Spatial ecology of blue shark and shortfin mako in southern Peru: local abundance, habitat preferences and implications for conservation

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ABSTRACT: While global declines of pelagic shark populations have been recognized for several years, conservation efforts remain hampered by a poor understanding of their spatial distribution and ecology. Two species of conservation concern are the blue shark *Prionace glauca* and the shortfin mako shark *Isurus oxyrinchus*. To improve management of these species, this study examined their local abundance patterns, habitat preferences, and distribution in the Southeast Pacific. Catch per unit effort (CPUE) data from an artisanal fishery in Peru were used to identify geographic hot spots and model abundance estimates as a function of environmental variables, including the El Niño Southern Oscillation (ENSO). A 10 yr data series revealed declining annual landings since 2012, despite no changes in management structures. Significant aggregations of both species were found in southwestern Peruvian waters (74–76° W, 17–19° S), with both species-specific hot spots targeted by major fishing efforts. *P. glauca* CPUE increased during La Niña conditions (i.e. low water temperature anomaly), and CPUE of both species declined when water depths exceeded 1000 m. Correlations with lunar illumination and chlorophyll *a* were revealed in *P. glauca* and *I. oxyrinchus*, respectively. Modeling explained 57 to 61 % of the deviance, indicating that other factors not included in the present study might account for unexplained variance in CPUE (e.g. thermocline depth, location of marine fronts, dissolved oxygen, and gear characteristics). Given the importance of the examined area to shark fisheries and the exploitation of multiple species of conservation concern, the information presented here can be used to inform management strategies designed to limit the depletion of pelagic sharks.

KEY WORDS: Artisanal fisheries · Blue shark · Catch per unit effort · Conservation · Spatial ecology · Generalized additive mixed model · Shortfin mako · Habitat preferences

INTRODUCTION

Recent studies have expressed concerns over the depletion of global pelagic shark populations (Dulvy et al. 2008, Worm et al. 2013, Queiroz et al. 2016) and the associated effects on ecosystem functioning (Myers et al. 2007). Declines in pelagic shark populations have been documented in many areas, including the South Atlantic (Barreto et al. 2016), Gulf of Mexico (Baum & Myers 2004, Hayes et al. 2009),

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Western Pacific (Robbins et al. 2006, Clarke et al. 2013), and the Mediterranean Sea (Ferretti et al. 2008). In the last century, growth in Asian shark fin markets (Dent & Clarke 2015) and rising global fishing demands have led to increased capture of pelagic sharks either as by-catch or by directed effort (Davidson et al. 2016). Research by Davidson et al. (2016) found that recent declines in the global chondrichthyan catches are strongly correlated to increased fishing pressure and weakly correlated to the often insufficient implementation of management regimes, indicating likely population declines. This is especially concerning as the population growth of many species is unable to match fishing mortality due to life-history constraints including low fecundity and late sexual maturity (Stevens et al. 2000, Worm et al. 2013).

Two species of conservation concern, because of declining populations and exposure to high fishing mortality, are the blue shark *Prionace glauca* and the shortfin mako *Isurus oxyrinchus. P. glauca* is the most commonly caught species of pelagic shark (Clarke et al. 2006, FAO 2011), mainly as by-catch of pelagic longline fisheries (Campana et al. 2006). Global *I. oxyrinchus* catches originate from both directed longline fleets and by-catch (Dulvy et al. 2008). Both species are globally distributed and highly migratory, making conservation and management an international effort. However, data are often geographically limited or inconsistent, adding high levels of uncertainty to assessments (Rice et al. 2014). In addition, both species are moderately productive (Dulvy et al. 2008), limiting recovery to high fishing pressure. *P. glauca* and *I. oxyrinchus* are therefore classified by the IUCN as Near Threatened and Vulnerable, respectively (Cailliet et al. 2009, Stevens 2009).

In the Southeast Pacific, shark fisheries are poorly monitored and regulated, because fisheries management agencies with limited resources tend to focus on the dominant fisheries of small pelagics and ignore the growing shark catches (Velez-Zuazo et al. 2015). This problem is exacerbated by the fact that most shark populations in the Southeast Pacific are targeted by artisanal fisheries (Bustamante et al. 2014, Gonzalez-Pestana et al. 2014), whose open access can lead to overexploitation and whose local management agencies often lack the capacity to undertake effective fishery assessments (Salas et al. 2007). However, despite the relatively small size of fishing vessels, artisanal fisheries can have large ecological impacts through destructive fishing techniques and large fleet size and activity (Alfaro-Shigueto et al. 2010, Shester & Micheli 2011).

Peru is the top shark-fishing nation in the Southeast Pacific (Fischer et al. 2012). *P. glauca* and *I. oxyrinchus* are the most caught shark species in Peru (Gonzalez-Pestana et al. 2014), with artisanal longline fisheries being the principal harvesters (Gilman et al. 2007). Artisanal vessels are defined in Peru as boats with a maximum of 32.6 m^3 gross registered tonnage (GRT), up to 15 m in length, and operating predominantly using manual labor (Alfaro-Shigueto et al. 2010). The longline artisanal fisheries have 2 distinct seasons: one for dolphinfish *Coryphaena hippurus* between December and February where shark catches, while retained, are mostly incidental; the second season is the directed shark fishery, which is mainly active between March and November (Doherty et al. 2014). The shark fishery principally targets *P. glauca* and *I. oxyrinchus* (Alfaro-Shigueto et al. 2010). Currently, there are no regulations on the finning of sharks, and there are no catch quotas in Peru. Although there is a minimum size limit for both shark species (160 and 170 cm total length for *P. glauca* and *I. oxyrinchus*, respectively), this is rarely enforced (Gilman et al. 2007, Fischer et al. 2012, Doherty et al. 2014). Concerns regarding the expansion of the longline fishery in Peru (>350% between 1995 and 2005; Alfaro-Shigueto et al. 2010), rising exports of shark products (Gonzalez-Pestana et al. 2014), and largely absent management warrant further study of these species to help address the status of shark fisheries in this region.

Understanding how and why animals are spatially and temporally distributed is a fundamental component of ecology and is essential for effective conservation and management (Arendt et al. 2012, Kessel et al. 2014, Stehfest et al. 2014, Afonso & Hazin 2015), partly because spatial ecology can be used to predict vulnerability to marine fisheries. For example, simple descriptors of habitat use can predict the probability of marine species being threatened as defined by the IUCN (Dulvy et al. 2014). Likewise, predictable geographic distributions and aggregations of sharks signal a high potential for overexploitation (Kessel et al. 2014), so distribution knowledge is crucial for the management of protected shark species, particularly if these are perceived as a nuisance or economic opportunity for other fisheries (Gilman et al. 2007). Understanding the biotic and abiotic factors driving shark abundance patterns is important in the context of environmental variation and future climatic scenarios (Kessel et al. 2014) and may help identify the mechanistic bases of species declines, because marine conditions (e.g. primary production and tempera-

ture) affect pelagic resources (Bigelow et al. 1999, Su et al. 2011). For example, interannual climate variation in the form of the El Niño Southern Oscillation (ENSO) has led to boom and bust fisheries in the Southeast Pacific because of poor knowledge of species' responses to ENSO and a lack of management (Wolff et al. 2007). ENSO greatly alters oceanographic conditions every 2 to 7 yr, which affects the status of pelagic fisheries (Ñiquen & Bouchon 2004, Su et al. 2011, Quiñones et al. 2015). However, the relationship between ENSO and the local abundance of pelagic shark species remains poorly understood, hampering conservation efforts.

