterion (AIC).

Following exploratory tests, we considered five candidate models: all uncorrelated variables, only static variables, static and broad scale dynamic variables, static and mesoscale dynamic variables, and only dynamic variables (model details in Table S2). We selected the final model based on percent deviance explained and AIC, as well as area under curve (AUC) (Delong, Delong, & Clarke-Pearson, 1988), and true skill statistic (TSS) (Allouche, Tsoar, & Kadmon, 2006) performance metrics with the R package ROCR (version 1.0.7). For AUC and TSS we took the average of five model iterations, with iterations trained on a random 75% subset of the data and tested with the remaining 25%. We evaluated the contribution of each individual variable to the

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best model by fitting models with each single explanatory variable, and then fitting the best model with each individual variable removed (Friedlaender et al., 2016), and comparing AIC values and percent deviance explained. We tested for spatial autocorrelation in model residuals with Moran's *I* statistics with R packages ncf (version 1.2.5) and spdep (version 0.7.8) (Dormann et al., 2007).

We used the final best model to predict hammerhead shark presence likelihood, which we used as a measure of habitat suitability, off the Peruvian coast. We predicted on environmental data from 2012, an example year which was an El Niño-Southern Oscillation "neutral" year, in the months respondents identified as the hammerhead fishing season (December–April). We interpolated all covariates to a 0.25° grid to match the resolution at which SLA was available.

2.3 | Interviews

We conducted 87 semistructured interviews between February 8 and March 11, 2018 in the three ports with the largest drift-gillnet fleets: San José ($n = 32$; 109 total vessels), Salaverry ($n = 26$; 70 total vessels), and Máncora ($n = 29$; 55 total vessels) (Alfaro-Shigueto, 2014) (Figure 1a). We specifically interviewed drift-gillnet captains or boat owners as experts who make decisions about where and when to fish; sampling was opportunistic and based on fishers' availability. Two of our respondents were not currently active gillnetters, and it is possible that some interviews were with the captains and owners of the same vessel, so our samples were not exact proportions of Alfaro-Shigueto's (2014) above estimates of vessel numbers. Interviews were conducted in Spanish and translated into English prior to analysis. The interview protocol was approved by Stanford University's Institutional Review Board for human subjects research on January 11, 2018, protocol #44763.

The interviewer first asked respondents demographic questions about their fishing experience and methods, including which months they most fish for hammerheads. The interviewer then conducted a participatory mapping exercise to characterize the spatial extent of juvenile hammerhead fishing grounds. This was done by asking respondents to draw on a printed map where they catch hammerheads. The map was labeled with a longitude and latitude grid at the degree scale, the names of major ports, coastal islands, and the 250 m isobath representing the continental shelf (see Figure S1, for example maps). Most fishers were familiar with maps and coordinates, but if they seemed unfamiliar the interviewer oriented them to the coast, their home port, and the islands.

The interviewer also asked a series of questions to characterize fishers' environmental niche. Respondents were first asked, "When you're fishing, what do you look for to know if there are hammerheads?" If needed, the interviewer clarified with the terms "indicators," "evidence," or "how do you know if hammerheads are in the water?" After recording responses to this open question, the interviewer asked specifically about environmental cues corresponding to variables used in the biophysical model including temperature, color of the water, currents or waves, distance from the coast, and distance from coastal islands if the respondent had not mentioned them.

2.4 | Interview analysis

We digitized and georeferenced participatory maps in ArcGIS ArcMap following Wahle and D'Iorio (2010) and Levine and Feinholz (2015). We categorized the polygons that respondents had indicated as their hammerhead fishing grounds based on which fishing months the respondent had specified and collated all responses onto the same 0.25° grid for each month (matching the biophysical model prediction grid), where any part of a polygon intersecting a grid cell marked a count. To characterize the environmental profile of these indicated fishing grounds, we overlaid the participatory grids with the same monthly biophysical predictor rasters, selecting only temperature and chl-a as they emerged as important in the interviews. From these rasters, we extracted environmental values, weighted by the number of polygons intersecting each grid cell. We hereafter refer to these distributions of values as the "fisher-mapped" hammerhead habitat.

