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Influence of Environmental Factors and Fishing Effort on Demersal Fish Species in Ghanaian Waters

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ABSTRACT

Separating effects of fishing from responses to environmental variables is a key problem for fisheries scientists. Data were collected from fishery-independent trawl surveys (6 years data between 1999 and 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, which calls for the documentation of the spatial patterns of fishing effort in future to help explain these shifts. Overall, the results showed that virtually all demersal species, targeted or not, appeared impacted by fishing and the species also track spatial and 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.

Keywords: spatial distribution, environmental variables, Ghana, marine ecosystems, anthropogenic pressures

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, Guimarães, & Costa, 2006; Collie, Wood, & Jeffries, 2008) and also to anthropogenic pressures including fishing (Bartolino, Ciannelli, Spencer, Wilderbuer, & Chan, 2012; Kendall, Bauer, & Jeffrey, 2008; Stelzenmüller, Rogers, & Mills, 2008) Fish species adapt to specific ranges of environmental variations, and significant alterations in these natural ranges could be stressful or fatal (Recsetar, Zeigler, Ward, Bonar, & Caldwell, 2012; Simpson et al., 2011). 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, Link, Hare, & Overholtz, 2009). Pihl, Baden, and Diaz (1991) also 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 similarly affected by high fishing pressure. The effect of fishing has led to a worldwide decrease, or even collapse of many fish species (Myers & Worm, 2003). In addition, fishing has been noted to 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 (Genner et al., 2010; Jennings, Greenstreet, & Reynolds, 1999; Pauly, Christensen, Dalsgaard, Froese, & Torres, 1998). Often the effects of changes in environmental factors and fishing activities develop simultaneously and may interact, thereby complicating their relative effects (Bartolino et al., 2012; Perry et al., 2010; Ter Hofstede & Rijnsdorp, 2011). 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 it caused a primarily eastward shift (Engelhard, Righton, & Pinnegar, 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 (Planque, Loots, Petitgas, Lindstrøm, & Vaz, 2011; Walters & Collie, 1988), however, tropical and sub-tropical regions are underrepresented in such analyses (Cheung et al., 2009).

In this study, 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 were determined. The demersal fishery in Ghana serves important roles for food security, income generation and employment (Ministry of Fisheries and Aquaculture Development, 2015). Demersal species of high economic value, including grouper (*Epinephelus aeneus*), seabream (*Pagellus bellottii*), cephalopods (*Sepia sp*.) and soles, together with other species make up about 23% of the total annual catch from the marine sector (Ministry of Fisheries and Aquaculture Development, unpublished report). Several fishing gears are employed by small-scale (or artisanal), semi-industrial (or inshore), and industrial vessels to target these demersal species (Aheto et al., 2012; Asiedu & 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, Olsen, Asante, Carocci, & Psomadakis, 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 (Ministry of Fisheries and Aquaculture Development, 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 the 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.

Materials and Methods

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 and 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, Yaqub, Mensah, & Frid, 2008).

Fish survey

The species for the analyses were chosen based on their economic value (target and bycatch) and data availability (Table 1). The target species were red pandora, bluespotted seabream, cuttlefish, goatfish and canary dentex, while the bycatch species were brown skate, red cornetfish and flying gurnard. These two groups were selected to test for the relative effects of fishing and climate. It was assumed that 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 therefore help to separate effects of climate from those of fishing.

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

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 (FAO) of the United Nations (UN) to assess status of fish stocks within Ghana's exclusive economic zone (EEZ). These years were selected because the surveys were conducted between February and June in each year. Each selected year's survey thus fell within the long thermally stratified period, making the data comparable across years (Mensah & Koranteng, 1988). Years which had surveys conducted during upwelling periods were excluded as a result of fish spawning migrations, plus changes in other environmental variables such as nutrient concentrations, which 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 (Figure 1). 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 & 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 (eg. Toresen, Olsen, Asante, Carocci, & Psomadakis, 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, Alveheim, & Zaera, 2008).