Understanding the distribution and ecology of sharks in Peru, and the effects of climate variation and fishing, can lead to a more accurate index of abundance which can increase the accuracy of future conservation and assessment efforts (Abascal et al. 2011, Doherty et al. 2014, Gonzalez-Pestana et al. 2014). To that end, we modeled *P. glauca* and *I. oxyrinchus* catch rates using a 10 yr data set from the small-scale longline fisheries in southern Peru. Using spatial-temporal and environmental variables, we aimed to (1) test the effects of ENSO on *P. glauca* and *I. oxyrinchus*; (2) investigate the ecology of these spe-

cies in Peruvian waters; (3) report on the spatial distribution of the shark fishery; and (4) examine the temporal development in annual landings.

MATERIALS AND METHODS

Catch data

Catch data for *Prionace glauca* and *Isurus oxyrinchus* captured by the artisanal longline fleet in the waters of southern Peru (i.e. Arequipa, Moquegua and Tacna Regions) between 2005 and September 2014 were provided by the Instituto del Mar del Perú (IMARPE; Fig. 1). The area covers the principal landing port (by biomass) for sharks in Peru (Ilo, Moquegua) as well as the principal *P. glauca* and *I. oxyrinchus* fishing grounds (Gonzalez-Pestana et al. 2014).

For each trip, port observers recorded catch per species (kg), vessel GRT, date of landing, and fishing area (Estrella et al. 1998, 1999). While gear and bait are not recorded by IMARPE observers for each fishing trip, on-board observers and port surveys have reported that artisanal longline shark fisheries typi-
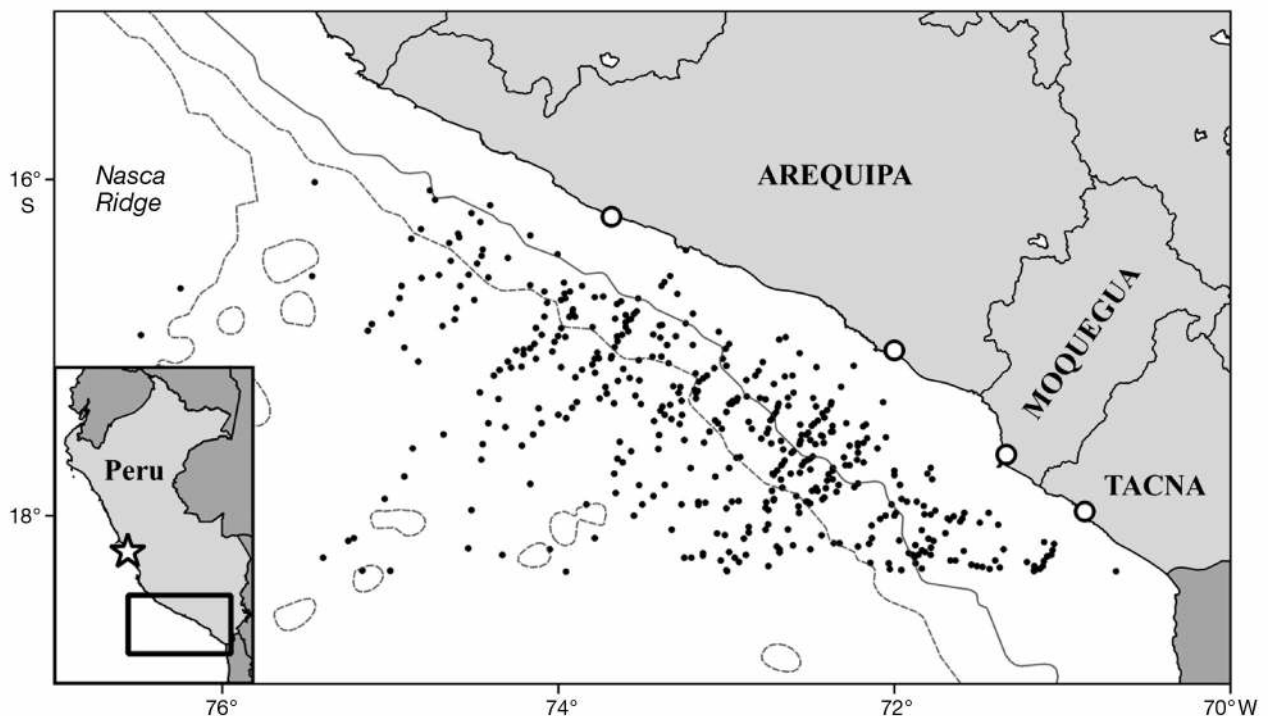

Fig. 1. Fishing locations of blue shark *Prionace glauca* and shortfin mako shark *Isurus oxyrinchus* caught by the pelagic artisanal longline fishery in southern Peru from January 2005 to September 2014. Fishing grounds are shown as black dots, landing ports as open circles, and the capital of Peru (Lima) as a star (inset). Depth contours represent the 2000 (solid line) and 4000 m (dashed lines) isobaths

cally use large J hooks, nylon multifilament cord branchlines and cable leaders with humboldt squid *Dosidicus gigas*, flying fish *Exocoetus volitans*, chub mackerel *Scomber japonicus*, porcupinefish *Diodon hystrix*, Peruvian Pacific sardine *Sardinops sagax sagax* and small cetacean meat as bait (Alfaro-Shigueto et al. 2010, Doherty et al. 2014). During the dolphinfish season, vessels deploy 7.4 ± 1.6 (mean ± SD) sets per trip with 676.6 ± 64.6 hooks per set and during the shark season vessels deploy 7.1 ± 0.9 sets per trip with 705.1 ± 89.8 hooks per set (Doherty et al. 2014). Nominal catch per unit effort (CPUE) was calculated as catch (kg) per day, which was estimated by dividing the recorded landings by the number of days at sea for each trip. Due to data quality constraints, the nominal CPUE could not be reported in more standardized units, such as catch per set or catch per 1000 hooks.