We coded the interviews for emergent themes in NVivo (QSR International, version 12) and extracted any quantitative environmental information, hereafter referred to as the "fisher-stated" hammerhead habitat. Only unprompted responses were used to characterize general patterns in hammerhead fishing behavior, while prompted responses were also included for subsequent qualitative and quantitative analysis of specific environmental cues. One such cue was temperature, for which we examined the distribution of fisher-stated temperature preferences from both prompted and unprompted responses. We categorized the distribution into quantiles: we classified "optimal" habitat as the mean reported temperature ± 0.5°, second most optimal as between the 0.25 or 0.75 quantiles and optimal temperature, and <0.25 or >0.75 quantiles as least optimal. We interpreted responses about color of water as pertaining to chl-a concentration, as measures of turbidity or other processes that may affect water color were less readily available. We used a cutoff of 0.2 chl-a (mg/m^3), or approximately −1.6 log chl-a (mg/m^3), which has been used to delineate oligotrophic from productive water masses in the north Pacific Ocean (Polovina, Howell, Kobayashi, & Seki, 2001) to differentiate between "blue" (i.e., clear) and "green" (i.e., colored, turbid) water.

2.5 | Biophysical model and interview comparisons

We employed two approaches to compare hammerhead shark habitat suitability between the biophysical model predictions and the fishers' knowledge. First, we qualitatively

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compared the spatial extent of hammerhead habitat from the biophysical model predictions, fisher-stated habitat, and participatory maps. To visualize fisher-stated habitat spatially, we classified the same monthly rasters used in the biophysical model prediction according to the optimal categories and cutoffs described above. Second, we compared the environmental profiles of predicted hammerhead habitat from the different methods. To compare biophysical model predictions and the fisher-mapped environmental variables, we extracted environmental values from the same cells where model predicted hammerhead suitability values were >0.5. We also determined the "background" environmental profile for each month for the overall fishing grounds, defined as a polygon surrounding all observed set nets with a 2° buffer (Figure 1a). We compared the density distributions of model-derived and fisher-mapped variables with biophysical model partial plot response curves and fisher-stated variables where applicable. We performed both these comparisons for each month in the peak fishing season (December–April) as well as for an aggregate over the peak season. In the spirit of epistemological pluralism (Miller et al., 2008), we present results from the biophysical model and the interviews side by side rather than use one method as the standard by which to evaluate the other.

3 | RESULTS

3.1 | Fisheries data

A total of 3,851 net sets from 125 boats and 13 ports were used to build the biophysical models, which included 1,644 juvenile hammerhead presences and 2,207 absences (Figure 1a). Fork lengths of hammerhead sharks caught in sets (n = 9,086 sharks) ranged between 11 and 274 cm, with the majority between 50 and 80 cm (Figure 1b). Net sets were primarily concentrated along the northern Peruvian coast. The majority of set data came from the port of Salaverry (n = 2,101), followed by San José (n = 950), then Mancora (n = 84). Hammerhead shark landings varied between months, with the majority of landings occurring from January to May. However, northern ports (notably Mancora, 4.10°S) showed peak catches between April and June (Figure 1c).

3.2 | Biophysical model

The best biophysical model was the full uncorrelated model containing 12 variables, with 31.9% deviance explained (see Table S1 for model summary). This model had good predictive performance with an AUC of 0.83 and a TSS of 0.49 (see Table S2 for model selection statistics). This model included year, month, port of departure, targeting of sharks, mesh size, distance to islands, log chl-a, SST, SST *SD*, SLA, FSLE, and FSLE direction as covariates; with points with missing environmental data removed, the final model included 3,212 net sets. We removed latitude and longitude as covariates because they resulted in extreme values at the edges of our predictions.

TABLE 1 Contribution of each variable to the best biophysical model deviance explained with individual variable model (Dev. explained, single), full—1 model (Dev. explained, drop), and the difference in deviance explained between the full model and full-1 model (Difference from full)

Variable	Dev. explained, single	Dev. explained, drop	Difference from full
Port	7.45	23.41	−8.52
SST	4.75	23.56	−8.36
Target	8.42	25.33	−6.60
Distance to islands	4.02	25.35	−6.58
Log chl-a	3.29	25.63	−6.30
Year	1.74	25.66	−6.27
SST *SD*	2.29	26.29	−5.64
FSLE	0.30	26.66	−5.27
SLA	1.09	26.68	−5.25
FSLE direction	0.33	26.68	−5.24
Month	1.36	26.75	−5.17
Mesh size	5.61	27.09	−4.83

Note. FSLE: finite-size Lyapunov exponents; SST: sea surface temperature; SLA: sea level anomaly.