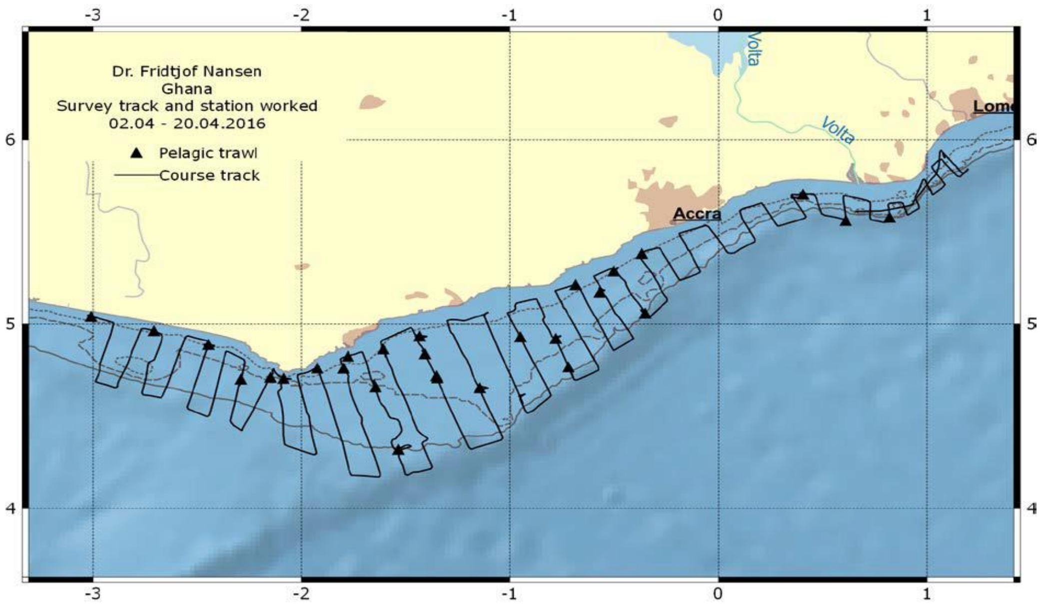


Figure 1: Coastal map of Ghana, showing trawl stations of 2016 survey. Source: (Toresen, Olsen, Asante, Carocci, & Psomadakis, 2016).

Environmental data and other predictors

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

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

Fishing effort was included in the model to test the relative effect of fishing on the abundance and distribution of the species. Since fishing effort is expected to have a lagged effect on fish abundance (Johnson & Carpenter, 1994), the mean effort over three years prior to the year of survey was used in the model. Finding the mean over three preceding years seemed ecologically reasonable as the study species are all relatively long-lived, with typical lifespans of 5-10 years (Ghorbel & Bertalanffy, 2004). Also changes in fishing effort occurred steadily over several years with modest inter-annual variations, apart from the year 2000. 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 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 & 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 (Dingsør, Ciannelli, Chan, Ottersen, & Stenseth, 2007; Hedger et al., 2004). The fish abundance data used for the analysis had a high percentage of zero observations and the data were also over-dispersed, hence a two-stage modelling approach was used (Guisan & Zimmermann, 2000; Maunder & Punt, 2004). 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, was used. Potential presence was modelled with one linear predictor and the second linear predictor modelled the Poisson mean abundance given potential presence (Wood, Pya, & Säfken, 2016). Abundance and presence/absence were modelled as:

$$Abundance\ or\ presence/absence$$
$$= s(Latitude, Longitude) + s(Depth) + s(Bottom\ temperature) + s(Salinity)$$
$$+ s(Oxygen) + Fishing\ efffort + Upwelling\ index$$

A set of candidate models was conducted to reflect 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. Due to 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, 2017). 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).

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

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. The relative importance of each variable included in the final model was assessed by excluding each variable individually from the best fit model and examining the change in both AIC and DE. Response plots were generated for each variable that had a significant influence ($p < 0.05$) on species distribution or abundance. To reduce model overfitting and the risk of generating ecologically unrealistic responses (Lehamnn, Overton, & Leathwick, 2002), a smooth term(k) value of 5 for all predictor variables and k value of 15 for the interaction between latitude and longitude 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 et al., 2007).

RESULTS

Environmental Variables

The study area spanned the shallow waters (sampled depths ranged from 17.5-115.5 m) of the relatively narrow Ghanaian continental shelf (30-90 km wide), and included 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 ˚C on average) and the years 2007 and 2016 (20˚C on average) were the coolest years. The spatial distribution of temperatures showed that it was generally cooler (< 22 ˚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˚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 3). 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 3).