Environmental data

Environmental data included in modeling of CPUE were ENSO anomalies, sea surface temperature (SST; °C), chlorophyll *a* (chl *a*) concentration (mg m^{-3}), water depth (bathymetry; μ), and lunar illumination (%). Monthly oceanic ENSO climate variation data were obtained from the Multivariate ENSO Index (MEI) provided by NOAA's Earth System Research Laboratory (http://www.esrl.noaa.gov/psd/enso/mei/). The MEI is calculated using the first principal component of sea-level pressure, zonal and meridional surface wind components, SST, surface air temperature, and total cloudiness fraction of the sky from the tropical Pacific (Niño 3.4 region) normalized for the reference period of 1950 to 1993 (Wolter & Timlin 2011). Positive MEI values represent El Niño phase-like conditions and negative values represent La Niña phase-like conditions. Monthly blended SST and chlorophyll *a* data with a 4 km^2 resolution were retrieved from the Moderate Resolution Imaging Spectrometer Aqua via the Oceancolor Data Downloader QGIS plugin developed by the Mapping and Geographic Information Centre at the British Antarctic Survey (Ireland & Connor 2015, QGIS Development Team 2015). Daily lunar illumination data at 12 noon (Peru time zone) were extracted from the 'lunar' package in R (R Core Team 2015, Lazaridis 2014). Lunar illumination is the proportion of the Moon's disk that is illuminated and, therefore, new moons have an illumination of 0.0, full moons have an illumination of 1.0, and quarter moons are intermediate (0.5). This means that lunar illumination corresponds directly to

lunar phase. Bathymetry data were obtained from the General Bathymetric Chart of the Oceans global 30 arc-second grid data set (IOC et al. 2003). While fishing area recorded by IMARPE is reported to be accurate within 1 nautical mile (Estrella Arellano & Swartzman 2010), locations of each set are not recorded and a single point denoting the fishing area is recorded for each trip. To account for possible vessel movement in relation to the recorded fishing area, SST, chl *a*, and depth within a 13.9 km radius from each fishing location were averaged. In addition, given the differences in time coverage between environmental variables and fishing trips, the weighted average of environmental variables was calculated over the duration of each fishing trip.

GAMM modeling

To examine the relationships of pelagic shark catch rates with spatial-temporal and environmental variables, generalized additive mixed models (GAMMs; Wood 2006) were fit to the CPUE data (Bigelow et al. 1999, Bustamante & Bennett 2013, Mitchell et al. 2014). Vessel-specific heterogeneity was included as a random effect (random intercept) to remove the assumption of homogeneity of gear and fishing characteristics among vessels and improve standardization of CPUE. To reduce Type I and II errors, GAMMs were constructed using cubic regression splines and fitted using restricted maximum likelihood to maximize stability (Marra & Wood 2011). In addition, the 'double penalty' shrinkage variable selection procedure was used to reduce uncertainty inherent in stepwise variable selection procedures (Marra & Wood 2011). Employing log transformed CPUE data for each species to meet the assumption of normality, GAMMs were fitted using a normal distribution and an identity link function to fit the response:

log(CPUE+1) ~ *s*(MEI) + *s*(SST) + *s*(chl *a*) + *s*(lunar illumination) + *s*(depth) + *s*(month) + *s*(year) + *s*(latitude) + *s*(longitude) + *s*(GRT) + α_i

where *s* is the smoothing function applied to each covariate, α_i is the vessel-specific random effect, and a constant of 1 was added to CPUE. The effect of month was modeled using cyclic cubic regression splines. Spatial prediction maps of CPUE were created for both species using the modeled effect of latitude and longitude. GAMM analyses were completed using the 'gamm4' package in R 3.2.1 (Wood & Scheipl 2014, R Core Team 2015), with significance accepted at p < 0.01.

Spatial distribution

Distributional patterns of pelagic sharks off the southeast coast of Peru were identified using the Optimized Hot Spot Analysis tool (Getis-Ord Gi* statistic) in ArcGIS 10.2.2 (Environmental Systems Research Institute), similar to Love et al. (2015) and Queiroz et al. (2016). CPUE of each species was averaged over $0.25 \times 0.25°$ grid cells for analysis by the Gi* statistic (Robinson & Graham 2013). The Gi* statistic indicates the level of clustering of CPUE, with positive and negative values noting areas where pelagic sharks are most (hot spots) and least (cold spots) encountered, respectively. A standard distance calculation was used to determine the optimal distance band based on the average distance to the 30 nearest neighbors after removing locational outliers, features more than 3 standard deviations away from their closest non-coincident neighbor. Areas were considered significantly hot (positive Gi*) or cold (negative Gi*) at $p \leq 0.05$. Catch data from March to November (i.e. shark season) and December to February (i.e. dolphinfish season) were analyzed separately because fishing techniques and gear characteristics of vessels vary for each distinct fishing season.

RESULTS

Between January 2005 and September 2014, 4971 fishing trips of the artisanal longline fleet in southern Peru landed 1621.2 t of *P. glauca* and 875.9 t of *I. oxyrinchu*s (Table 1). Landings increased during the beginning of the study period and started declin-

ing after 2012 (Fig. 2). Data were excluded from further analyses if departure date was not recorded (i.e. trip duration could not be calculated). Thus, 1253 t of *P. glauca* and 697 t of *I. oxyrinchus* landings from 3025 artisanal longline trips in Peruvian waters were used in GAMMs and hot spot analyses. The majority of catches observed occurred during the shark season, when trip length and CPUE were greater, rather than the dolphinfish season (Table 1).

Effects of environmental and spatial-temporal variables on CPUE

For *Prionace glauca*, results of the GAMMs indicated that all input variables except chlorophyll *a*
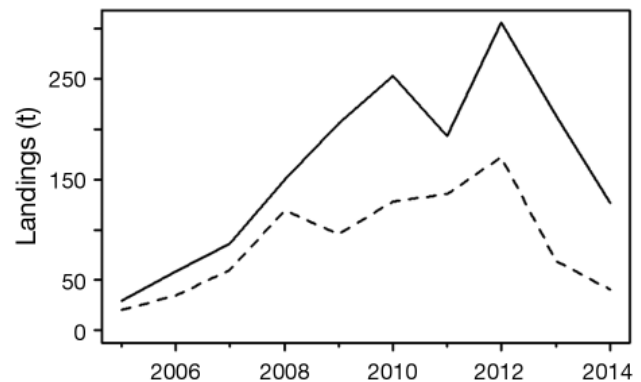

Fig. 2. Yearly landings in metric tonnes (t) of blue shark *Prionace glauca* (solid line) and shortfin mako shark *Isurus oxyrinchus* (dashed line) from the artisanal longline fleet in southern Peru, January 2005–September 2014. For both species, landings peaked in 2012, followed by a declining trend

Table 1. Catch and effort data for the study period by fishing season (shark and dolphinfish). Note that summary statistics were calculated only from data with complete landing and departure date information and are included under 'GAMM and hot spot analyses.' Data are displayed as mean ± SD with ranges in parentheses. GRT: gross registered tonnage; CPUE: catch per unit effort