The port of departure and SST emerged as the most important explanatory variables in terms of lost deviance explained when dropped from the model, and targeting of sharks had the most explanatory power when considered independently (Table 1). The mesoscale variables (SLA and FSLE) had only a minor effect in describing shark habitat. Spatial predictions of shark habitat suitability (as measured by presence likelihood) are closely associated with coastal temperature and log chl-a distributions (Figure 2a,e). The SST response curve showed peak predicted habitat between 20 and 22°C (Figure 3c). The log chl-a response curve has an inflection point approaching 0 at −1.6 mg/m^3 (Figure 3d), further supporting our cutoff defining fisher-stated "green water." We did not find significant autocorrelation spatial structure in the residuals (Moran's I statistic = -3.13×10^{-4}, standard deviate = −2.13, p = 0.98), justifying running a model without latitude and longitude.

3.3 | Interviews

Respondents drew a total of 269 polygons spanning 17.42° of latitude (0.22°–17.64°S) and 12.80° longitude (76.54°–89.34°W) (Figure 2b,f). The highest overlap was 24 polygons in December, January, and February. Based on respondents' reports of the months they most fish for hammerheads, we defined the peak fishing season for all ports as December through April.

Respondents' most common unprompted explanation of drivers of hammerhead fishing behavior was that fishers cue to prey aggregations, such as anchovy, which they know

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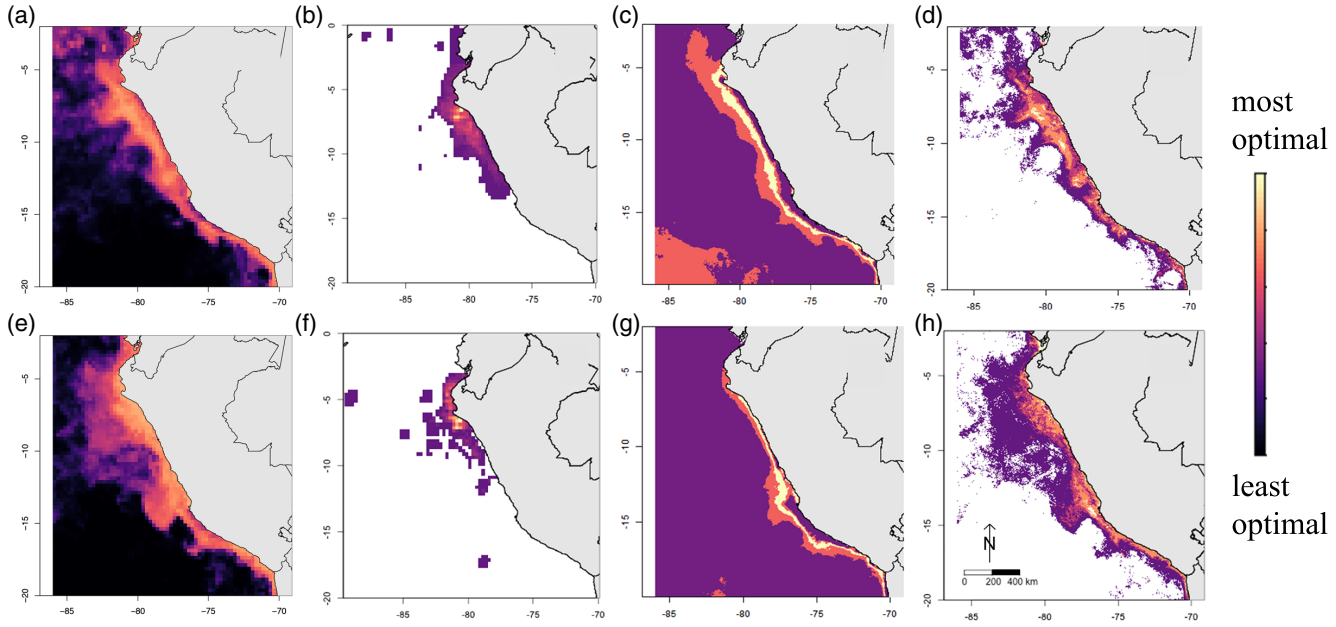