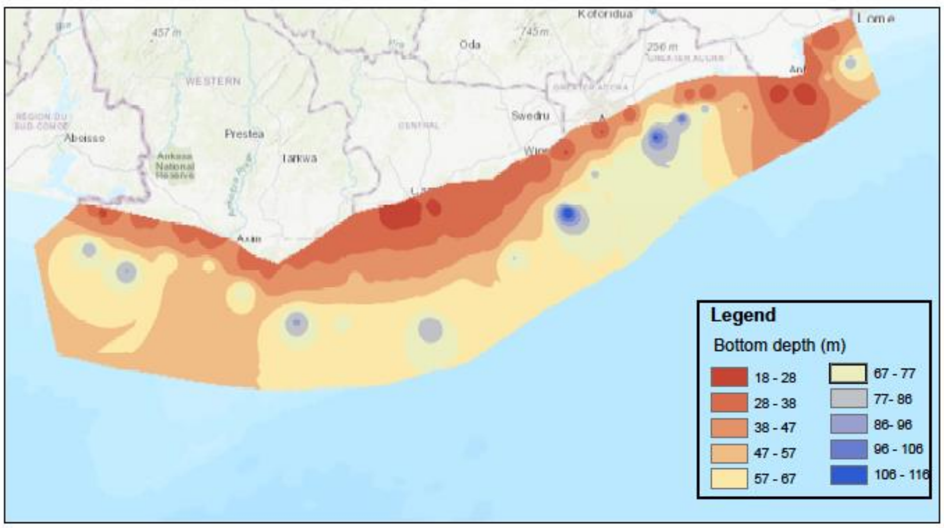


Figure 2: Spatial representation of bottom depth on the continental shelf. Note: the shaded area is the area surveyed