	Shark season (Mar–Nov)	Dolphinfish season (Dec–Feb)	Total
Total			
Prionace glauca landed (t)	1377.3	243.9	1621.2
Isurus oxyrinchus landed (t)	707.6	168.3	875.9
Number of trips	1711	3260	4971
GAMM and hot spot analyses			
P. glauca landed (t)	1072.8	179.2	1253
I. oxyrinchus landed (t)	566.8	130.2	697
Number of trips	1160	1865	3025
Fishing days	21938.5	18566.7	40505.2
GRT	5.4 ± 2.1 (1.5–16)	6.3 ± 2.6 (2–20)	5.7 ± 2.4 (1.5–20)
Mean trip length (d)	12 ± 6.3 (1–31)	7.9 ± 2.9 (1–27)	9.7 ± 5.1 (1–31)
Mean CPUE (kg d^{-1})	63.3 ± 68.6 (0.6–483.9)	12.9 ± 32.1 (0.4–478.5)	35 ± 57 (0.4–483.5)

were significant predictors of CPUE (Table 2). For *Isurus oxyrinchus*, 8 of the 10 input variables were significant predictors of CPUE (Table 2). Modelling explained the majority of the deviance for *P. glauca* (adjusted r^2 = 0.58) and *I. oxyrinchus* (adjusted r^2 = 0.61). Standard model diagnostics suggested that both models fit the data well (Fig. A1 in the Appendix).

The effect of the MEI variable on *P. glauca* and *I. oxyrinchus* peaked at −2.0, dropping as MEI increased, indicating a positive correlation between CPUE and La Niña ENSO phase-like conditions (i.e. cooling events; Fig. 3). MEI values between 0.5 and 1.5 had no effect on *P. glauca* CPUE. Peak *P. glauca* CPUE occurred when lunar illumination was 0 and 100% (Fig. 3a). The influence of SST on *P. glauca* CPUE peaked between 14.5 and 20°C, while 20°C SST coincided with elevated CPUE in *I. oxyrinchus* (Fig. 3b). CPUE of *I. oxyrinchus* was much greater at chl *a* values approaching 0 mg m^{-3}, then decreased drastically to plateau until 4 mg m^{-3} (Fig. 3b). The depth covariate demonstrated much higher *P. glauca* and *I. oxyrinchus* CPUE at ~1000 m sea depth, decreasing as depth increased. The month predictor

Table 2. Summary of generalized additive mixed models (GAMMs), relating blue shark *Prionace glauca* and shortfin mako shark *Isurus oxyrinchus* catch per unit effort (kg d^{-1}) data to spatial-temporal and environmental variables in southern Peru (cutoff for significance set at α = 0.01). Data for the analyses are described in detail in Table 1. MEI: Multivariate ENSO Index; SST: sea surface temperature; GRT: gross registered tonnage; edf: estimated degrees of freedom

Predictor	edf	*F*	p-value
P. glauca			
MEI	3.0	8.8	≪0.0001
SST	4.0	4.7	≪0.0001
Lunar illumination	2.5	2.0	0.0038
Depth	3.3	5.6	≪0.0001
Month	7.0	98.9	≪0.0001
Year	5.7	7.8	≪0.0001
GRT	4.7	32.8	≪0.0001
Latitude	4.4	10.9	≪0.0001
Longitude	7.1	16.0	≪0.0001
I. oxyrinchus			
SST	5.1	3.8	0.002
Chlorophyll *a*	6.6	6.6	≪0.0001
Depth	4.0	17.6	≪0.0001
Month	5.9	67.2	≪0.0001
Year	5.1	11.0	≪0.0001
GRT	3.0	15.9	≪0.0001
Latitude	1.0	109.4	≪0.0001
Longitude	1.3	44.9	≪0.0001

showed that CPUE of *P. glauca* is highly seasonal, with elevated values from April to October (Fig. 3a). For *I. oxyrinchus,* peak CPUE was between April and July (Fig. 3b). For both species, the year predictor demonstrated steady declines in CPUE until 2008 (*P. glauca*) and 2010 (*I. oxyrinchus*), followed by increasing and plateauing trends for *P. glauca* and *I. oxyrinchus* towards the end of the study period, respectively (Fig. 3). CPUE also increased for both species with increasing GRT, at least up to 10 to 15 GRT (Fig. 3).

CPUE spatial predictions (based on GAMMs) indicated much higher CPUE of *P. glauca* in the southwest and north of the study area (Fig. 4a). In contrast, *I. oxyrinchus* CPUE was greatest in the southwest corner of the study area, declining steeply north and eastwards (Fig. 4b). However, the extent of spatial predictions for *I. oxyrinchus* CPUE was less than for *P. glauca*, given the lack of captures beyond ~75.5°W.

