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# Influence of Environmental Factors and Fishing Effort on Demersal Fish Species in Ghana

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# INFLUENCE OF ENVIRONMENTAL FACTORS AND FISHING EFFORT ON DEMERSAL FISH SPECIES IN GHANA

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## ABSTRACT

Separating effects of fishing from responses of environmental factors is a key problem for fisheries scientists. I used data from fishery-independent trawl surveys (6 years data from 1999 – 2016) to test influences of fishing effort and environmental factors (temperature, oxygen salinity) on the abundance and spatial distribution of two species groups: 5 economically important species and 3 non-commercial species on the continental shelf of Ghana. Fishing effort, measured for the entire study area, affected year-to-year changes in the abundance of all but one species (5 species negatively, 2 positively, and 1 species unaffected). All species also showed significant spatio-temporal associations with temperature, salinity and oxygen levels. There was some year-to-year consistency in spatial distributions because each of these environmental variables was correlated with depth. Nonetheless, some inter-annual changes in species distribution appeared to reflect tracking of year-to-year shifts in climatic variables, e.g. inshore-offshore shifts in goatfish, red pandora and red cornetfish were associated with shifts in temperature and oxygen levels. The causes of other inter-annual changes in spatial distribution were not readily linked to climatic variables, and I argue that documenting spatial patterns of fishing effort in future might help explain these shifts. Overall, my results show that virtually all demersal species, targeted or not, appear impacted by fishing but also track spatial-temporal changes in environmental conditions from year-to-year. Improved management should thus incorporate spatially resolved measures of fishing effort alongside measures of climatic variables.

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## TABLE OF CONTENTS

ABSTRACT ........ ii

ACKNOWLEDGMENTS ........ iii

TABLE OF CONTENTS ........ iv

LIST OF TABLES ........ v

LIST OF FIGURES ........ vi

MANUSCRIPT ........ 1

ABSTRACT ........ 2

INTRODUCTION ........ 3

METHODOLOGY ........ 5

- Study Area ........ 5
- Fish survey ........ 5
- Environmental data and other predictors ........ 7
- Data analysis ........ 8

RESULTS ........ 11

- Environmental Variables ........ 11
- Fish abundance and distribution ........ 12
- Factors predicting ........ 12
- fish distribution and abundance ........ 12

DISCUSSION ........ 15

ACKNOWLEGEMENTS ........ 18

REFERENCES ........ 18

SUPPLEMENTARY MATERIALS AND APPENDICES ........ 42

## LIST OF TABLES

**Table 1**: List of species studied showing common names, economic value in Ghana (High = targeted Low = by-catch) and distribution. Distribution information from http://www.fishbase (Froese and Pauly 2018)........................................................ 24

**Table 2**: List of candidate GAM models used to test the influence of predictors on fish abundance........................................................................................................ 25

**Table 3**: Degrees of freedom (df) and AIC values for each of the eight GAM models. For each species, bold text indicates the best fitting model ...................................... 26

**Table 4**: Results of tests for the significance of parameters and model deviance (DE) of GAMs for the five target species. ........................................................................ 27

**Table 5**: Results of tests for the significance of parameters and model deviance (DE) of GAMs for the three bycatch species. .................................................................. 28

**Table 6**: A summary of the specific effects of predictor variables of the abundance of each species. ........................................................................................................ 29

**Table 7**: Relative importance of independent variables as predictors of target species distribution and abundance. ......................................................................... 29

**Table 8**: Relative importance of independent variables as predictors of bycatch species distribution and abundance. ......................................................................... 29

## LIST OF FIGURES

**Figure 1**: Coastal map of Ghana, showing trawl stations of 2016 survey................. 32

**Figure 2**: Spatial representation of bottom depth on the continental shelf. ............... 33

**Figure 3**: Spatial distribution of bottom temperatures on the continental shelf in two representative years. ........................................................................................ 34

**Figure 4**: Spatial distribution of oxygen concentrations on the continental shelf in two representative years. ........................................................................................ 35

**Figure 5**: Spatial distribution of salinity on the continental shelf in two representative years. ........................................................................................................... 36

**Figure 6**: Spatial distribution of red pandora in two representative years................. 37

**Figure 7**: Spatial distribution of goatfish in two representative years. ....................... 38

**Figure 8**: Spatial distribution of brown skate in two representative years................. 39

**Figure 9**: Spatial distribution of bluespotted seabream in two representative years. 40

**Figure 10**: Spatial distribution of flying gurnard in two representative years. ............ 41

**MANUSCRIPT**

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Influences of Climatic Variables and Fishing on Demersal Species in Ghana

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## ABSTRACT

Separating effects of fishing from responses to environmental variables is a key problem for fisheries scientists. I used data from fishery-independent trawl surveys (6 years data from 1999 – 2016) to test influences of fishing effort and environmental variables (temperature, oxygen salinity) on the spatial distribution of two species groups: 5 economically important species and 3 non-commercial species on the continental shelf of Ghana. Fishing effort, measured for the entire study area, affected year-to-year changes in the abundance of 6 species negatively, 2 species positively, and 1 species was unaffected. All species also showed significant spatio-temporal associations with temperature, salinity and oxygen levels. There was some year-to-year consistency in spatial distributions because each of these climatic variables was correlated with depth. Nonetheless, some inter-annual changes in species distribution appeared to reflect tracking of year-to-year shifts in climatic variables, e.g. inshore-offshore shifts in goatfish, red pandora and red cornetfish were associated with shifts in temperature and oxygen levels. The causes of other inter-annual changes in spatial distribution were not readily linked to climatic variables, and I argue that documenting spatial patterns of fishing effort in future might help explain these shifts. Overall, my results show that virtually all demersal species, targeted or not, appear impacted by fishing but also track spatial-temporal changes in environmental conditions from year-to-year. Improved management should thus incorporate spatially resolved measures of fishing effort alongside measures of environmental variables.

## INTRODUCTION

Numerous studies around the world have revealed that the dynamics of the demersal fish community in marine ecosystems are linked with oceanographic and climatic variability (Araújo *et al.*, 2006; Collie *et al.*, 2008) and also to anthropogenic pressures including fishing (Kendall *et al.*, 2008; Stelzenmüller *et al.*, 2008; Bartolino *et al.*, 2012). Fish species adapt to specific ranges of environmental variations and significant alterations in these natural ranges could be stressful or fatal (Simpson *et al.*, 2011; Recsetar *et al.*, 2012). An effect of changing environment on fish populations was illustrated by fish species changing their distribution to new depths due to increasing water temperatures (Nye *et al.*, 2009). As another example, Pihl and coworkers (1991) demonstrated the effect of oxygen deficiency on three demersal fish species in York river, Chesapeake Bay, USA. They found that the fish species migrated from deeper to shallower water when the oxygen levels were low, but then returned to the deeper waters when the levels of oxygen improved.

Apart from the effects of environmental variability, fish populations are affected by high fishing pressure. The effect of fishing has led to a worldwide decrease, or even collapse of many fish species (Myers and worm, 2003). Fishing can also alter community structure by removing large body size predatory fish, which can trigger gradual increases in species at lower trophic levels due to predation release (Pauly et al 1998, Jennings et al., 1999b; Genner et al., 2010). Often the effects of changes in environmental factors and fishing activities develop simultaneously and may interact, thereby complicating their relative effects (Perry *et al.*, 2010; Ter Hofstede and Rijnsdorp, 2011; Ciannelli *et al.*, 2012). For example, increasing temperature appears to have shifted the distribution of North Sea cod northwards and into deeper water over the past 100 years, while at the same fishing pressure caused a primarily eastward shift (Engelhard *et al.*, 2014). Understanding factors that influence changes in the distribution of demersal fish populations is critical for their conservation. In particular, knowledge of the factors regulating species distributions could provide useful information to manage fisheries (Walters & Collie 1988, Planque et al. 2011), but tropical and sub-tropical regions are underrepresented in analyses of this issue (Cheung *et al.*, 2009)

Here, I present an analysis of how variations in the environment and fishing pressure influence the distribution of demersal fish populations in the shallow sub-tropical waters off the coast of Ghana. The demersal fishery in Ghana serves important roles for food security, income generation and employment (MOFAD, 2015). Demersal species of high economic value, including grouper (*Epinephelus aeneus*), seabreams (*Pagellus bellottii*), cephalopods (*Sepia sp.*) and soles, together species make up about 23% of the total annual catch from the marine sector (MOFAD unpublished report). Several fishing gears are employed by small-scale (or artisanal), semi-industrial (or inshore), and industrial vessels to target demersal species (Aheto et al., 2012; Asiedu and Nunoo, 2013). The most recent report on the assessment of the status of demersal species in the eastern central Atlantic by the Scientific Working group of the Fisheries Committee for the eastern central Atlantic Subgroup South of the Food and Agriculture Organisation (FAO/CECAF) classified most of the demersal species within the region as either fully exploited or overexploited (FAO, 2015). In addition, independent fishery surveys conducted in Ghana report a decline in the biomass of important demersal species from about 25000 mt in 1999 to about 15000 mt in 2016 (Toresen et al, 2016), while the reported annual catch has remained relatively constant since 2002. The current status of demersal fish populations has been linked to effects of high fishing pressure (MOFAD, 2015) however, it is not clear whether trends in the abundance of these important demersal populations are influenced primarily by fishing or changes in the environment, or a combination of the two, and whether the influence is similar across species. Also unknown is whether there are spatial, as well as temporal, changes in species distribution in response to changing conditions.

The objective of my study was to explore, through statistical modelling, the influence of fishing and environmental factors on the abundance and distribution of demersal fish populations in Ghana. Selected demersal fish species representing economically important (target) and by-catch (non-target) species were used as indicators to examine the influence of environmental variables and fishing effort on abundance and distribution. Short term spatio-temporal analysis of the distribution of species were explored in relation to changes in bottom temperature, salinity and oxygen.

## METHODOLOGY

### *Study Area*

The area considered in this study is the coastal zone of Ghana which is 550 km long and geographically located between 3° 06' W to 1° 10' E latitude and between longitude 4° 30' and 6° 6' N (Mensah & Koranteng 1988). The area experiences four distinct hydrographic regimes; a major upwelling period and a minor upwelling period, interspersed with two periods of thermal stratification. The upwelling periods are characterized by low sea surface temperature, low dissolved oxygen, high salinity and high biological productivity (Wiafe et al., 2008).

### *Fish survey*

The species to be modelled were chosen based on their economic value (target and bycatch) and data availability (Table 1). The target species include red pandora, bluespotted seabream, cuttlefish, goatfish and Canary dentex and the bycatch species were brown skate, red cornetfish and flying gurnard. These two groups were selected as a way to test the relative effects of fishing and climate. I assumed the abundance and distribution of fish species that are not predominantly harvested (bycatch) would change in response to climatic (or other natural) factors alone. However, heavily fished species would respond to both fishing and climate. Differential responses of these two groups of fish would thus help to separate effects of climate from those of fishing.

The data were obtained from demersal trawl surveys conducted in 1999, 2004, 2005, 2006, 2007 and 2016 by the Government of Ghana, the Institute of Marine Research (IMR) and the Food and Agriculture Organisation of the United Nations (FAO) to assess status of fish stocks within Ghana's exclusive economic zone (EEZ). These years were selected because surveys were conducted between February to June. Each year's survey thus fell within the long thermally stratified period, making the data comparable across years (Mensah, M. A., and Koranteng, 1988). Years when surveys were performed during upwelling periods were excluded because fish spawning migrations, plus changes in other environmental variables such as nutrient concentrations, would complicate the interpretation of responses to the environmental factors of interest.