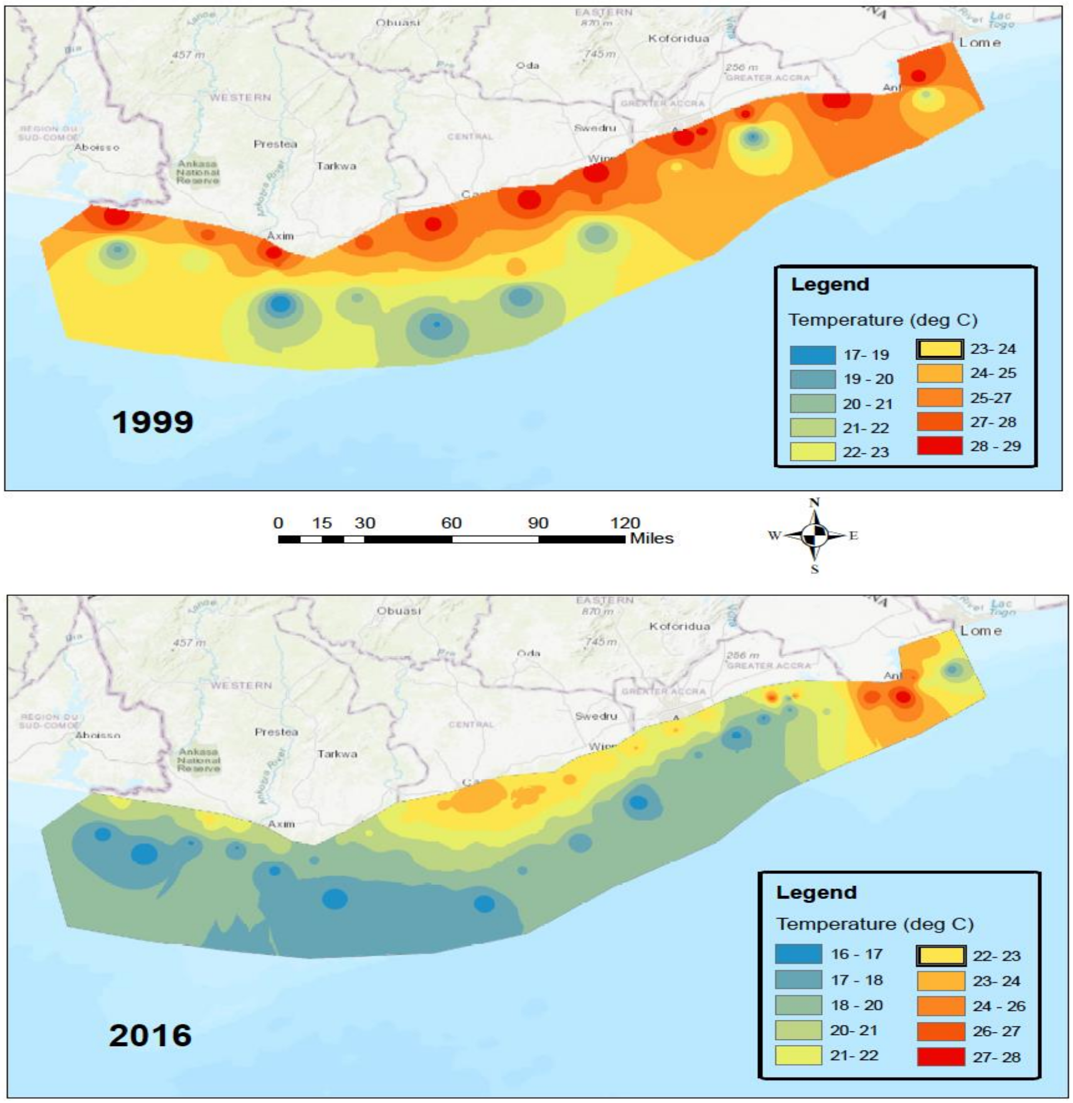


Figure 3: Spatial distribution of bottom temperatures on the continental shelf in two representative years. For each year, the spatial distribution of bottom temperatures within the study area is indicated by the brightness of the contours

Table 3: 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

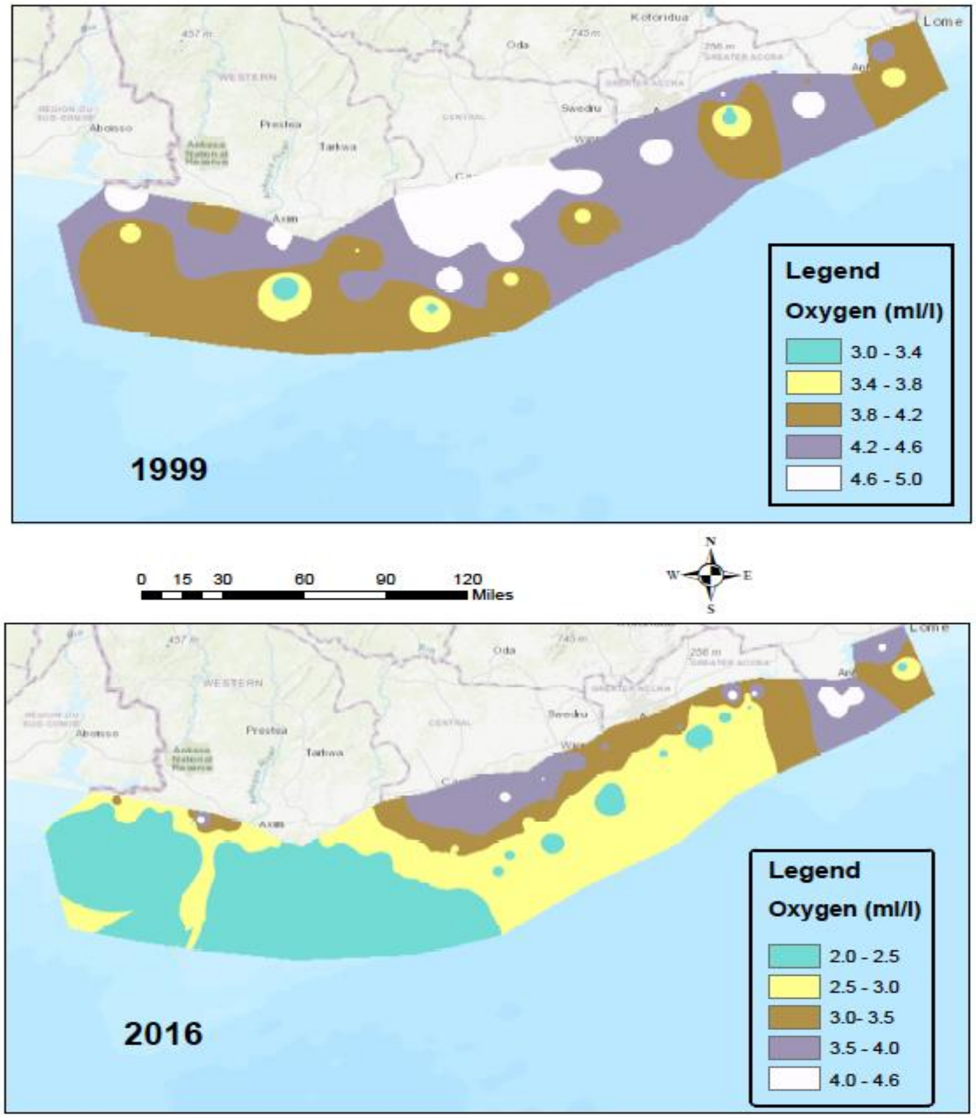


Figure 4: Spatial distribution of oxygen concentrations on the continental shelf in two representative years. For each year, the spatial distribution of oxygen concentration within the study area is indicated by the brightness of the contours