CPUE spatial distribution and hot spots

Hot spot analyses revealed 3 distinct, and highly overlapping (i.e. sympatric), clusters of greater probability of encountering *P. glauca* and *I. oxyrinchus* (CPUE) by artisanal longline fisheries during both the dolphinfish season (December to February) and the shark fishing season (March to November; Fig. 5). For *P. glauca*, 16.5 and 5.4% of the area examined in which sharks were present was considered a hot spot during the shark and dolphinfish season, respectively (i.e. 15 of 91 and 5 of 93 grid cells, respectively). Hot spots of *P. glauca* CPUE were located in the southwest corner of the study area (Fig. 5). For *I. oxyrinchus,* 10 and 8% of the area in which sharks were captured was considered a hot spot during the shark and dolphinfish season, respectively (i.e. 8 of 80 and 6 of 75 grid cells, respectively). The *I. oxyrinchus* hot spots were located in the southwest and southeast corner of the study area (Fig. 5). In addition, cold spots for each species and season were identified along the coast (Fig. 5, blue region). Overall, 775.1 and 34.7 t of *P. glauca* and 489 and 82.4 t of *I. oxyrinchus* were caught from the identified hot spots during the shark and dolphinfish seasons, respectively, indicating the importance of these areas to pelagic sharks in the region. However, only 3.5 and 2.2 t of *I. oxyrinchus* were captured during the shark and dolphinfish seasons, respectively, from the hot spot in the southeast of the study area.
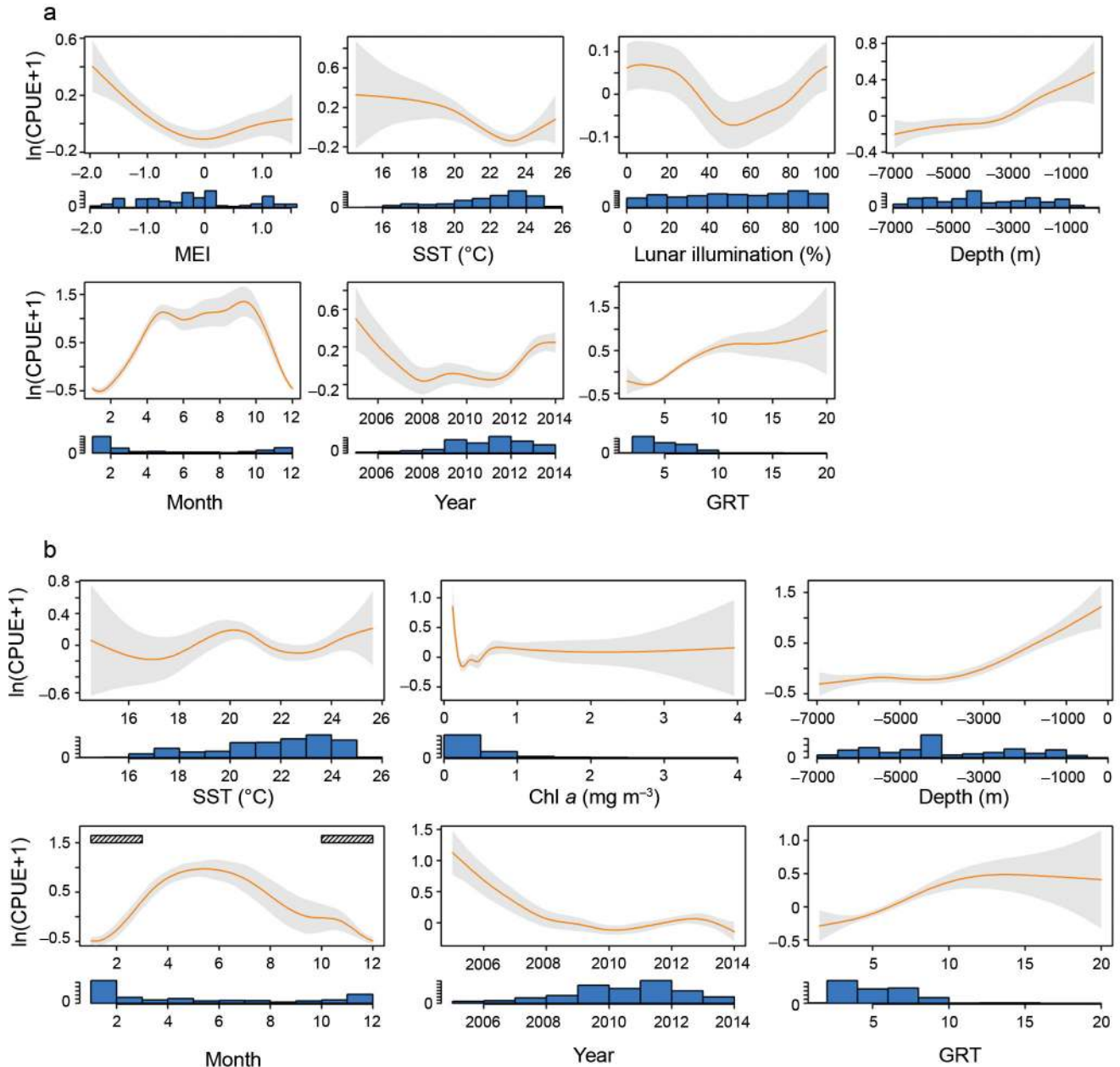
Fig. 3. GAMM analyzed and fitted partial response curves showing the effects of spatial-temporal and environmental variables on catch per unit effort (CPUE; kg d^{-1}) for artisanal longline fisheries in southern Peru, January 2005–September 2014 (see Table 2) of (a) blue shark *Prionace glauca* and (b) shortfin mako shark *Isurus oxyrinchus* (bars in 'Month' panel mark the pupping season; Bustamante & Bennett 2013). Negative Multivariate ENSO Index (MEI) values correspond to La Niña phase-like conditions involving cold water anomalies. Grey shading indicates the 95% confidence interval. Note that *y*-axes differ between panels, with zeros corresponding to the centered values. Fishing effort (number of trips) is indicated in the lower panels with blue vertical bars. CPUE: catch per unit effort; SST: sea surface temperature; GRT: gross registered tonnage

DISCUSSION

This study provides the first assessment of the distribution and spatial ecology of *Prionace glauca* and *Isurus oxyrinchus* in the Southeast Pacific using data from the artisanal longline fishery in the southern

Peru. GAMMs presented here explain a large proportion (>57%) of the deviance of shark catch rates using predictors that are known to influence the spatial and temporal distribution, and local abundance of sharks (Bigelow et al. 1999, Carvalho et al. 2011, Bustamante & Bennett 2013), thus providing a mean-
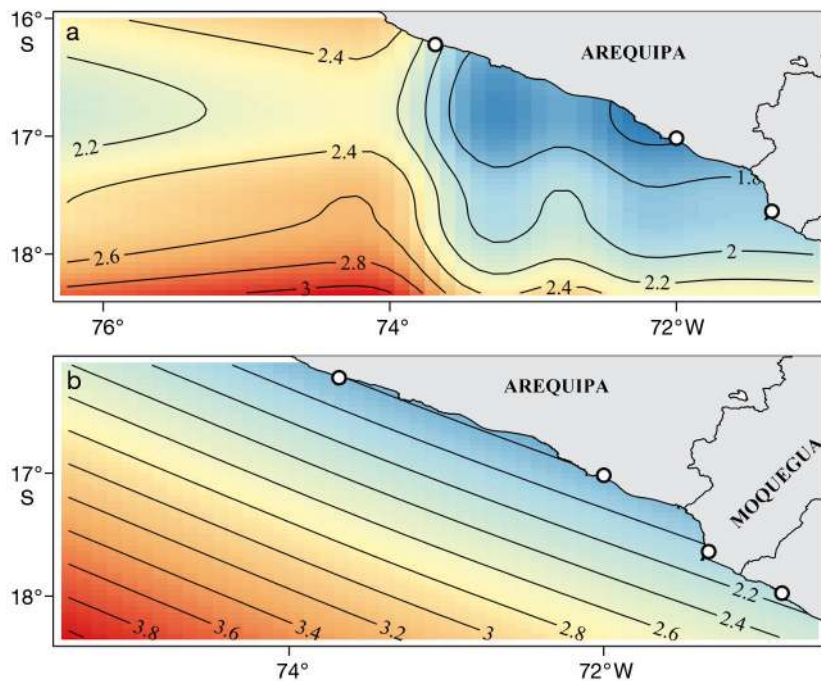
Fig. 4. Spatial distribution of GAMM-predicted natural log-transformed catch per unit effort (CPUE; kg d⁻¹) of (a) blue shark *Prionace glauca* and (b) shortfin mako shark *Isurus oxyrinchus* caught by the artisanal longline fleet in southern Peru, January 2005–September 2014. Colour scale indicated by the numbers next to the isopleths

ingful interpretation of the ecological processes that may affect these species in the Southeast Pacific. Given the importance of artisanal fisheries in the region (Alfaro-Shigueto et al. 2010, Estrella Arellano & Swartzman 2010) and related conservation concerns, the present study addresses pertinent gaps in our understanding of the distribution and ecology of pelagic sharks in the Southeast Pacific.