Trawl surveys were conducted by the R/V "Dr. Fridtjof Nansen" research vessel. Trawling was done using the "Gisund super bottom trawl", with a 20-mm mesh in the cod-end and an inner net of 10-mm mesh and a wing spread of 21 m. The survey boundaries were constant throughout, but within the survey boundary, the specific location of each trawl haul differed among years. Each year, the study area was sub-divided into three depth strata (0-30 m, 30-50m and 50-100m), and a set of semi-random swept-area hauls was carried out within each depth stratum. Trawling took place during day-time hours (0600 to 1800) at a towing speed of 2.9 to 3.1 knots and a haul duration of close to 30 minutes. The net was retrieved after each tow and the contents emptied onto the deck of the vessel. All fish collected were identified to the lowest taxon possible (Carpenter and De Angelis, 2002), counted, weighed, and the length-frequency of some commercially important species was compiled. Further details of sampling can be found in country reports on Dr. Fridtjof Nansen Surveys for Ghana (e.g. Toresen et al, 2016). Fish abundance was measured as the number of individuals per unit area of seabed swept by the trawl (fish $km^{-2}$). The area swept was the distance trawled multiplied by the trawl width (21 m) (Krakstad et al. 2007).

***Environmental data and other predictors***

Selection of explanatory variables to include in the model was based on ecological considerations and data from several different sources were used. Data on bottom temperature, salinity and oxygen were collected during the trawl survey, and were obtained from the electronic database of the Institute of Marine Research (IMR) in Norway. A Seabird 911 Conductivity Temperature Depth plus sensor was used to obtain vertical profiles of these variables from the surface to few meters above the bottom at majority of the trawl locations. Measurements close to the seabed were extracted and used in the analysis because the species considered in this study dwell near the seabed. Bottom depth, temperature, salinity and oxygen were found to be correlated (Table S1), however since there was no prior knowledge of which of the variables were important for the studied species, all variables were included in the model.

For other environmental variables, spatially resolved data to match the trawl stations were not available, so I calculated annual means for the entire study area corresponding to years of the survey. Data on sea surface temperature were obtained from the database of the Fisheries Scientific Survey Division in Ghana. An annual upwelling index was estimated using daily sea surface temperature (SST) recordings from eight stations (Keta, Tema, Winneba, Elmina, Takoradi, Axim, Half Assini) located along the coast by the Fisheries Scientific Survey Division of Ghana. The upwelling index (UI) was estimated by subtracting annual mean SST from 25°C. The value 25°C is the temperature threshold below which upwelling occurs in the Gulf of Guinea (Bakun,1978).

A term for fishing effort was included in the model to test the relative effect of fishing on the abundance distribution of the species. Because fishing effort is expected to have a lagged effect on fish abundance (Johnson and Carpenter, 1994), effort averaged over three years prior to the year of survey was used in the model. Averaging over three preceding years seemed ecologically reasonable because the study species are all reasonably long-lived, with typical lifespans of 5-10 years (Ghorbel and Bertalanffy, 2004), and because changes in fishing effort occurred steadily over several years, with modest inter-annual variations (apart from 2000) (Figure S1). Annual fishing effort was estimated as the total number of fishing days by all vessels. Fishing effort data from the three fishing sectors in Ghana (artisanal canoes, semi-industrial trawlers and industrial trawlers) were standardized and combined (Appendix S1) before use in the analysis (following Stamatopoulos and Abdallah, 2015). Standardization of effort was needed because the different classes of fishing vessel vary greatly in size, speed, and gears used and so differ greatly in relative fishing power (Robson, 1966).

***Data analysis***

Graphs of the spatial distribution of the environmental parameters and the spatial distribution of the eight fish species per year were obtained by interpolating data between stations to create surface layer maps. This was done using the inverse distance weighting (IDW) method in ArcGIS software. For each variable, raster size was maintained at a constant level and the smoothing power (p) was equal to 2.

Generalized additive models (GAM) were used to assess the relationships between fish distribution and the selected explanatory variables (Venables and

Dichmont, 2004). GAMs are a nonparametric extension of general linear models, and their flexibility allows for effective modelling of the frequently complex and nonlinear relationships between multiple environmental factors and species distributions (Hedger et al., 2004; Dingsør et al., 2007). The fish abundance data used for the analysis had a high percentage of zero observations and the data were also over-dispersed (Table 2); hence a two-stage modelling approach was used (Guisan and Zimmermann, 2000; Maunder and Punt, 2004). I used the Zero Inflated Poissson location scale model (using the ziplss function in the mgcv package within R), which is a two stage zero inflated Poisson model with two components; potential presence is modelled with one linear predictor and the second linear predictor models the Poisson mean abundance given potential presence (Wood et al., 2016). Abundance and presence/absence were modelled as:

$$\begin{aligned} &Abundance\ or\ presence/absence \\ &\quad = s(Latitude, Longitude) + s(Depth) + s(Bottom\ temperature) + s(Salinity) \\ &\quad\quad + s(Oxygen) + Fishing\ effort + Upwelling\ index \end{aligned} \tag{2}$$

I constructed a set candidate models that reflected plausible alternative hypotheses about the effect of environmental variables, fishing effort and upwelling on demersal fish presence and abundance (Table 2). The simplest reference model (Model 1) assumes that the presence and abundance of fish is described by location (latitude and longitude) and depth. Because of the potential for spatial autocorrelation, which would violate the assumption that data are independent, terms for location were included as smoothing terms in all GAM models to account for spatial autocorrelation on the broad scale (Wood 2006). Water depth was also included in all candidate models because it affects the distribution of most fish species, and the goal was to identify spatially and temporally dynamic influences of the other environmental variables after accounting for the (static) influence of depth. Models 2-4 include the individual or combined effects of the non-spatial predictors, for which we tested only the effect of year-to-year changes. Model 5 includes only the spatially-resolved environmental variables collected during the trawl surveys (temperature, oxygen and salinity). Models 6 and 7 include combinations of both spatial and non-spatial predictor variables and, finally, all predictor variables were included in the final model (Model 8).

Model fits were calculated using Akaike's Information criterion (AIC; Akaike, 1973) and model deviance (DE), and the model with the lowest AIC value and highest deviance was selected as the model that best described the data (Table 3). I assessed the relative importance of each variable included in the final model by excluding each variable individually from the best fit model and examining the change in both AIC and DE (Table 6 and 7). Response plots were generated for each variable that had a significant influence ($p < 0.05$) on species distribution or abundance (Figure S4). To reduce model overfitting and reduce the risk of generating ecologically unrealistic responses (Lehmann etal., 2002), a k value of 5 and 15 for all predictor variables and the interaction between latitude and longitude respectively were used. The "gam.check" function in the "mgcv" package in R was used to check that the basic dimension value was adequate for each model. Model performance was also evaluated by visually comparing the observed values at each point with the model predictions and using model diagnostics generated from the gam.check function in R. Spatial autocorrelation in the residuals of the model was judged to be minimal based on visual examination of the semivariogram as a function of the measured sample points (Dormann etal., 2007).

## RESULTS

### *Environmental Variables*

The study area spans the shallow waters (sampled depths ranged from 17.5-115.5 m) of the relatively narrow Ghanaian continental shelf (30-90 km wide), and includes deeper areas offshore at the beginning of the continental slope (the Côte d'Ivoire Escarpment) (Figure 2). The mean bottom temperature in the study area varied among years. The warmest year was 1999 (25 $^{\circ}$C on average) and the years 2007 and 2016 (20$^{\circ}$C on average) were the coolest years. The spatial distribution of temperatures showed that it was generally cooler (< 22 $^{\circ}$C) in deeper water offshore, however inshore areas were sometimes cooler in years when the overall mean temperature was low (Figure 3). For example, in 1999 warmer temperatures were recorded throughout most of the study area, except for the deepest areas furthest offshore. In contrast, in 2016, warmer waters (> 26$^{\circ}$C) were found only in inshore areas at the eastern edge of the study area (Figure 3). The inter-annual trends, and spatial distribution of oxygen concentrations appeared to correlate reasonably closely with those described for temperature (Table S1). Oxygen concentrations were generally higher in years when temperatures were higher, and oxygen concentrations were typically reduced in deeper offshore areas (Figure 4). Instances of higher oxygen concentrations in shallow inshore areas tended to coincide with warmer temperatures in those areas. Salinity concentrations showed different patterns, with no clear trend in mean salinity concentrations from year to year. Spatial variation in salinity concentrations appeared to be driven by intrusion of fresh water from estuaries along the coast especially in the west, which reduced salinity concentrations in shallow areas in some years (Figure 5) and may be responsible for the weak negative correlation of salinity levels with those of oxygen and temperature (Table S1).

### ***Fish abundance and distribution***

Overall, the target species were more abundant than the bycatch species but both target and bycatch species displayed large fluctuations in their annual mean abundance from 1999 to 2016 (Figure S3). Locations of high and low abundances for these species were highly variable, and for most species, patches of high abundance were in different locations across years (Figures 6-10). Also, there was little consistency among species in the exact locations where abundance was high in a given year (Figures 6-10). For example, red pandora tended to be more abundant in offshore deeper waters, but patches of high and low abundance were in different areas each year. Other species, like bluespotted seabream, goatfish (both target species) and red cornetfish (a bycatch species) were typically more abundant offshore, but increased numbers of fish were observed in inshore areas in some years. Species like Canary dentex, cuttlefish and flying gurnard, on the other hand, displayed less consistent changes in their distribution from year to year.

### ***Factors predicting fish distribution and abundance***

The model selection procedure showed that model 8 performed better than the other models for 7 of the 8 species (Table 3), which means distribution and abundance was driven by both environmental variability and fishing effort. However, Model 5 was the best model for the brown skate, reflecting the lack of significant effects of fishing and upwelling on this species. In general, the deviance explained in each model ranged from 45% for brown skate to 66.6% for Canary dentex, suggesting that the models have adequate power and predictability (Table 4).

Red Pandora abundance was negatively affected by fishing effort, whilst upwelling had a positive influence (Table 6 and Figure S4). Abundance was higher at depths between 40-60 m, and at temperatures between 21-27 $^{\circ}$C and oxygen concentrations < 3 ml $l^{-1}$ (Table 6 and Figure S4). The strongest effects on red pandora abundance were those of temperature, oxygen and salinity (Table 6).

Bluespotted seabream presence and abundance was positively associated with depths between 30-60 m (Table 6 and Figure S4). There were weak negative effects of fishing and upwelling on abundance (Tables 6 and 7), and effects of oxygen, temperature and salinity that were of greater magnitude (Tables 6 and 7). Abundance was higher at temperatures between 16-21 °C and at salinities between 34.3-35.3 psu (Table 6 and Figure S4).

Higher abundance of cuttlefish was associated with temperatures between 17-21°C, oxygen levels between 1.5-3.5 ml $l^{-1}$ salinities between 35-35.5 psu. Cuttlefish abundance was higher in deeper water between 60-115 m (Table 6 and Figure S4). Both fishing effort and upwelling index had a positive influence on abundance (Table 6). The strongest effects on abundance were those of fishing effort and temperature (Tables 6 and 7).

Goatfish were most abundant at depths from 40-70 m, at temperatures of 20-26 °C and salinities between 3-4 psu (Table 6 and Figure S4). Temperature, fishing effort and oxygen were the three most important predictors from the best fitting GAM model (Table 7). However, the relationship of goatfish abundance with oxygen from the response plots was unclear. The influence of fishing effort on goatfish abundance was positive, but the effect of upwelling was negative.

Response plots generated from the GAM, indicated that the abundance of Canary dentex was highest at depths from 70-110 m and at temperatures from 17-21 °C (Table 6 and Figure S4). The most influential effects on Canary dentex were those of temperature, salinity and a negative effect of fishing (Table 7).

Red cornetfish were more abundant at depths from 40-115 m, at temperatures between 18-26 °C and salinities between 34.5-35.5 psu (Table 6 and Figure S4).

Calculating the magnitude of influence of each variable indicated that temperature, oxygen, salinity and fishing effort all had appreciable influences on red cornetfish abundance (Table 8). The effects of fishing effort and upwelling index were both negative (Table 6)

The brown skate was most abundant at depths between 40-115 m, at temperatures between 16-24 $^{\circ}$C, salinities between 34.8-35.6 psu and oxygen concentrations between 2.5-3.2 ml $l^{-1}$ (Table 6 and Figure S4). Effects of these environmental variables were of large magnitude (Table 8), and fishing effort and upwelling had no detectable influence on brown skate abundance.