FIGURE 2 Median generalized additive model prediction (GAM) of juvenile hammerhead shark catch (a, e), aggregated participatory map polygons (b, f), fisher-stated temperature niche (c, g), and fisher-stated ocean color niche (d, h) for January (top row) and April (bottom row), 2012. Habitat suitability in each map goes from low (dark) to high (bright), measured as 0–1 presence likelihood for GAM predictions, 1–24 overlapping polygons for participatory maps, three discrete categories based on fisher-stated temperature quantiles (°C, see Figure 3) for sea surface temperature, and −1.6 to 3.0 mg/m^3 for log chl-a

attract sharks (30 respondents, 34%). The next most common unprompted answer had to do with the color of the water: green, brown, turbid, dark (30%). Eighteen percent of respondents explained that they share fishing information via radio communication, including providing specific coordinates, in social networks that may bridge ports. Fifteen percent described a "trial and error" strategy, emphasizing that with gillnets, the catch can be a surprise. Including prompted responses, 74% of respondents use temperature to fish for hammerheads, usually specifying warmer waters, and 48% (42) gave a specific degree or range; these specific responses comprise our fisher-stated hammerhead habitat temperature distribution (Figure 3a). Ninety percent of respondents use dark, turbid, or greenish waters to locate hammerheads (Figure 3b), and two respondents noted a relationship between warmer and greener water. Some respondents also noted when prompted that hammerheads are closer to the coast in the summer than in the winter, but in general did not cue to this distance or the other prompted variables as much as those described above. In subsequent results and discussion of fishers' knowledge, we focus on temperature and chl-a as they were the most commonly reported environmental drivers of fishing behavior.

3.4 | Biophysical model and interview comparisons

The spatial distributions of fisher-stated environmental variables, participatory maps, and biophysical model predictions all follow similar patterns, with highest predicted habitat close to shore, particularly the coastal waters off San José (Figure 2). The participatory maps tended to have a smaller and more northward footprint than the biophysical model predictions. The fisher-mapped temperature distribution for the peak fishing season (Figure 3e) had a warmer peak (mean [*SD*] = 22.74°C [1.62]) than fisher-stated temperature (Figure 3a) (mean [*SD*] = 21.36°C, [2.29]), which showed a similar pattern to the biophysical model partial plot relationship of SST (Figure 3c) (peak ~20–22°C). The distributions of SST from the biophysical model prediction (mean [*SD*] = 22.32°C [1.97]) and fisher-mapped values are more similar to each other and distinct from the background environmental signal (mean [*SD*] = 24.05°C [1.83]) (Figure 3e). The temperature distributions of biophysical model predictions tend toward the warmer quantiles of fisher-stated temperature in later months, with the most overlap in January and the least in December (Figure S2). During the peak fishing season, the model prediction and fisher-mapped log chl-a distributions had similar peaks (model mean [*SD*] = −0.41 mg/m^3 [0.73]; maps mean [*SD*] = −0.46 mg/m^3 [0.62]) higher than background log chl-a (mean [*SD*] = −1.29 mg/m^3 [0.81]) (Figure 3f), again with least overlap in December (Figure S2).

4 | DISCUSSION

This study is one of the first to assess the complementarity of fishers' knowledge and biophysical models in describing catch patterns, lending further credence to the utility of fishers' knowledge for conservation planning in data-poor situations. The convergence of results across three methods (biophysical model, fishers' maps, and fishers' descriptions