Impacts of ENSO

The study assessed for the first time the non-linear effects of ENSO on *P. glauca* and *I. oxyrinchus* in southern Peru. Previously, Gonzalez-Pestana et al. (2014) found a positive correlation between ENSO and *P. glauca* and *I. oxyrinchus* monthly landings by the artisanal longline fishery in Peru using linear regression. The use of CPUE and GAMMs suggests that these models more accurately reveal possible non-linear effects of ENSO on shark fisheries in southern Peru. In contrast to Gonzalez-Pestana et al. (2014), the present study found that *P. glauca* is impacted by strong La Niña events (i.e. when MEI was negative) and ENSO has no significant impact on *I. oxyrinchus*. Further differences between the

results of the present study and those of Gonzalez-Pestana et al. (2014) may be due to latitude, interdecadal climate regime (i.e. El Viejo vs. La Vieja), or area-specific effects of ENSO, as Gonzalez-Pestana et al. (2014) analyzed data from the entire country covering multiple interdecadal climate regimes. The time period of the present study lacked strong El Niño events and represents the La Vieja regime, marked by cooler waters and the dominance of anchovies over sardines (Chavez et al. 2003). Thus, further study is warranted to examine the impacts of El Viejo and strong positive ENSO anomalies. Given the large horizontal distributions of the examined species beyond the study area and exclusion of a temporal lag to account for possible population growth, ENSO most likely alters the local abundance of *P. glauca* in southern Peru. ENSO anomalies influence the distribution of large pelagic species such as blue marlin *Makaira nigricans* by altering the location of favorable habitat (i.e. temperature and primary production) (Su et al. 2011). In addition, alterations in the horizontal distribution and abundance of prey species due to ENSO (Ñiquen & Bouchon 2004, Adams & Flores 2016) could act as a driver of local shark abundances, as documented for other upper trophic level species (Cury et al. 2000).

Ecology

Environmental predictors such as SST and chl *a* play significant roles in the local abundance patterns of pelagic sharks due to optimal thermal ranges and food availability (Bigelow et al. 1999, Carvalho et al. 2011, Mitchell et al. 2014). As demonstrated by our results, CPUE was greatest at 14.5 to 20°C for *P. glauca* and 20°C for *I. oxyrinchus*. These results are similar to studies in the North Pacific (Walsh & Kleiber 2001) and South and North Atlantic (Carvalho et al. 2011, Vandeperre et al. 2014) which reported that *P. glauca* CPUE was greatest at temperatures ranging from 16 to 21°C. Furthermore, tagging of *I. oxyrinchus* by Abascal et al. (2011) in Chilean waters found that relative time spent at a certain temperature peaked between 20 and 22°C. Similar to work in the northern Pacific (Walsh & Kleiber 2001),
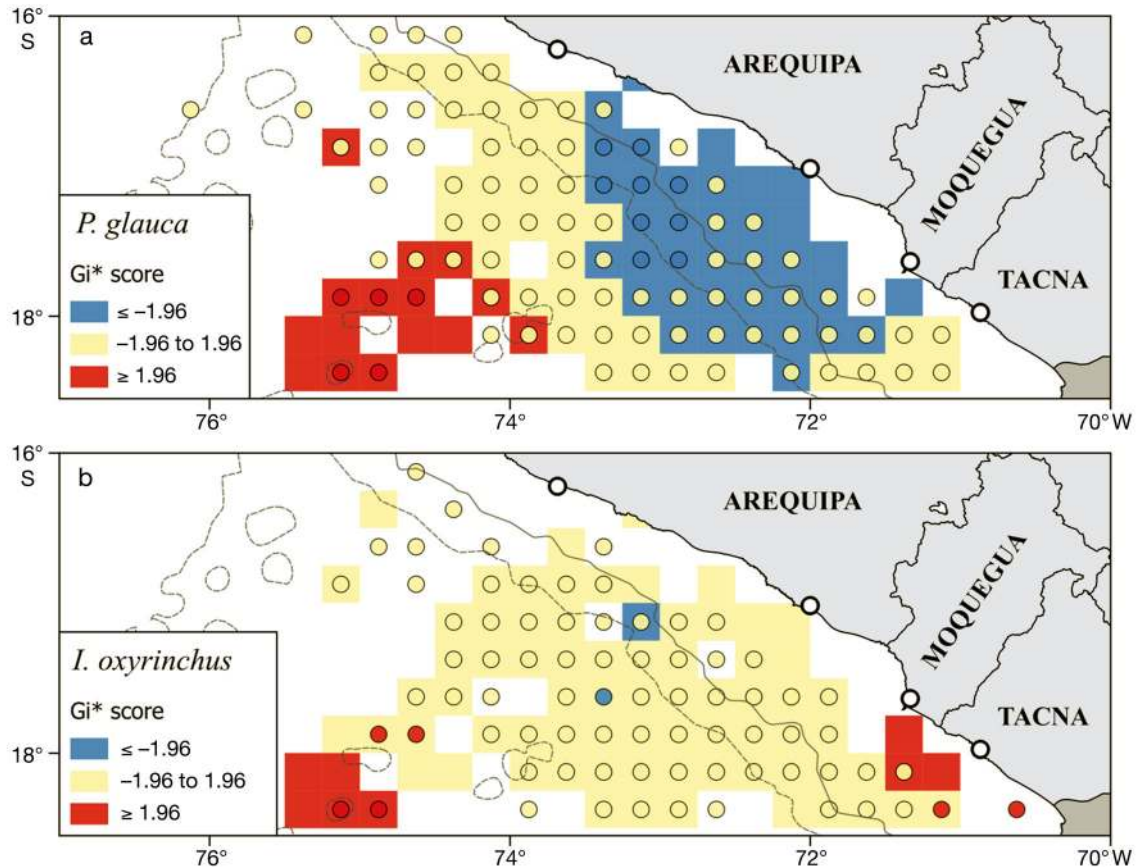
Fig. 5. Long-term distributional patterns in (a) blue shark *Prionace glauca* and (b) shortfin mako shark *Isurus oxyrinchus* catch per unit effort (CPUE; kg d^{-1}). Spatial patterns for each species were computed using the Getis-Ord hot spot analysis Gi* statistic (z-score), with positive and negative Gi* statistics indicating hot (red) and cold (blue) areas, respectively, for the probability of encountering each species in southern Peru. Circles represent CPUE hot spots during the dolphinfish season (December to February) and squares represent CPUE hot spots from the shark fishing season (March to November). Areas were considered significantly hot or cold at p ≤ 0.05 (|Gi*| ≥ 1.96). Open circles along the shoreline indicate ports significant to the pelagic artisanal fishery. Depth contours represent the 2000 (solid line) and 4000 m (dashed lines) isobaths

we noticed an increase in *P. glauca* CPUE at the highest temperatures observed, although the underpinning mechanism is unknown.