Both fishing effort and upwelling index had a negative influence on flying gurnard abundance (Table 6). Flying gurnard were also positively associated with water depths between 50-90 m, and with temperatures between 16-22 $^{\circ}$C and oxygen levels 4.2-5 ml $l^{-1}$ (Table 6 and Figure S4), with the effects of temperature and oxygen have the strongest influences (Table 8).

Overall, most species tended to avoid the shallowest inshore parts of the study area (Table 8). Three of the target species were associated with intermediate depths (red pandora, bluespotted seabream and goatfish), whereas the other two target species and the three bycatch species were associated with deeper water (Table 8). Deeper water was generally cooler, less oxygenated, and at higher salinity than shallower water inshore (Figures 2-5). Despite these broad associations with depth, all of the species were influenced by spatio-temporal variation in temperature, oxygen and salinity levels. Temperature explained the largest (4 species) or second largest (3 species) percentage of model deviance for 7 of the 8 species, and so was generally the most important predictor of fish distributions. Visual inspection of the spatial plots, suggests that some inter-annual changes in species distribution appear to reflect tracking of year-to-year shifts in environmental variables. For example, the distribution of red pandora was shifted inshore and eastward in 1999 relative to 2016 (Figure 6), apparently matching the associated shift in temperature (Figure 3). Similarly, the inshore shift of goatfish in 2016 relative to 1999 may also reflect tracking of cooler water from year-to-year (Figure 7).

Of the two non-spatial predictors, fishing effort had a much stronger effect on the eight study species than upwelling (Tables 7 and 8). Surprisingly, effects of fishing were both positive and negative. Regardless of the direction of the fishing effect (positive or negative), there was some evidence that the influence of the fishing effect was of greater magnitude on target species than on bycatch species (Tables 7 and 8). Fishing explained the largest (1 species) or second largest (2 species) percentage of model deviance for 3 of the 5 target species, whereas for the three bycatch species it always explained a lower percentage of model deviance than all three environmental predictors (temperature, oxygen and salinity) (Tables 7 and 8).

## DISCUSSION

Overall, the GAM models revealed influences of all predictor variables on the abundance of the species. The model revealed that geographical location and depth were the main determinants of the presence and abundance of the study species. This is because depth is often found to be a key predictor of variability in spatial distribution of demersal fish populations due to its close relationship to many environmental features such as temperature and oxygen (Damalas et al., 2010). These results were consistent with other findings on distribution of demersal species in other parts of the world (Russell et al. 2014., Grüss et al., 2016; Parra et al., 2016). The preferred depth range was species specific but generally most of the species were more abundant in the offshore areas on the continental shelf at depths greater than 40m. The findings suggest some degree of niche overlap in the spatial distribution of these species. This may reflect tracking the spatial distribution of resources such as food. For instance, both Canary dentex and Bluespotted seabream both feed on small fish and crustaceans (Russel et al., 2014), which may create overlap in their distributions and create the potential for interspecific interactions

Broadly similar associations between abundance and environmental variables were observed for target and bycatch species. All the environmental variables were important in describing the dynamics in species abundance distribution. Bottom temperature was a very influential variable on both target and bycatch species, however the magnitude of influence was species specific. Many studies have demonstrated the influence of these variables on fish assemblage structure and distribution (Harman *et al.*, 2003; Anderson and Millar, 2004; Araújo *et al.*, 2006; Simpson *et al.*, 2011; Recsetar *et al.*, 2012; Anderson *et al.*, 2013). In addition to the above, our analysis revealed insight into ecological preferences of these species on the continental shelf of Ghana. Most species were associated with cooler, less oxygenated and more saline conditions that are typically found offshore. Based on this information, future management and conservation efforts for demersal species in Ghana could focus on these areas.

The findings also demonstrated that fish spatial distributions were tracking short term spatial and temporal changes in environmental variables, especially temperature. This was evident in the distribution of some target species (goatfish and red pandora) and bycatch species (red cornetfish). These species avoided coastal areas in 1999 when it was generally warmer everywhere, but increased in abundance in both inshore and offshore areas when temperature was cooler in 2016. Other species, however, like Canary dentex and flying gurnard did not show any clear pattern in their year-to-year shifts in distribution. The shifts in abundance distribution of these species could not be explained by changes in either temperature, salinity or oxygen. Perhaps other factors like spatial patterns in fishing pressure, prey distribution patterns, the type of substratum, or other habitat features may explain the distribution of these species.

The dynamics of fish communities are often considered to be controlled primarily by fishing, but influences of fishing and of environmental variation are often similar and complicated to disentangle (ter Hofstede & Rijnsdorp 2011). The use of two species groups, one being a target of the fishery and the other; bycatch species allowed the comparison of influence of fishing on these species. Fishing effort was an important predictor variable influencing the dynamics of the both target and bycatch species, and there was only weak support for the hypothesis that the influence of fishing effort will be greater for the target species than the bycatch species. One possible explanation is the unselective nature of most fishing gears used in Ghana, coupled with high and increasing effort from all sectors of the fishery (Koranteng and Pauly, 2004; MOFAD, 2015) and the use of unsustainable fishing practices like light fishing (Ameyaw,G., Asare *et al.*, 2012). There is also a vibrant market for some bycatch species especially in the central region of Ghana, hence classifying them as bycatch may be innacurate (Nunoo et al., 2009). I suggest that these bycatch species should no longer be classified as a bycatch for the demersal fishery and should be added to the species that are rountinely assessed and monitored.

To conclude, this study has demonstrated that both environmental variability and fishing effort are generally important in explaining the dynamics of demersal fish populations. Comparing target and bycatch species provided an understanding of how environmental variables and fishing effort influence these species and it also offered a way to disentangle the effect of fishing and environmental variability. Having knowledge of the factors driving demersal fish populations in Ghana is essential for effective monitoring and management of these important organisms. Findings from the study provide a baseline against which future changes in fish distributions, and the effects of environmental variability and fishing effort may be monitored and compared.

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## TABLES

**Table 1**: List of species studied showing common names, economic value in Ghana (High = targeted Low = by-catch) and distribution. Distribution information from http://www.fishbase (Froese and Pauly 2018)

| **Species** | **Common Name** | **Economic Value (Ghana)** | **Distribution** |
|---|---|---|---|
| *Pagrus caeruleostictus* | Bluespotted seabream | High | E Atlantic: Portugal to Angola; Mediterranean |
| *Pagellus bellottii* | Red pandora | High | E Atlantic: Strait of Gibraltar – Angola; SW Mediterranean; Canary Islands |
| *Sepia hierredda* | Cuttlefish | High | E Atlantic; Mediterranean |
| *Pseudupeneus prayensis* | Goatfish | High | E Atlantic: Morocco - Angola; Mediterranean; Catalan Sea |
| *Dentex canariensis* | Congo dentex | High | E Atlantic: Cape Bojador, W Sahara – Angola, South Spain |
| *Raja miraletus* | Brown skate | Low | E Atlantic, Mediterranean, W Indian ocean |
| *Fistularia petimba* | Red cornetfish | Low | E Atlantic, W Atlantic, Indo-West Pacific, Australia, Hawai. |
| *Dactylopterus volitans* | Flying Gurnard | Low | E Atlantic: English Channel – Angola, W Atlantic: Canada – Massachusetts, Mexico – Argentina |

**Table 2**: List of candidate GAM models used to test the influence of predictors on fish abundance

| Model | Model formulation - explanatory variables |
|---|---|
| 1 | Depth + Location |
| 2 | Depth +Location + Fishing |
| 3 | Depth + Location + Upwelling Index |
| 4 | Depth + Location + Fishing + Upwelling Index |
| 5 | Depth + Location +Temperature + Oxygen + Salinity |
| 6 | Depth + Location + Temperature + Oxygen + Salinity + Fishing |
| 7 | Depth + Location + Temperature + Oxygen + Salinity + Upwelling Index |
| 8 | Depth + Location + Temperature + Oxygen + Salinity + Fishing + Upwelling Index |

**Table 3**: Degrees of freedom (df) and AIC values for each of the eight GAM models. For each species, bold text indicates the best fitting model

| | | **Model 1** | **Model 2** | **Model 3** | **Model 4** | **Model 5** | **Model 6** | **Model 7** | **Model 8** |
|---|---|---|---|---|---|---|---|---|---|
| **Red pandora** | df | 35.4 | 52.1 | 37.4 | 37.4 | 56.1 | 55.3 | 39.4 | **57.7** |
| | AIC | 108154.6 | 85386.3 | 104561.9 | 108136.8 | 85063.7 | 84655.2 | 104130.7 | **84561.3** |
| **Bluespotted** | df | 32.4 | 45.7 | 34.8 | 34.4 | 49.7 | 50.3 | 36.9 | **55.1** |
| **seabream** | AIC | 8702.2 | 6942.5 | 8591.9 | 8699.8 | 6932.4 | 6917.3 | 8593.8 | **6876.2** |
| **Cuttlefish** | df | 27.8 | 41.8 | 30.2 | 29.8 | 46.6 | 43.6 | 32.2 | **48.0** |
| | AIC | 3149.4 | 3007.7 | 3033.8 | 3140.7 | 2891.1 | 3009.1 | 2987.2 | **2856.1** |
| **Goatfish** | df | 33.6 | 48.4 | 35.9 | 35.9 | 52.4 | 51.3 | 38.1 | **53.6** |
| | AIC | 19076.7 | 17003.3 | 18590.5 | 18727.6 | 16481.3 | 16866.5 | 18448.0 | **16476.3** |
| **Canary dentex** | df | 32.6 | 46.3 | 34.9 | 34.7 | 49.3 | 49.7 | 36.9 | **51.2** |
| | AIC | 5013.9 | 4319.3 | 4919.3 | 4885.9 | 4262.4 | 3996.3 | 4815.3 | **3992.3** |
| **Brown skate** | df | 29.7 | 45.5 | 32.3 | 31.9 | **49.1** | 48.4 | 34.4 | 51.1 |
| | AIC | 1518.0 | 1094.1 | 1473.2 | 1520.5 | **1095.6** | 1097.4 | 1469.8 | 1099.3 |
| **Red cornetfish** | df | 34.8 | 50.1 | 36.5 | 36.8 | 53.0 | 53.6 | 38.5 | **55.0** |
| | AIC | 4228.6 | 3496.2 | 3838.8 | 4188.6 | 3294.6 | 3387.6 | 3841.3 | **3276.6** |
| **Flying gurnard** | df | 34.1 | 47.7 | 36.3 | 36.2 | 55.1 | 51.5 | 38.5 | **56.4** |
| | AIC | 3782.33 | 2661.81 | 3660.77 | 3772.75 | 2612.37 | 2605.28 | 3607.79 | **2471.84** |

**Table 4**: Results of tests for the significance of parameters and model deviance (DE) of GAMs for the five target species. Covariates with *p* values < 0.05 are in bold

| Model | Covariate | Red pandora | Bluespotted seabream | Cuttle fish | Goatfish | Canary dentex |
|---|---|---|---|---|---|---|
| **Abundance** | Location | **<0.001** | **<0.001** | **<0.001** | **<0.001** | **<0.001** |
| | Bottom depth | **<0.001** | **<0.001** | **<0.001** | **<0.001** | **<0.001** |
| | Temperature | **<0.001** | **<0.001** | **<0.001** | **<0.001** | **<0.001** |
| | Oxygen | **<0.001** | **<0.001** | **<0.001** | **<0.001** | **<0.001** |
| | salinity | **<0.001** | **<0.001** | **<0.001** | **<0.001** | **<0.001** |
| | Fishing effort | **-0.001** | **-0.001** | **0.001** | **0.001** | **-0.001** |
| | Upwelling Index | **0.001** | **-0.001** | **0.001** | **-0.001** | |
| **Presence/Absence** | Location | 0.100 | **0.001** | **0.024** | **0.001** | **0.011** |
| | Bottom depth | **0.001** | **0.001** | 0.843 | **0.001** | 0.093 |
| | Temperature | 0.434 | 0.796 | **0.007** | 0.819 | 0.277 |
| | Oxygen | 0.408 | 0.984 | **0.012** | 0.270 | 0.163 |
| | salinity | 0.449 | 0.373 | **0.025** | 0.323 | **0.007** |
| | Fishing effort | **0.001** | **0.001** | **0.001** | **0.001** | **0.001** |
| | Upwelling Index | **0.037** | 0.003 | -0.011 | -0.066 | |
| **DE (%)** | | **53.6** | **54.4** | **45.6** | **48.2** | **66.6** |