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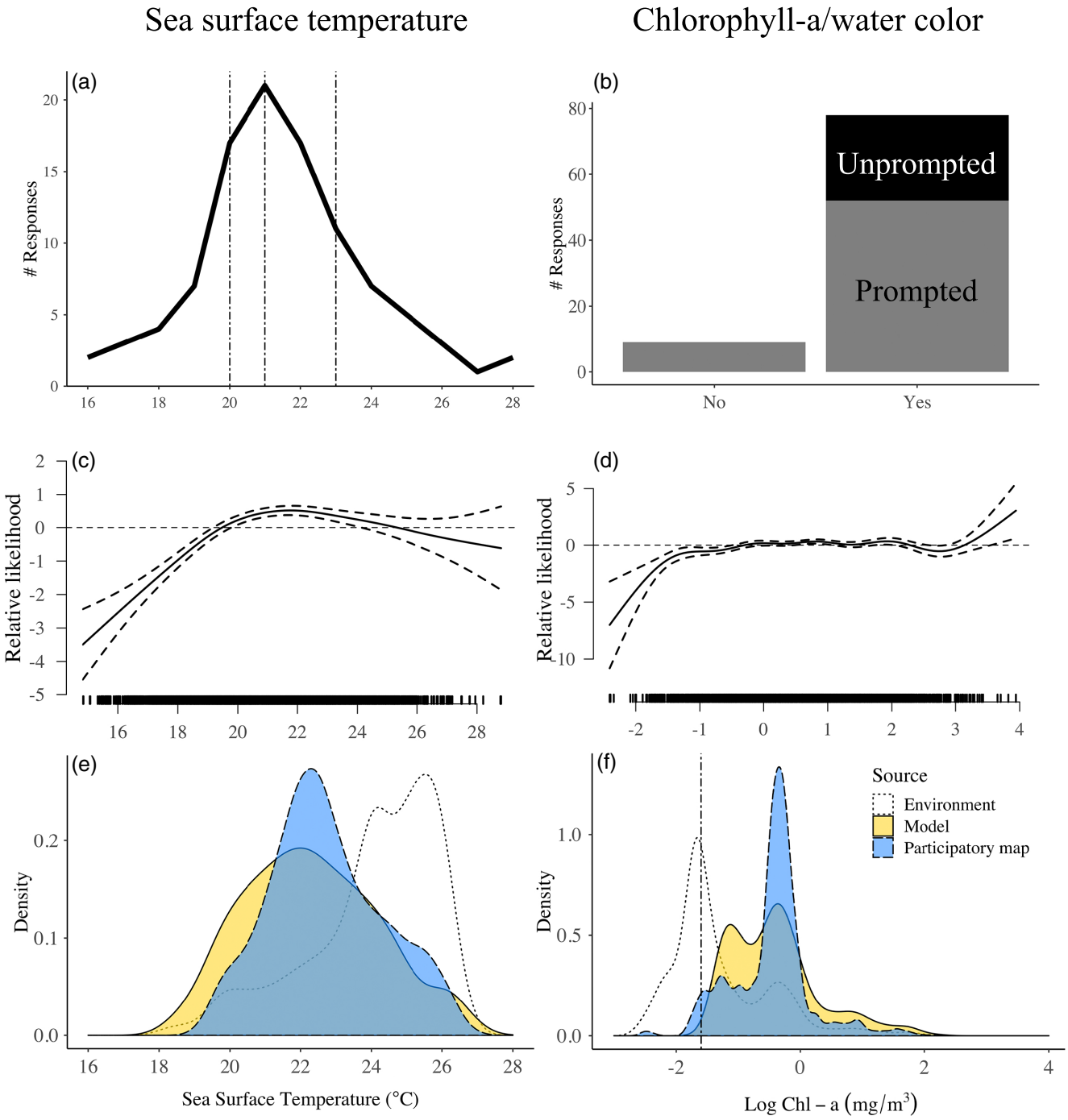


FIGURE 3 Model and interview comparison of sea surface temperature (a, c, e) and log chlorophyll-a (b, d, f) distributions, including fisher-stated variables (a, b), biophysical model partial plots (c, d), and density distributions (e, f) of fisher-mapped variables (dashed line), biophysical model prediction values >0.5 (solid line), and background environment (dotted line) for the peak fishing season (December–April) 2012. For fisher-stated temperature (a), vertical dashed lines indicate quartiles used to categorize "optimal" habitat in Figure 2. For fisher-stated chlorophyll (b), we show the number of respondents that did (yes) and did not (no) indicate that they use the color of the water to fish hammerheads, with prompted responses in black and unprompted in gray. Vertical dashed line in (f) indicates −1.6 cutoff representing green water

of their environmental niche) is encouraging for bringing together these different sources of knowledge. The dynamic nature of juvenile hammerhead shark habitat shown here suggests that including sea surface temperature and chlorophyll-a patterns in conservation planning may allow fishers and conservation practitioners to refine spatiotemporal management approaches for these sharks, with the potential for incorporating more dynamic approaches (Alfaro-Shigueto, Mangel, Dutton, Seminoff, & Godley, 2012; Hazen et al., 2018; Howell, Kobayashi, Parker, Balazs, & Polovina, 2008).

Both our model and respondents' accounts of how they use environmental variables emphasized temperature, with fishers also cuing to color of water, which may refer to a

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complex combination of productivity, turbidity, and fronts; these results are broadly similar to other published studies of juvenile shark habitat (Cartamil et al., 2010; Oh et al., 2017). Aggregations of prey fish, which fishers emphasized in their fishing strategies, are also linked to these productive oceanographic conditions (Polovina et al., 2001). Mesoscale covariates, including FSLE and SLA, which are often proxies for productive feeding areas, did not have a large effect in predicting hammerhead habitat. Similarly, fishers did not emphasize currents or waves in their environmental responses. These mesoscale covariates may not be effective predictors for juvenile sharks within their nursery grounds, and perhaps are more appropriate predictors for adult predators (e.g., swordfish; Scales et al., 2018). Some fisher responses pertained to optimal fishing practices broadly, not just for targeting hammerheads. For example, a few respondents explained that dark and turbid water obscures their nets, promoting catch of many species. Nevertheless, these results show that both juvenile hammerheads and fishers have a distinct niche separate from the background environment, even when fishers may be fishing by trial and error or sharing information.