Primary production may act as a proxy of prey availability because many of the prey species of pelagic sharks are reliant on primary production (Chassot et al. 2010). Correspondingly, chl *a* plays a significant role in abundance patterns of pelagic sharks (Carvalho et al. 2011). In eastern boundary upwelling ecosystems (EBUEs) migratory sharks forage primarily on the edge of highly productive upwelling environments (Chavez & Messié 2009). Thus, as expected, *I. oxyrinchus* catch rates were highest when primary production was lowest.

Lunar illumination and lunar phase affect fish species in multiple manners, including visual detection of prey and predator camouflage, and may change fish distribution, thermal exposure, and activity patterns (Metcalfe et al. 1997, Hanson et al. 2008, Aarestrup et al. 2009, Afonso & Hazin 2015, Papastamatiou et al. 2015, Schabetsberger et al. 2015). Shark prey species may modify vertical distributions according to the lunar phase (Schabetsberger et al. 2013, 2015), suggesting that lunar phase (and illumination) influences the distribution of foraging sharks. Because lunar effects on pelagic sharks are unknown in the Southeast Pacific, the effects of lunar illumination were tested on *P. glauca* and *I. oxyrinchus* CPUE. Despite the fact that the 2 species are sympatric and may have been foraging on similar prey species, results revealed contrasting findings, with no lunar effects on *I. oxyrinchus*, whereas *P. glauca* CPUE varied with lunar illumination. Previous studies of lunar effects on *P. glauca* and *I. oxyrinchus* have not reported consistent findings. In the northern Atlantic Ocean, Vandeperre et al. (2014) found that

P. glauca CPUE peaked at intermediate moons, partly supported by Lowry et al. (2007) who reported that CPUE of *P. glauca* and *I. oxyrinchus* peaked during the waxing crescent in the western South Pacific. Poisson et al. (2010) reported no lunar effects on CPUE of *P. glauca* and *Isurus* spp. in the western Indian Ocean. In support of the present study, Bigelow et al. (1999) found that *P. glauca* CPUE tended to peak during new moon and full moon in the North Pacific. The varying findings indicate that the mechanistic basis for lunar effects on shark CPUE may comprise a complex array of factors, perhaps including the behavior of various prey species. However, the effects of mixed-layer depth, thermocline, locations of marine fronts, oxygen concentration, and other oceanographic factors not included in the present study may contribute to unexplained deviance in the present modeling approach.

Spatial distribution

Both *I. oxyrinchus* and *P. glauca* are primarily pelagic species with global distributions (Compagno 2001). Many shark species, however, aggregate for foraging or reproduction purposes, and hot spots in abundance and aggregations of pelagic sharks have been found in the Northeast Pacific (Williams et al. 2010) and the North Atlantic (Vandeperre et al. 2014, Queiroz et al. 2016). The present study adds to these findings by describing hot spots in the Southeast Pacific. Hypotheses for the importance of shark aggregation include reproductive and feeding opportunities. Comparable with other species (Williams et al. 2010), the tendency of many pelagic sharks to aggregate makes them especially vulnerable to overexploitation (Litvinov 2006, Dulvy et al. 2008). In the present study, the greatest abundance of *P. glauca* and *I. oxyrinchus* was found far offshore (>150 km from the shore) in the southwest corner of the study area where there was a statistically significant clustering of elevated CPUE (hot spots), corroborating high catch rates in the study area identified by onboard observers (Doherty et al. 2014). The importance of the hot spots in the southwest is indicated by the fact that a greater percentage of all shark captures originated from these hot spot areas. However, hot spots for *I. oxyrinchus* in the southeast of the study area were primarily driven by 2 fishing trips with relatively high CPUE and therefore these areas are likely not as significant to local shark populations and the artisanal fishery. GAMMs indicate another concentration of elevated CPUE for *P. glauca* further north in

the study area. While fishing effort is minimal in this region, aggregations of *P. glauca* have previously been found associated with the Nasca Ridge (Litvinov 2006; Fig. 1). Given that GAMMs standardize CPUE to vessel size (GRT), temporal, and environmental predictors, spatial distribution of CPUE as predicted by GAMMs may more accurately portray the true distribution of the examined species than hot spot analysis. In addition, both methods indicate that the study area does not completely cover the population centers of these sharks, and international effort is required to fully elucidate the distribution of both species.

Temporal patterns

As described previously, the shark fishery in Peru is seasonal (Doherty et al. 2014). Bait species described by Doherty et al. (2014) follow seasonal abundance patterns (Estrella Arellano & Swartzman 2010) that correspond to peak shark CPUE. Thus, shark abundance patterns in the study area may follow seasonal prey abundance patterns to take advantage of greater prey availability. However, because gear characteristics and fishing techniques change depending on the season (Alfaro-Shigueto et al. 2010), seasonal trends in CPUE in our GAMMs may partly reflect gear-specific selectivity and fleet direction. Therefore, fishery-independent research is needed to examine seasonal migration and abundance patterns.

Corroborating the increasing landings up until 2010 (Gonzalez-Pestana et al. 2014) and contrary to CPUE reported by previous studies (Doherty et al. 2014), the present study found a decline in the CPUE of *P. glauca* and *I. oxyrinchus* from the beginning of the study period to around 2009. In more recent years, annual landings of *P. glauca* have declined although CPUE has increased. While assessments of *P. glauca* and *I. oxyrinchus* are absent for the Southeast Pacific, assessments from the North Pacific found declining trends of *P. glauca* abundance in the 2000s when using CPUE data from the Secretariat of the Pacific Community's observer program and observers on longline vessels based in Hawaii (Rice et al. 2014). However, when CPUE series from the Japanese longline fleet were used, abundance estimates were more optimistic. In the Southwest Pacific, CPUE for *P. glauca* and *I. oxyrinchus* generally increased between 2005 and 2013 (Francis et al. 2014). Differences between studies are likely due to geographic differences in local population dynamics, fishing pressure and mortality, temporal span of the CPUE series, and CPUE standardization techniques.