**Table 5**: Results of tests for the significance of parameters and model deviance (DE) of GAMs for the three bycatch species. Covariates with *p* values < 0.05 are in bold

| **Model** | **Covariate** | **Brown skate** | **Red cornetfish** | **Flying gurnard** |
|---|---|---|---|---|
| **Abundance** | Location | **<0.001** | **<0.001** | **<0.001** |
| | Bottom depth | **<0.001** | **<0.001** | **<0.001** |
| | Temperature | **<0.001** | **<0.001** | **<0.001** |
| | Oxygen | **<0.001** | **<0.001** | **<0.001** |
| | salinity | **<0.001** | **<0.001** | **<0.001** |
| | Fishing effort | | **-0.001** | **-0.001** |
| | Upwelling Index | | **-0.001** | **-0.001** |
| **Presence/Absence** | Location | 0.378 | **0.001** | **0.001** |
| | Bottom depth | 0.730 | **0.001** | **0.001** |
| | Temperature | 0.192 | 0.335 | **0.018** |
| | Oxygen | 0.428 | 0.203 | 0.054 |
| | salinity | 0.697 | 0.151 | **0.030** |
| | Fishing effort | | **0.001** | **0.001** |
| | Upwelling Index | | -0.038 | 0.090 |
| **DE (%)** | | **47.6** | **55.9** | **60.5** |

**Table 6**: A summary of the specific effects of predictor variables of the abundance of each species. For depth, temperature, salinity and oxygen, the table indicates apparent preferences inferred from ranges of the predictor over which a response plot indicated a positive additive effect of that predictor on presence and/or abundance (Figure S4). When the response to a variable was complex or difficult to interpret, the response is entered as "?". For effects of fishing and upwelling, the table indicates whether the effect was positive ("+") or negative ("-"). Cells are left empty when the response was not significant ($p < 0.05$)

| | Depth (m) | Temperature (°C) | Salinity (psu) | Oxygen (ml $l^{-1}$) | Fishing Effort | Upwelling Index |
|---|---|---|---|---|---|---|
| **TARGET SPECIES** | | | | | | |
| **Red pandora** | 40-60 | 21-27 | ? | 1.5-3 | - | + |
| **Bluespotted seabream** | 30-60 | 16-21 | 34.3-35.3 | ? | - | - |
| **Cuttlefish** | 60-115 | 17-21 | 35-35.5 | 1.5-3.5 | + | + |
| **Goatfish** | 40-70 | 20-26 | ? | 3-4 | + | - |
| **Canary dentex** | 70-110 | 17-21 | ? | ? | - | |
| **BYCATCH SPECIES** | | | | | | |
| **Brown skate** | 40-115 | 16-24 | 34.8-35.6 | 2.5-3.2 | | |
| **Red cornetfish** | 40-115 | 18-26 | 34.5-35.5 | ? | - | - |
| **Flying gurnard** | 50-90 | 16-22 | ? | 4.2-5 | - | - |

**Table 7**: Relative importance of independent variables as predictors of target species distribution and abundance. Relative importance was calculated as the change in AIC (ΔAIC) and change in deviance explained (ΔDE) when each predictor variable was excluded from the final GAM model for each species

| | **Red pandora** | | **Bluespotted seabream** | | **Cuttle fish** | | **Goatfish** | | **Canary dentex** | |
|---|---|---|---|---|---|---|---|---|---|---|
| | ΔAIC | ΔDE (%) | ΔAIC | ΔDE (%) | ΔAIC | ΔDE (%) | ΔAIC | ΔDE (%) | ΔAIC | ΔDE (%) |
| **Oxygen** | 2683 | 1.9 | 448 | 3.8 | 18 | 0.7 | 228 | 0.9 | 38 | 0.4 |
| **Salinity** | 4167 | 3 | 50 | 0.5 | 51 | 1.7 | 197 | 0.8 | 233 | 2.5 |
| **Bottom temperature** | 8117 | 5.8 | 143 | 1.3 | 75 | 2.4 | 591 | 2.2 | 379 | 3.5 |
| **Fishing effort** | 240 | 0.2 | 28 | 0.3 | 163 | 4.6 | 390 | 1.5 | 279 | 2.8 |
| **Upwelling Index** | 34 | 0 | 19 | 0.2 | 43 | 1.2 | 21 | 0.1 | 4 | 0 |

**Table 8**: Relative importance of independent variables as predictors of bycatch species distribution and abundance. Relative importance was calculated as the change in AIC (ΔAIC) and change in deviance explained (ΔDE) when each predictor variable was excluded from the final GAM model for each species

| | Brown skate | | Red cornet fish | | Flying gurnard | |
|---|---|---|---|---|---|---|
| | ΔAIC | ΔDE (%) | Δ AIC | ΔDE (%) | ΔAIC | ΔDE (%) |
| **Oxygen** | 92 | 6.6 | 140 | 2.8 | 428 | 7 |
| **Salinity** | 151 | 10.3 | 100 | 2.1 | 35 | 0.7 |
| **Bottom temperature** | 39 | 2.9 | 271 | 5.5 | 134 | 2.4 |
| **Fishing Effort** | | | 108 | 2.1 | 52 | 1 |
| **Upwelling Index** | | | 13 | 0.3 | 96 | 1.7 |

## FIGURES

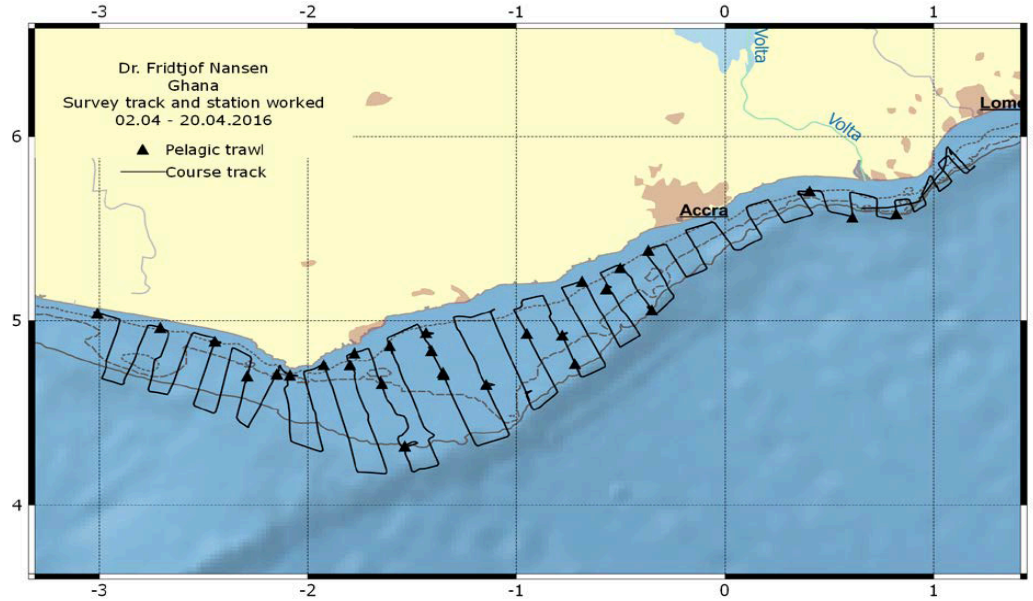



**Figure 1**: Coastal map of Ghana, showing trawl stations of 2016 survey. Source: Toresen et al. 2016

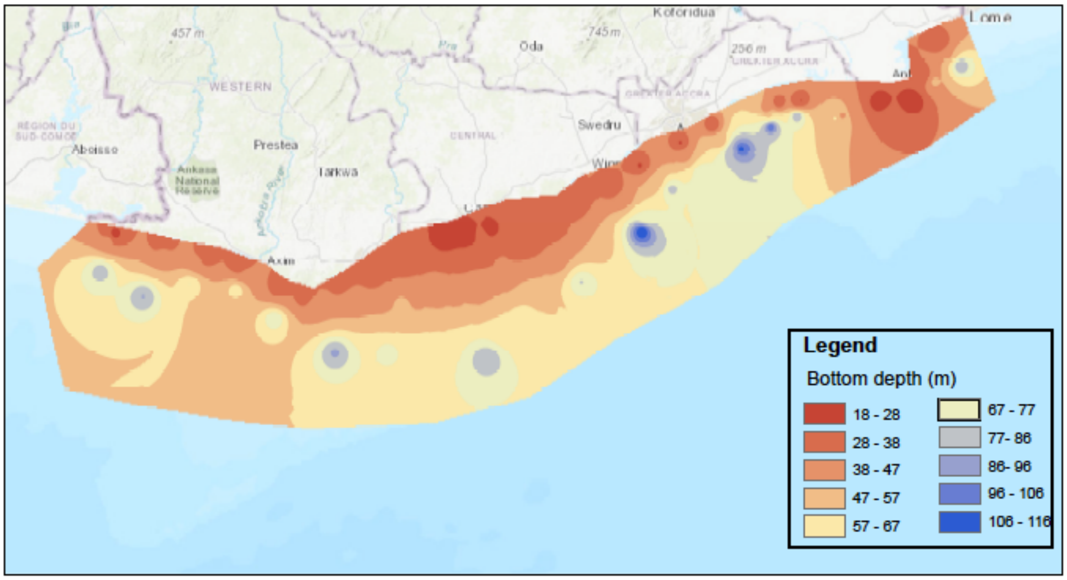



**Figure 2**: Spatial representation of bottom depth on the continental shelf. Note: the shaded area is the area surveyed

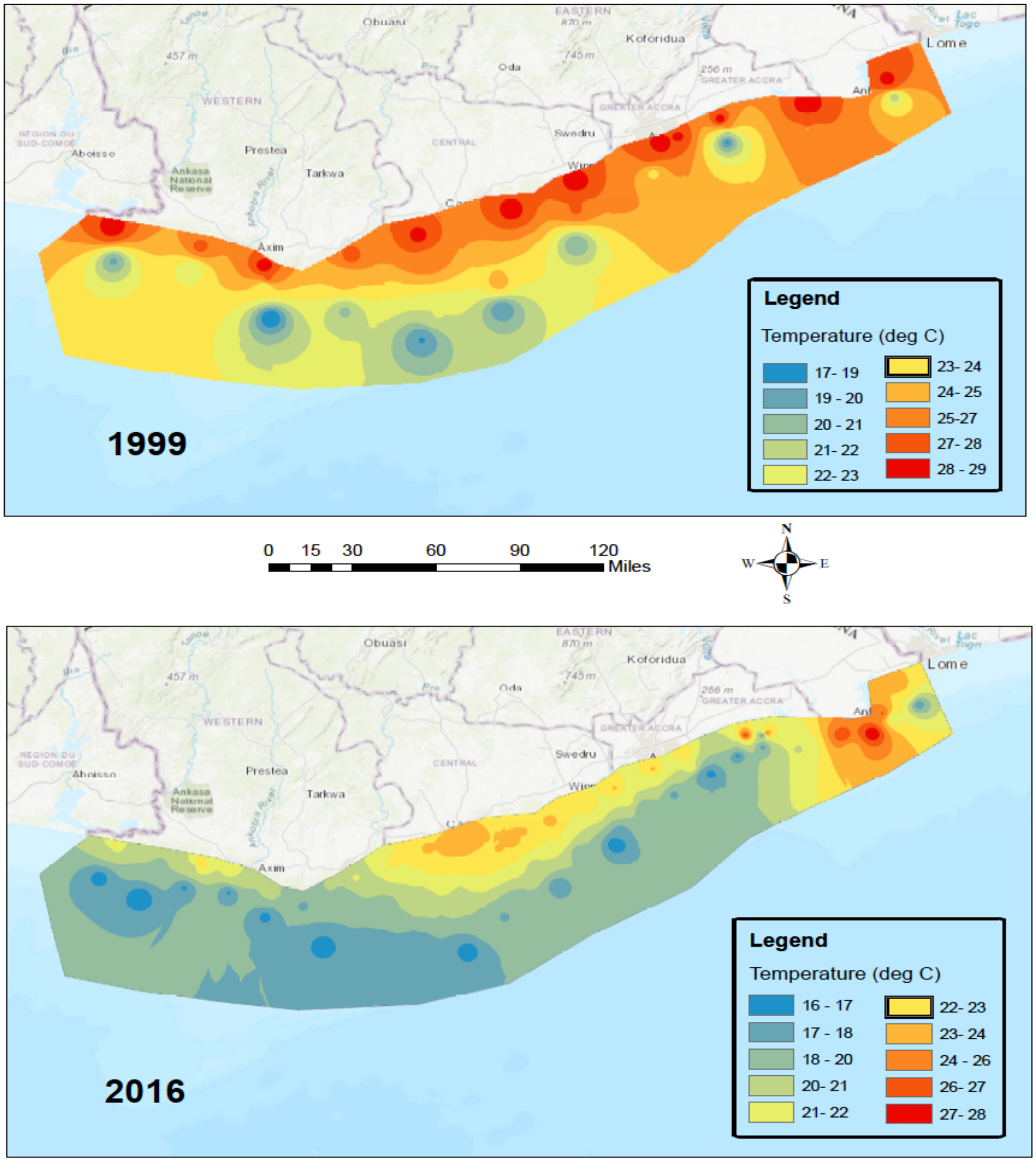



**Figure 3**: Spatial distribution of bottom temperatures on the continental shelf in two representative years. For each year, the spatial distribution of bottom temperatures within the study area is indicated by the brightness of the contours