In particular, the spatial and temporal variability of this catch vulnerability niche has implications for the 2016 hammerhead fishing ban. The ban may not adequately protect juvenile hammerhead sharks near northern ports operating later in the season. Anomalous oceanographic years may also result in greater vulnerability outside of the closed season (Hazen et al., 2018; Oliver et al., 2018). Further study of the avenues for dynamic approaches and incorporating fishers' knowledge and perspectives may be a productive pathway toward more effective management. Similarly, better understanding of smooth hammerhead population dynamics and ontogenetic niche separation might help ensure that management measures protect appropriate life stages (Kinney & Simpfendorfer, 2009).

From an epistemological standpoint, where the two methods diverge may highlight biases in either approach. The biophysical model leaves the majority of the deviance unexplained, which may be due to social factors or individual variability in fishing cues. Because the observer dataset included several projects with different objectives, observer coverage for ports is not necessarily representative of the entire population of fishers. In particular, the observer dataset has disproportionately fewer records from Máncora than our interview dataset and from the overall hammerhead fishery, and greater representation of more southern ports. This bias may explain the overall more northern and warmer patterns from fishers' knowledge than the biophysical model predictions. Fishers' knowledge may also vary based on age, experience, port, and other factors, but these were not examined here. The implementation of the hammerhead fishing ban in 2016 may have altered fishing behavior, and although we asked questions specifying conditions before the ban, respondents tended to speak in recent terms. There was also potential sampling bias in that we could only talk to fishers who were in port, so the fishers at sea for the duration of the interviews may utilize different fishing strategies. However, as we covered between ~30 and ~50% of drift-gillnet captains in these ports and reached general convergence in responses, this bias may be negligible.

Our methods of combining fishers' knowledge and a biophysical model could be improved with future research to elicit the multivariate relationships in fishers' environmental niche, rather than comparing single variable distillations to the multivariate model. Yet, the similarity between niche maps based on temperature and chl-a and model predictions is encouraging on its own, as many aspects of fishers' decision-making are complex and not easily quantified. Further work integrating fishers' knowledge and biophysical models would be particularly useful for predicting conditions under climate change and extreme climatic events including El Niño and La Niña. Species distribution models, as done here, are fit on observed environmental conditions and may not hold up to novel conditions as the environment changes (Franklin, 2010; Guisan & Thuiller, 2005). Iterative work that incorporates fishers' understanding and perceptions of these changing relationships to existing distribution models may be useful for updating them for changing conditions. Some respondents also reflected that they have had to adapt their knowledge to novel conditions; the methods they previously used no longer apply because there are too few fish or because the environment has changed. This points to the urgency of iterative work that further applies fishers' knowledge in what Bélisle et al. (2018) terms the instrumental, or empowering use: knowledge sharing platforms for scientific study may also be a valuable means of sharing knowledge among generations of fishers.

This study points to the utility of integrating local knowledge and biophysical modeling for conservation and management of the hammerhead shark fishery in Peru. It also shows promise for other data-poor fisheries where spatially explicit data is limited, absent, or difficult to obtain. Interviewing fishers or other resource users may provide sufficient information for prioritizing research and implementing conservation planning in data-poor systems. In addition, fishers' knowledge may prove useful as a component of ensemble modeling efforts. These findings may encourage use the of fishers' knowledge in Peru and elsewhere to inform conservation decision-making for data-poor fisheries.

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CONFLICTS OF INTEREST

The authors declare no conflicts of interest.

DATA ACCESSIBILITY

Interview protocols and full transcript data are available at https://purl.stanford.edu/wv848yd6100.

Author contributions

J.G.M. conducted the interviews, performed the analysis, and wrote the paper. J.A.-S. and J.C.M. designed and directed onboard observer data collection, provided access to fishermen, and identified hammerheads as a research priority. E.L.H., S.J.B., and S.B. contributed to the biophysical model analysis and critical revision of the manuscript. L.B.C. contributed to critical revision of the manuscript.

ORCID

Julia G. Mason https://orcid.org/0000-0002-8828-353X

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