CONCLUSION

Due to biological constraints related to life history, combined with increasing fishing pressures, *P. glauca* and *I. oxyrinchus* have been listed as species of conservation concern by the IUCN Red List. Despite these concerns, the availability of fishery and biological data continues to be limited, especially in the Southeast Pacific, thus restricting conservation possibilities for these species. In particular, while Estrella Arellano & Swartzman (2010) note that the accuracy of location of fishing site recorded by IMARPE is to within 1 nautical mile, the present study is limited by the lack of information on the start and end locations of sets. Soak time, bait, and gear for each trip, which can affect catch rates of pelagic sharks, are not recorded by port observers (Gallagher et al. 2014). Furthermore, due to a lack of available information on the number of sets per trip and hooks per set, the definition of CPUE used here may be biased. The present study addressed these issues by averaging environmental data over large grid space to account for possible vessel movement, using the most detailed definition of CPUE possible given the data available from the fishery, and using a mixed model structure to account for inter-vessel heterogeneity in gear and fishing techniques. The similarity between these results and previous studies (Walsh & Kleiber 2001, Chavez & Messié 2009, Abascal et al. 2011, Doherty et al. 2014, Vandeperre et al. 2014) in terms of greater CPUE on the southern border of the study area, seasonality of the fishery, associations between CPUE at SST, and greater CPUE of *I. oxyrinchus* at low chlorophyll levels adds credibility to the findings, despite the apparent limitations. However, more extensive data from fishery (e.g. number of sets per trip, number of hooks per set, and negative catch data) and fishery-independent studies are needed to better evaluate and understand the status, ecology, and distribution of *P. glauca* and *I. oxyrinchus* in this region. For example, effort by the artisanal longline fleet has been recorded in Chilean waters (Doherty et al. 2014); however, catch data from these areas are not accurately georeferenced. Therefore, further effort to improve portside data collection and fisheries-independent surveys are necessary to examine the ecology and distribution of pelagic sharks to the south of the present study.

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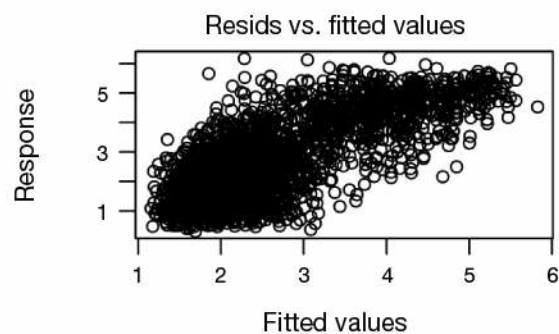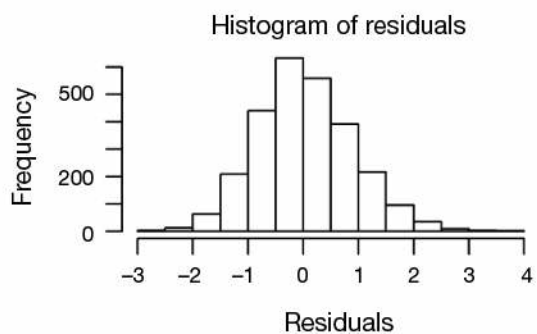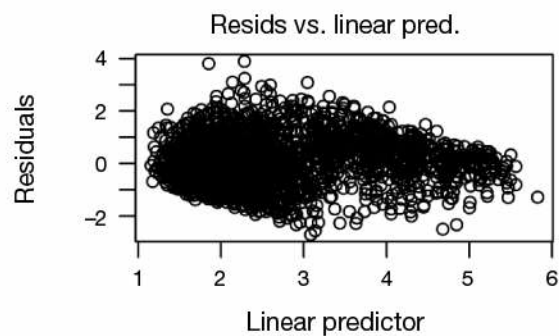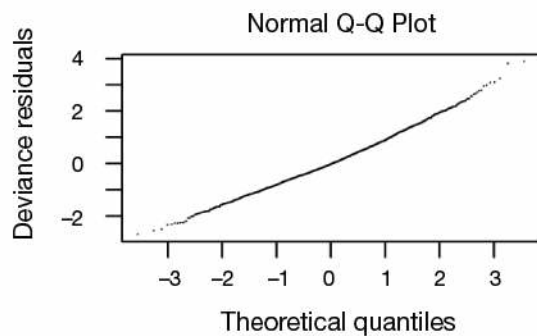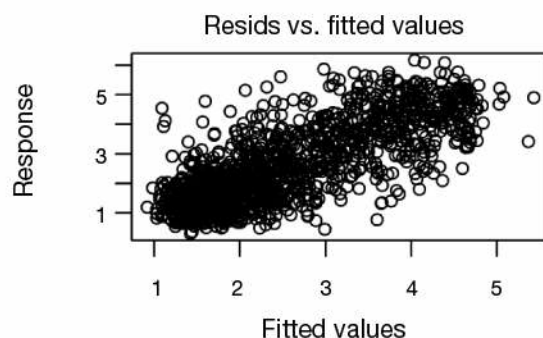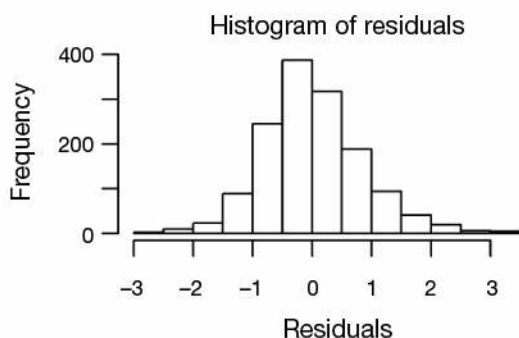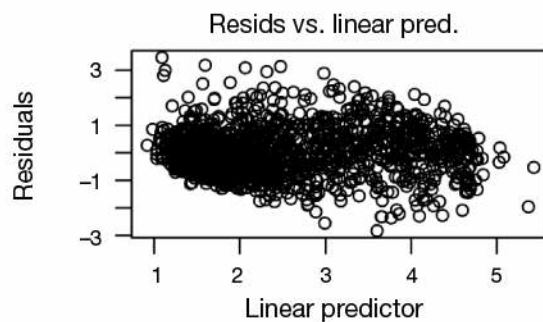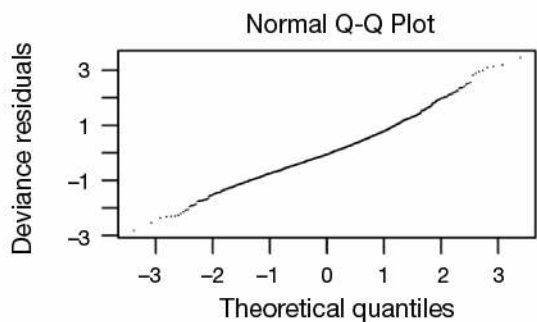
Appendix

a) *P. glauca*

b) *I. oxyrinchus*

Fig. A1. Standard model diagnostics of generalized additive mixed models (GAMMs), relating (a) blue shark *Prionace glauca* and (b) shortfin mako shark *Isurus oxyrinchus* catch per unit effort (kg d^{-1}) data to spatial-temporal and environmental variables in southern Peru