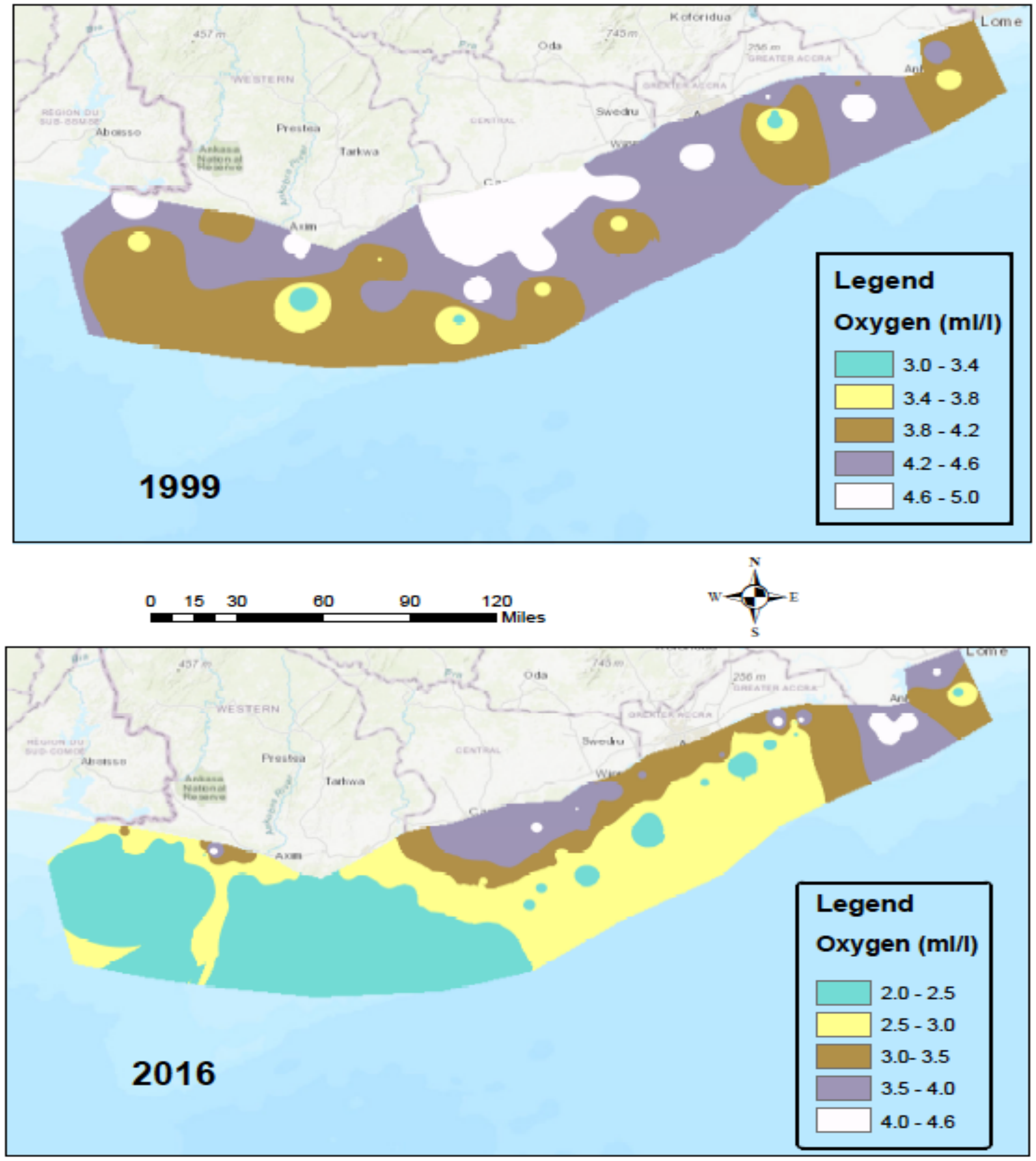



**Figure 4:** Spatial distribution of oxygen concentrations on the continental shelf in two representative years. For each year, the spatial distribution of oxygen concentration within the study area is indicated by the brightness of the contours

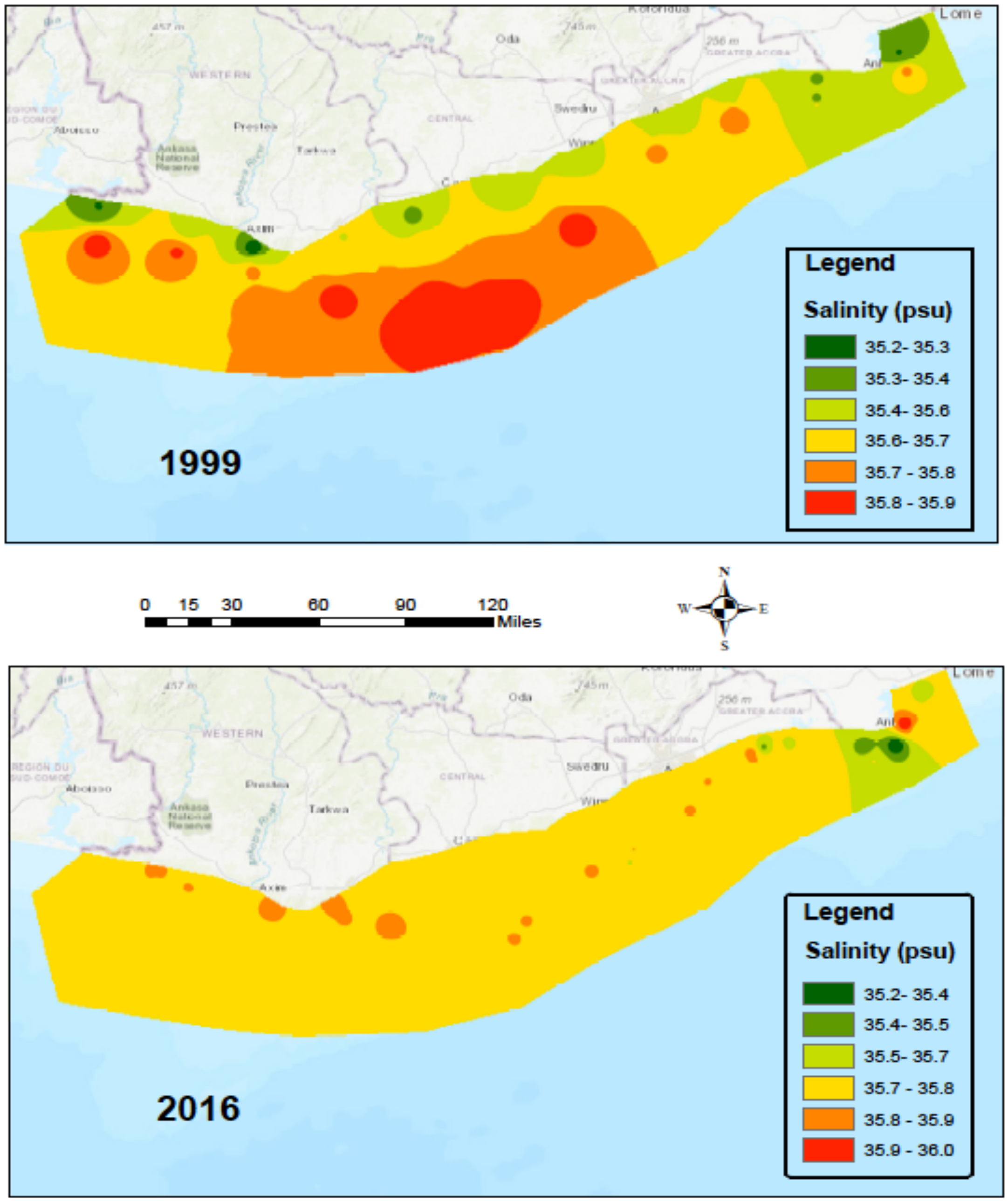



**Figure 5:** Spatial distribution of salinity on the continental shelf in two representative years. For each year, the spatial distribution of salinity within the study area is indicated by the brightness of the contours.

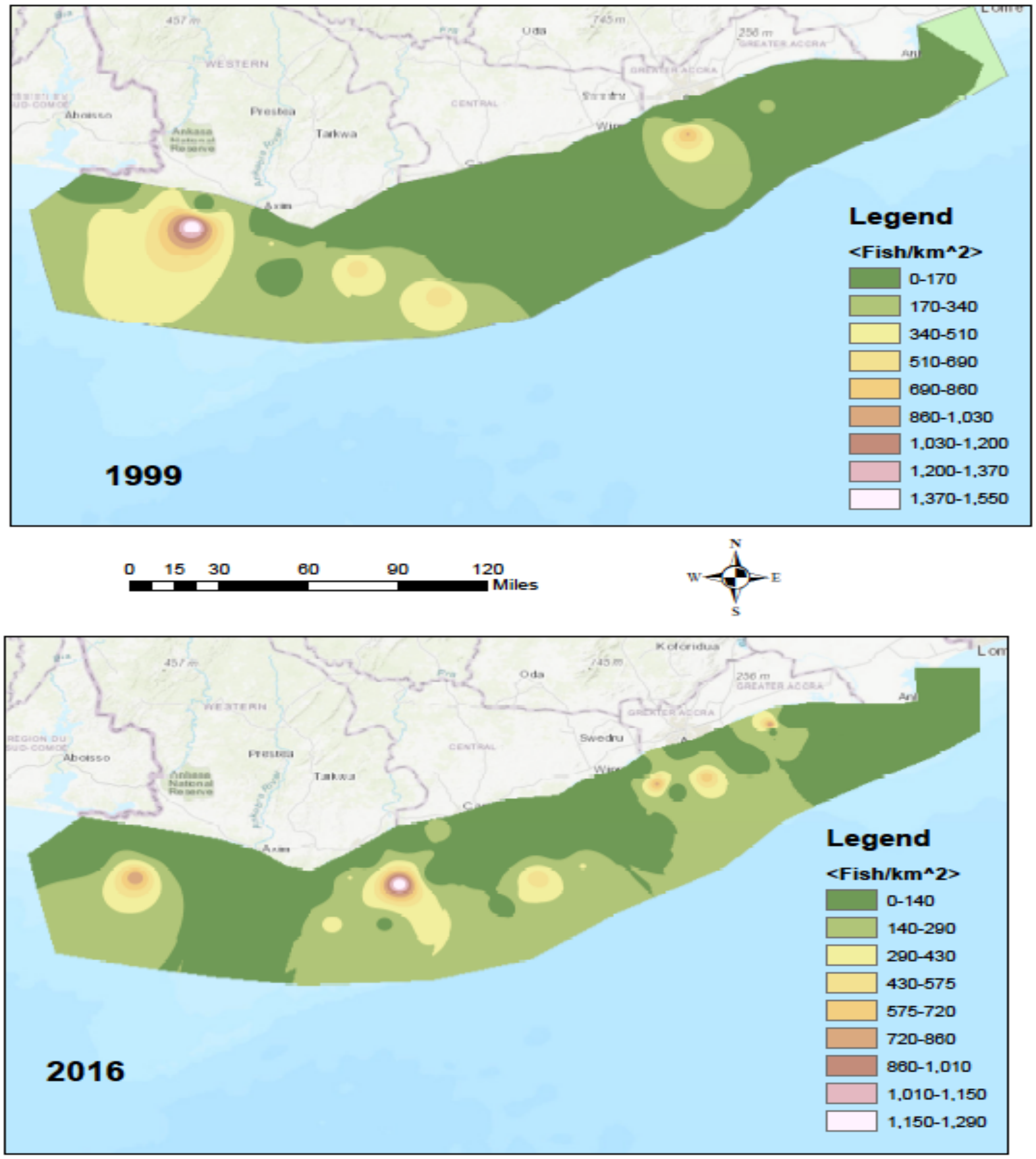



**Figure 6**: Spatial distribution of red pandora in two representative years. For each year, the brightness of the contours is proportional to fish population density

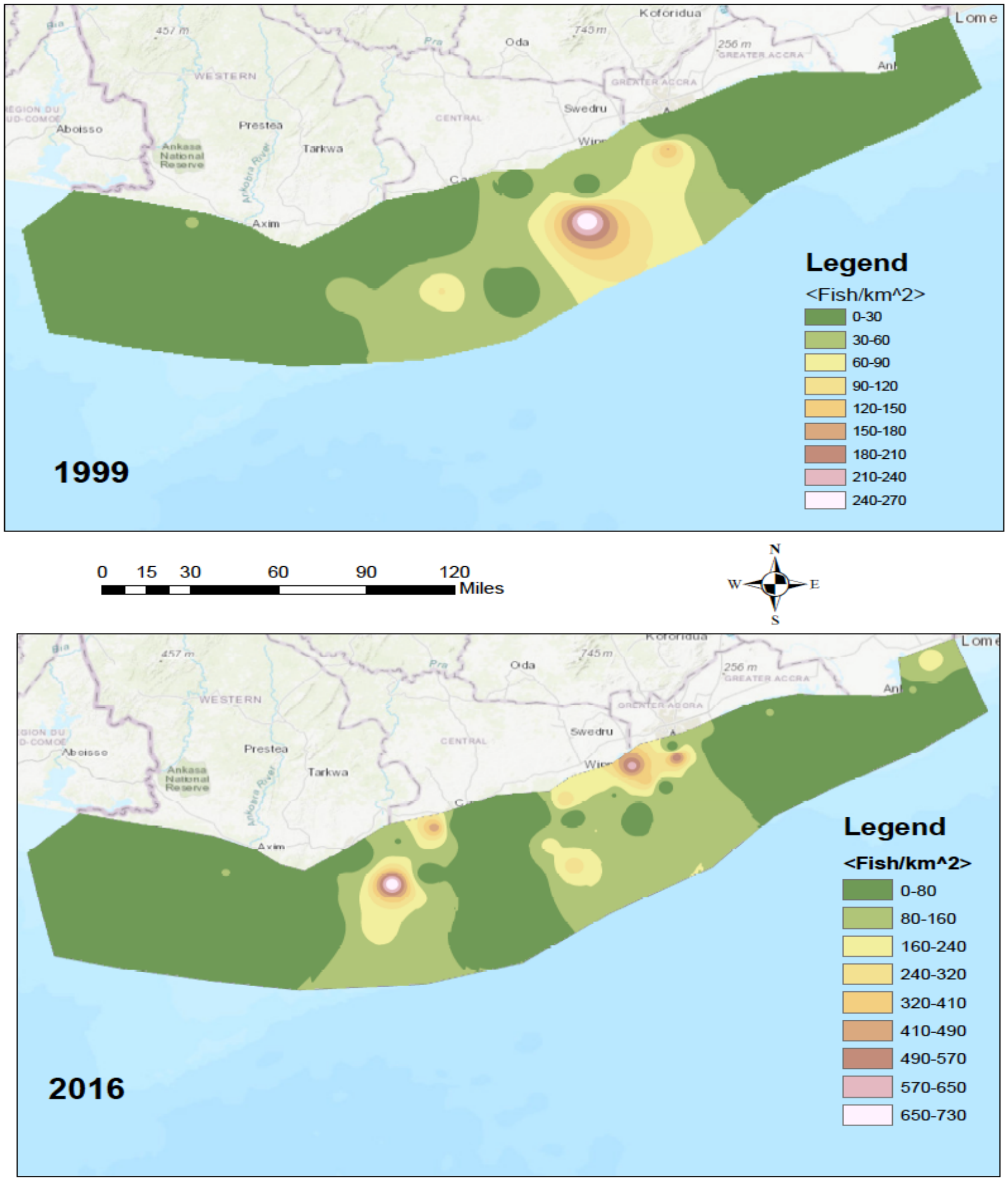



**Figure 7**: Spatial distribution of goatfish in two representative years. For each year, the brightness of the contours is proportional to fish population density

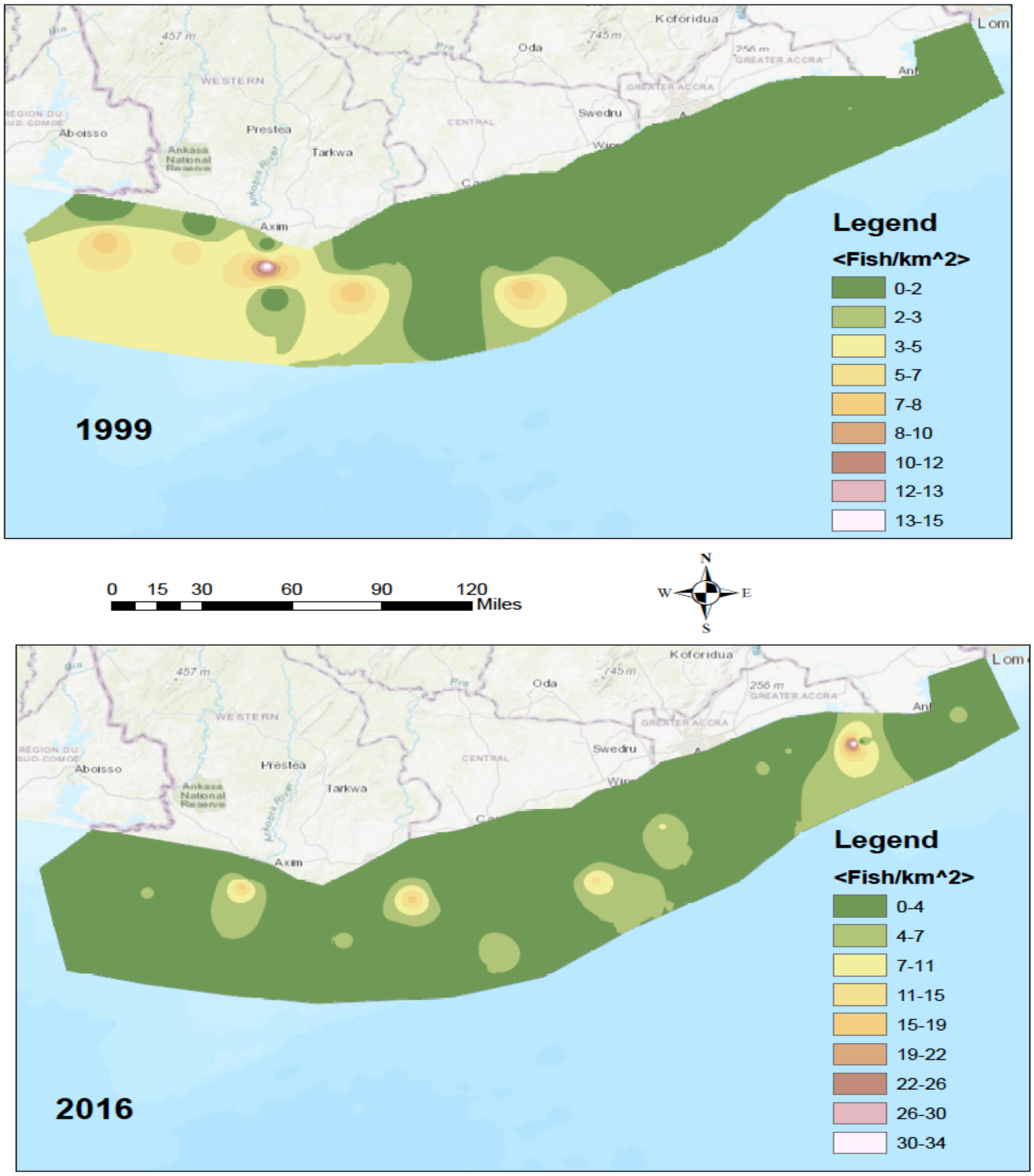



**Figure 8**: Spatial distribution of brown skate in two representative years. For each year, the brightness of the contours is proportional to fish population density

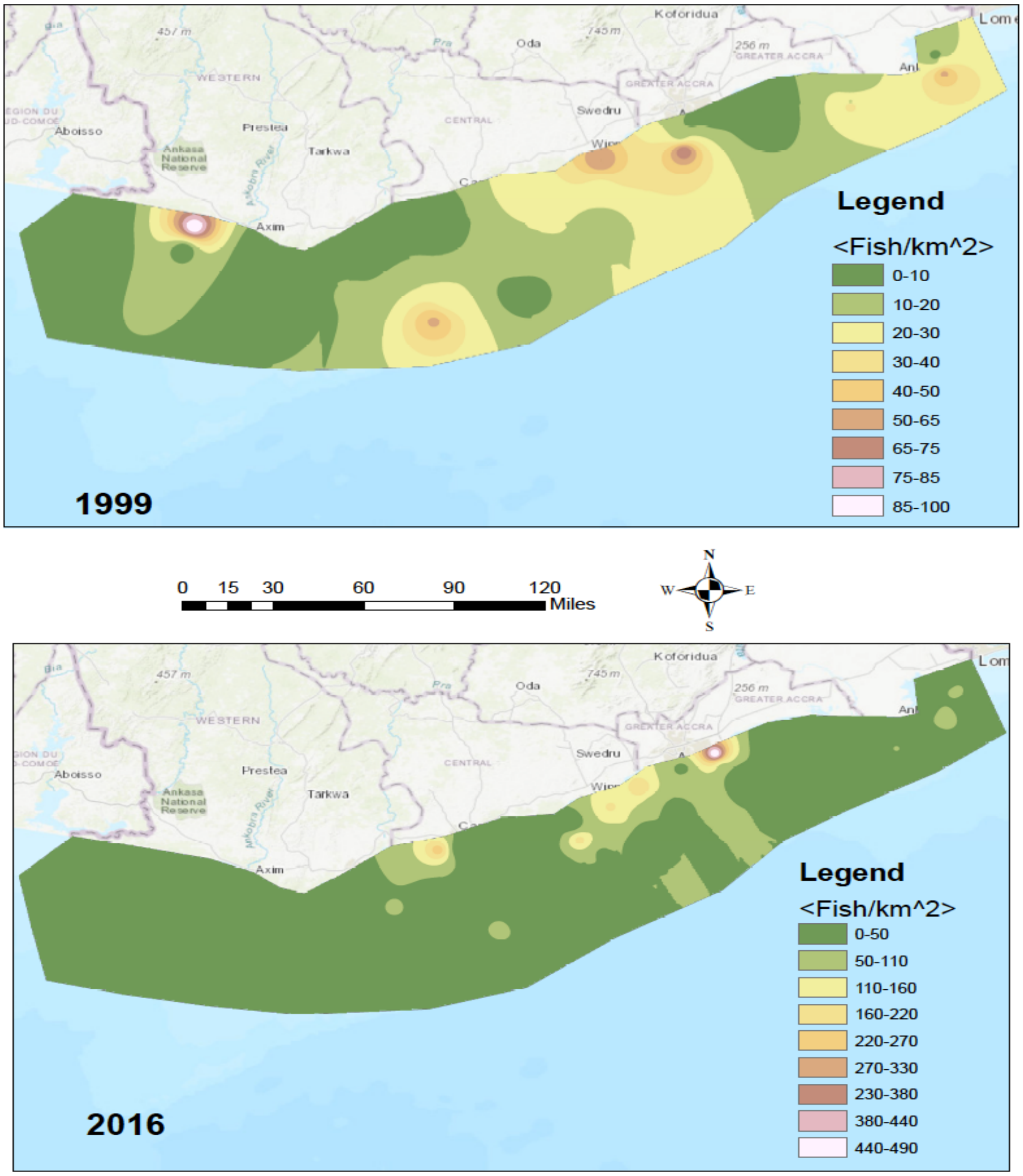



**Figure 9**: Spatial distribution of bluespotted seabream in two representative years. For each year, the brightness of the contours is proportional to fish population density

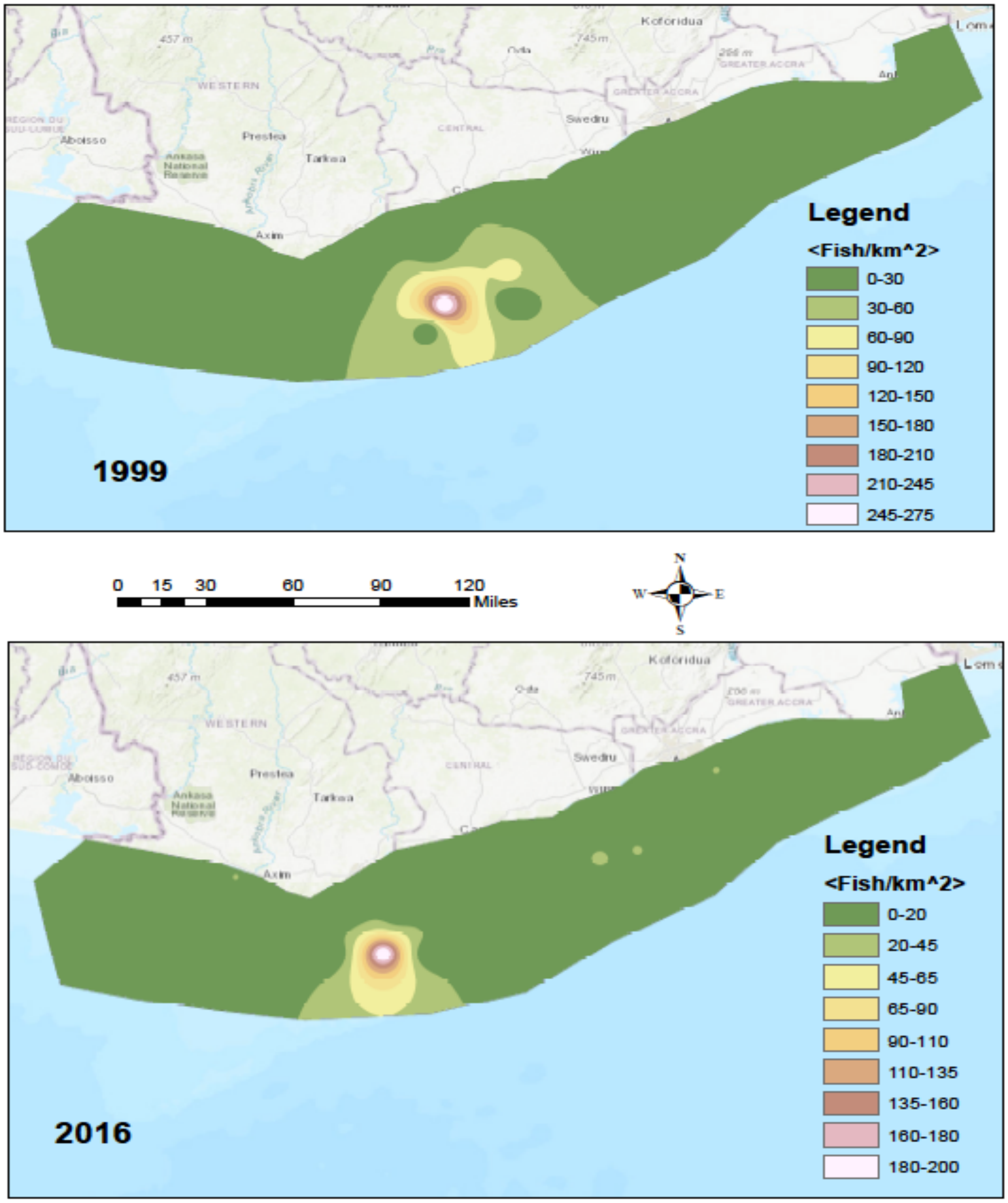



**Figure 10**: Spatial distribution of flying gurnard in two representative years. For each year, the brightness of the contours is proportional to fish population density

## SUPPLEMENTARY MATERIALS AND APPENDICES

**Table S1**: Table showing correlation (Pearson's *r*) between explanatory variables used to predict fish distributions

| | Depth | Bottom temperature | Salinity | Oxygen | Upwelling Index | Fishing Effort |
|---|---|---|---|---|---|---|
| Depth | 1.00 | -0.76 | 0.32 | -0.63 | -0.06 | 0.02 |
| Bottom temperature | | 1.00 | -0.63 | 0.89 | 0.07 | -0.26 |
| Salinity | | | 1.00 | -0.48 | 0.01 | 0.12 |
| Oxygen | | | | 1.00 | 0.05 | -0.29 |
| Upwelling Index | | | | | 1.00 | -0.23 |
| Fishing Effort | | | | | | 1.00 |

**Table S2**: Summary statistics from the trawl survey for each fish species (fish km$^{-2}$). There were 259 trawl samples in total

| | Red Pandora | Bluespotted seabream | Cuttlefish | Goatfish | Canary dentex | Brown skate | Red cornetfish | Flying gurnard |
|---|---|---|---|---|---|---|---|---|
| Mean | 221.7 | 28.4 | 9.6 | 55.1 | 14.4 | 2.9 | 13.2 | 8.3 |
| SD | 629 | 60 | 19.5 | 131 | 78.5 | 9 | 27 | 35.8 |
| % Zero Observations | 25.5 | 32.1 | 37.8 | 35.1 | 51.4 | 61.4 | 36.3 | 61 |

**Table S3**: Estimates of preferred water temperatures for the study species in degrees centigrade (from Froese and Pauly 2018)

| Species | Common Name | Mean | Range |
|---|---|---|---|
| *Pagrus caeruleostictus* | Bluespotted seabream | 17.5 | 13.3-25.2 |
| *Pagellus bellottii* | Red pandora | 25.2 | 18.5-28 |
| *Sepia hierredda* | Cuttlefish | 26.5 | 22.2-32.14 |
| *Pseudupeneus prayensis* | Goatfish | 25.2 | 18.1-27.9 |
| *Dentex canariensis* | Congo dentex | 14.5 | 12.8-16.1 |
| *Raja miraletus* | Brown skate | 17.6 | 13.1-25.6 |
| *Fistularia petimba* | Red cornetfish | 27.5 | 21.3-29 |
| *Dactylopterus volitans* | Flying gurnard | 23.9 | 13.3-27.8 |

**Figure S1**: Long-term trend of standardized fishing effort for Ghanaian coastal waters.

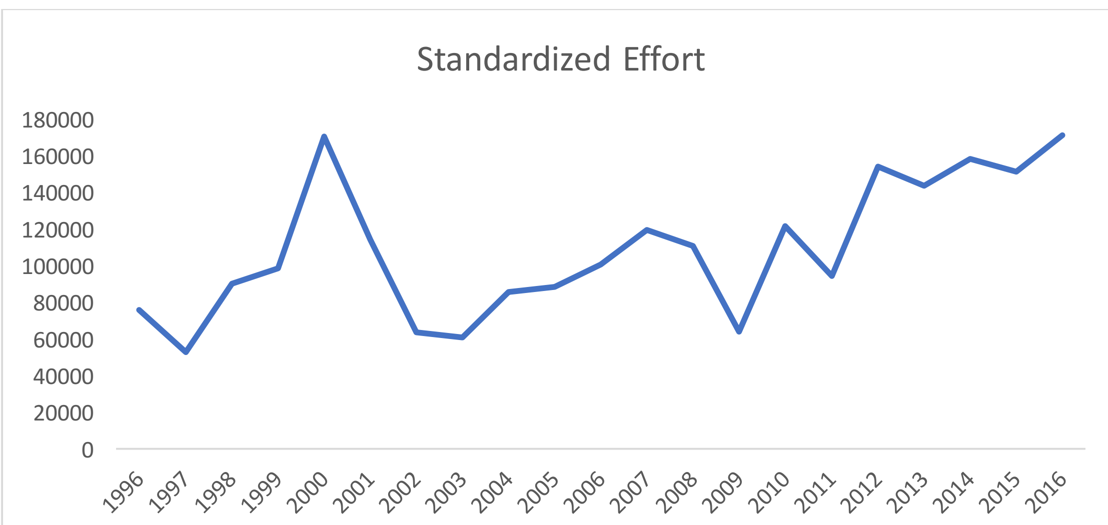


**Figure S3**: Mean (± SE) population density (fish km$^{-2}$) of each target species collected during the trawl survey each year

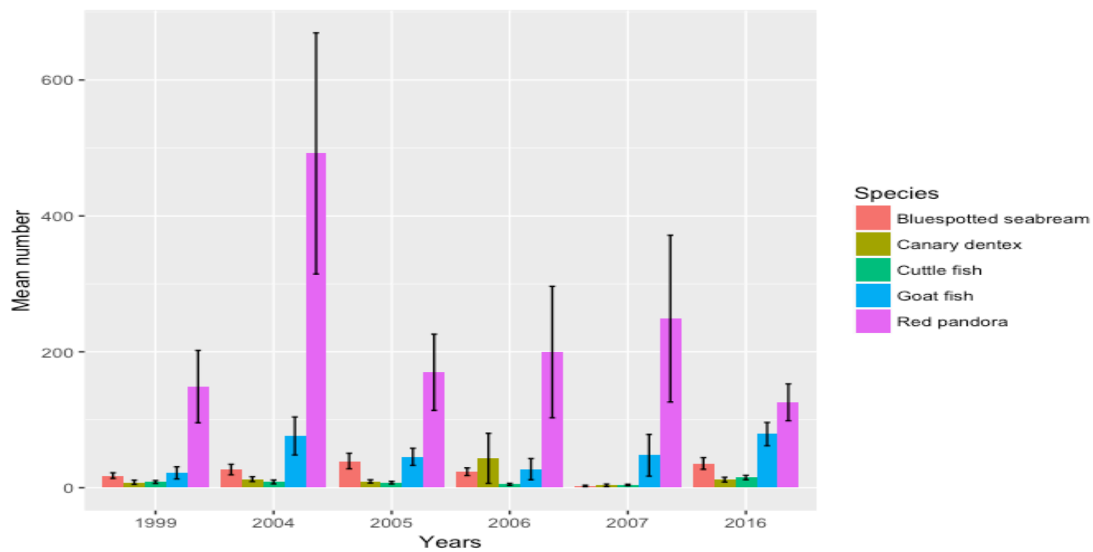



**Figure S4**: Mean (± SE) population density (fish km$^{-2}$) of each bycatch species collected during the trawl survey each year

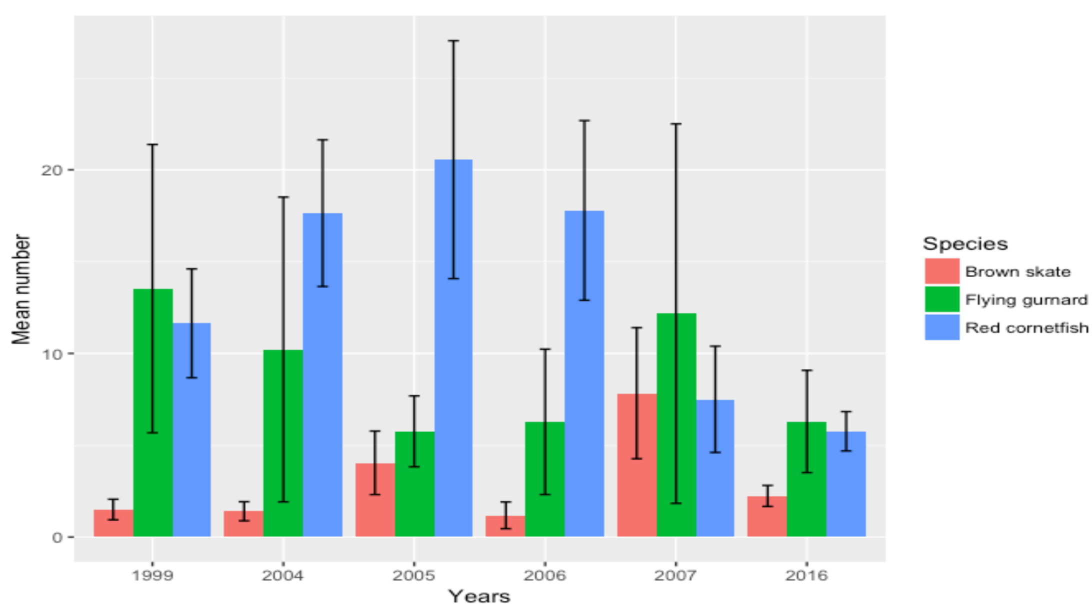
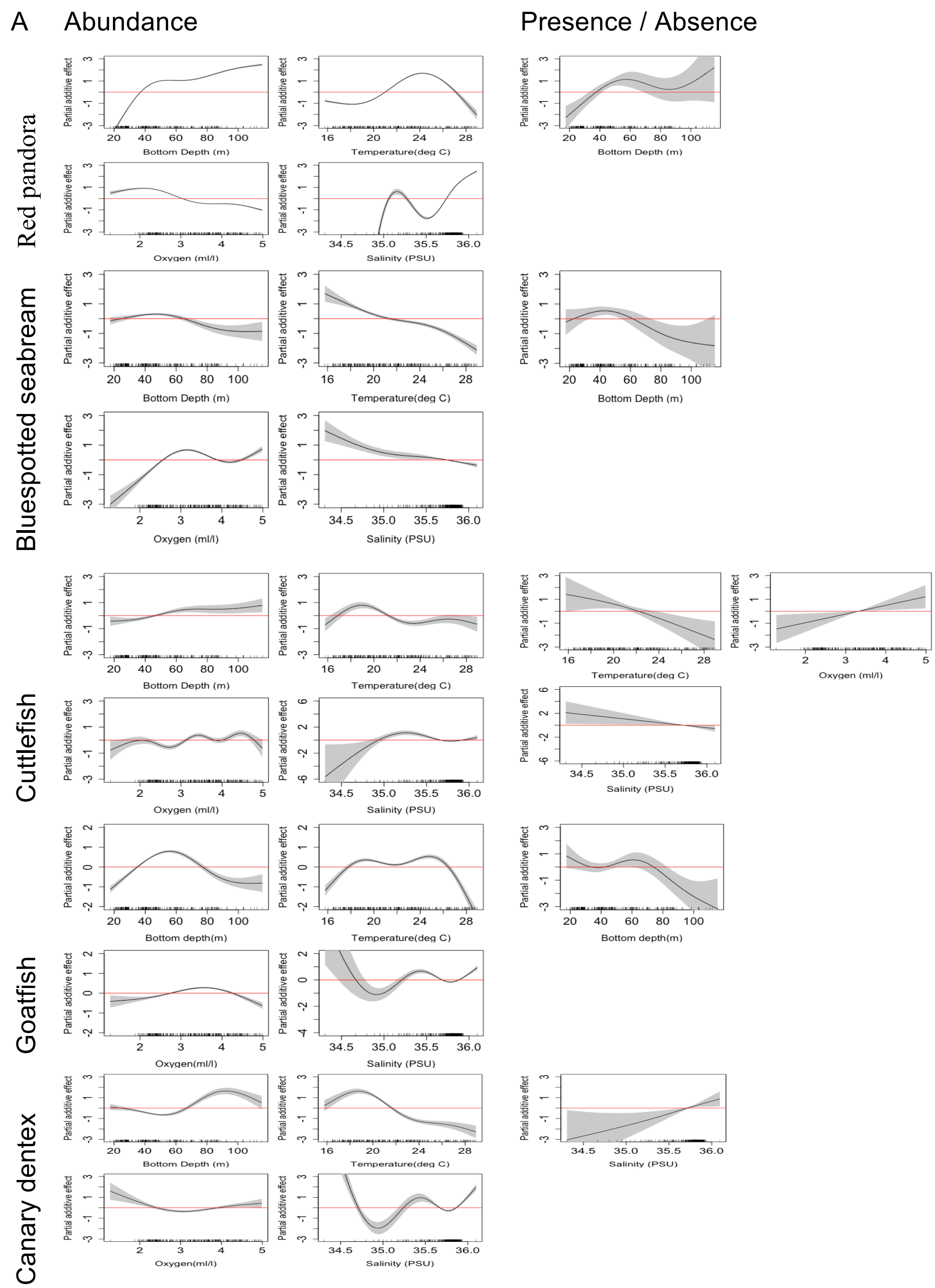
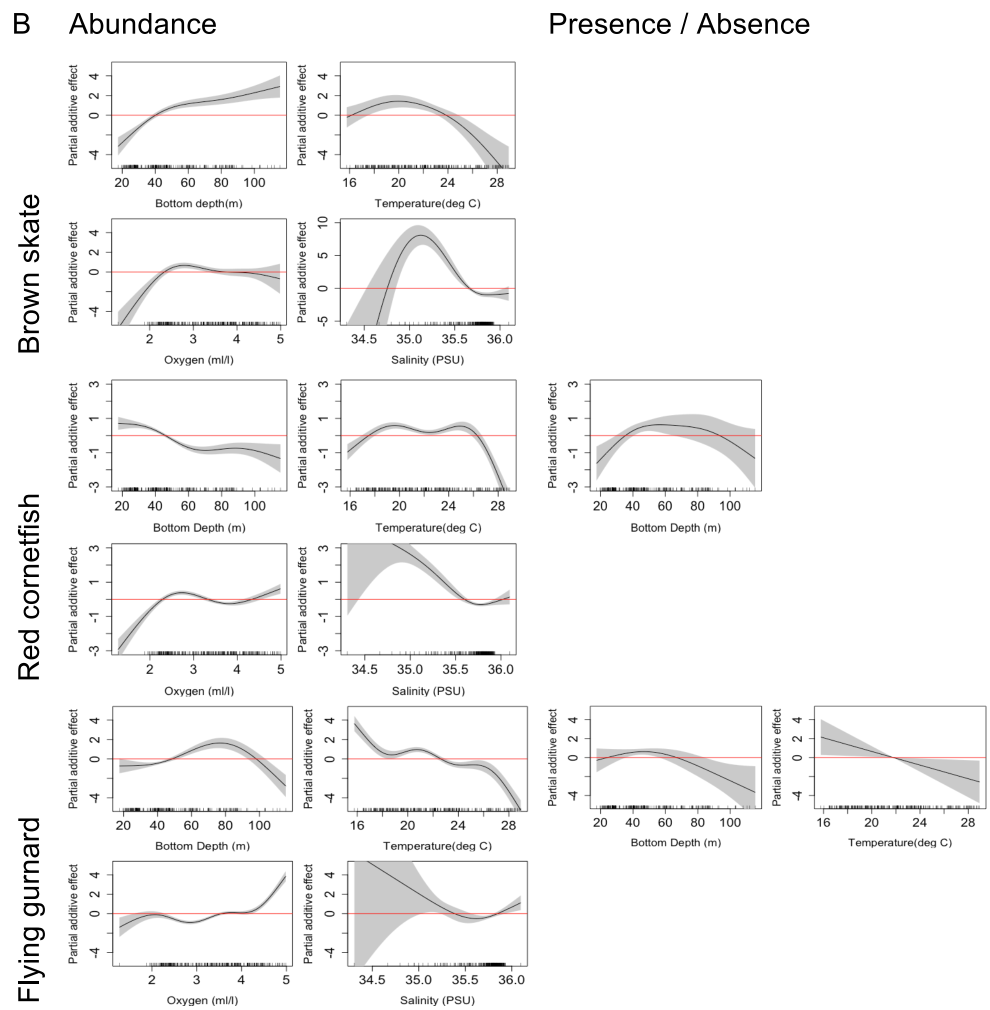


**Figure S5**: Response plots to visualize effects of environmental variables on the distribution of each fish species from best fitting GAM models. Plots are grouped by fishing status: (A) = plots for target species and (B) = plots for by-catch species. Plots are presented only for significant predictors ($p < 0.05$), and significant predictors of presence/absence and abundance are plotted separately. On each plot, solid lines indicate smoothed values and shaded areas indicate the 95% confidence interval. The red line at y = 0 represents no effect on abundance or presence/absence for a given covariate.


A
Abundance
Presence / Absence
Red pandora
Bluespotted seabream
Cuttlefish
Goatfish
Canary dentex
Partial additive effect
Bottom Depth (m)
Temperature(deg C)
Oxygen (ml/l)
Salinity (PSU)
Bottom depth(m)
Oxygen(ml/l)


B
Abundance
Presence / Absence
Brown skate
Red cornetfish
Flying gurnard
Partial additive effect
Bottom depth(m)
Temperature(deg C)
Oxygen (ml/l)
Salinity (PSU)
Bottom Depth (m)

*Appendix S1: Method of standardizing fishing effort*

Data on catch and fishing effort were used to determine the catch per unit effort (CPUE) of the three types of fishing vessel in the demersal fishery based on the level of technology and fishing power. The three types are vessel are: (1) artisanal canoes (smaller wooden vessels powered by sail or outboard motors), semi-industrial vessels (wooden vessels 8-37 m in length with up to 400 hp inboard engines) and (3) industrial vessels (large steel-hulled trawlers usually > 25 m in length). Annual catch per a fishing unit ($C_a$) was determined as the sum of all the monthly catch landed in a specific fishing sector using that fishing unit. Similarly, the annual fishing effort per a fishing unit ($E_a$) was determined as the sum of all the monthly fishing effort recorded within each year for that fishing unit. Fishing effort of a fishing unit was measured as the number fishing days carried out by a fishing unit (vessel). The annual catch per unit effort for each category of the fishing units ($CPUE_v$) was computed as:

$$CPUE_v = C_a/E_a$$

Given that data were collected for 6 years, the arithmetic mean of $CPUE_v$ was calculated as:

$$\mathrm{CPUE}_{\mu} = \frac{\sum_{y=1}^{6} \mathrm{CPUE}_{\mathrm{v}}}{6}$$

The arithmetic mean of the annual catch per unit effort ($CPUE_a$) for all the 3 fishing units over the six-year period was determined as:

$$\mathrm{CPUE}_{\mathrm{T}} = \frac{\sum_{v=1}^{3} \sum_{y=1}^{6} \mathrm{CPUE}_{\mathrm{v}}}{3\ X\ 6}$$

To standardize the fishing effort for each fishing unit, a standardized factor ($SF_v$) was determined as:

$$SF_v = \frac{\mathrm{CPUE}_{\mu}}{\mathrm{CPUE}_{\mathrm{T}}}$$

Using the standardized factor, the actual annual fishing effort ($E_a$) was standardized as:

$$E^{STD} = SF_v \, E_a$$