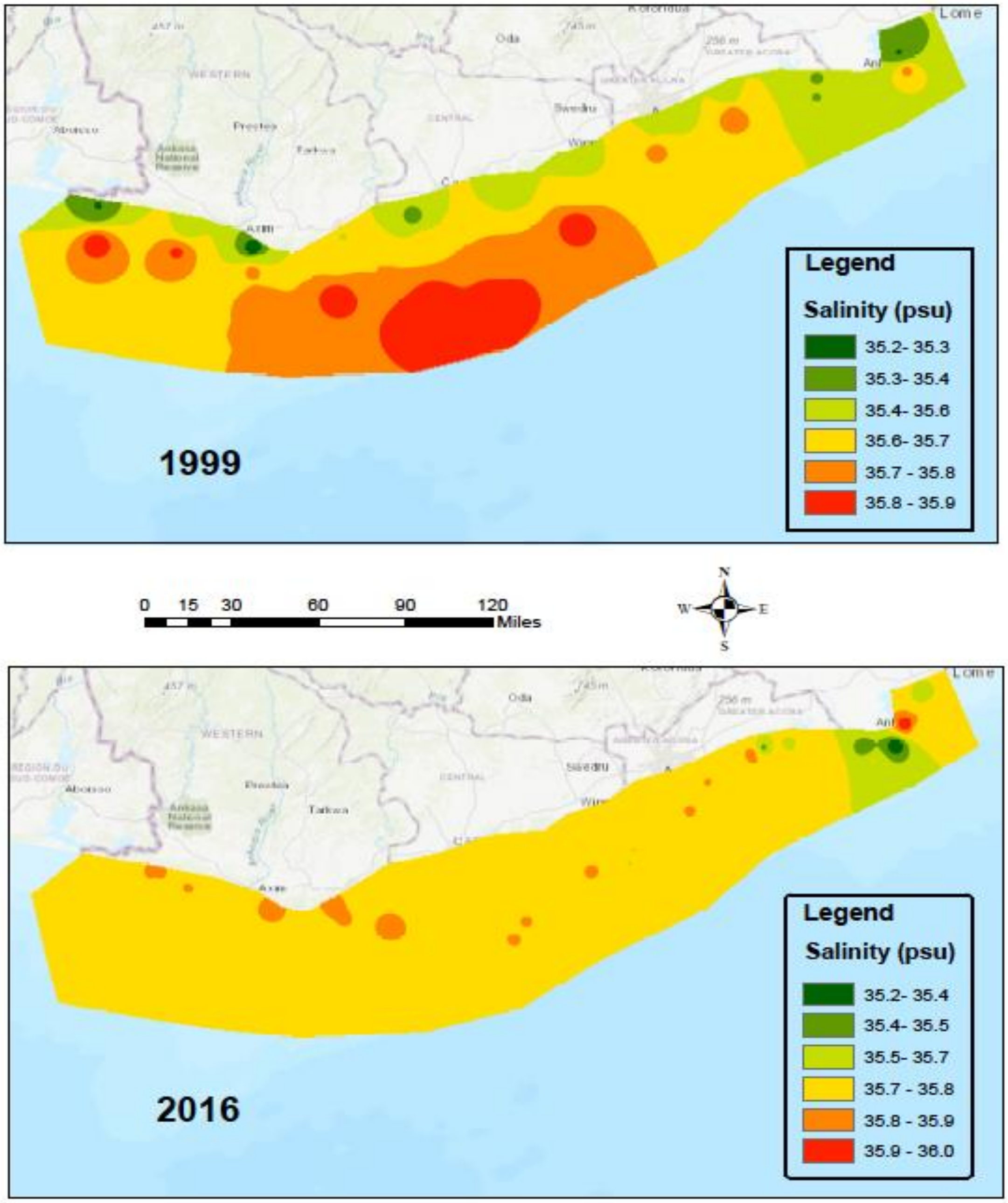


Figure 5: Spatial distribution of salinity on the continental shelf in two representative years. For each year, the spatial distribution of salinity within the study area is indicated by the brightness of the contours.

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. 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 (Figure 6). Other species, like bluespotted seabream (Figure 7), goatfish (both target species) (Figure 8) 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 (Figure 9), on the other hand, displayed less consistent changes in their distribution from year to year.

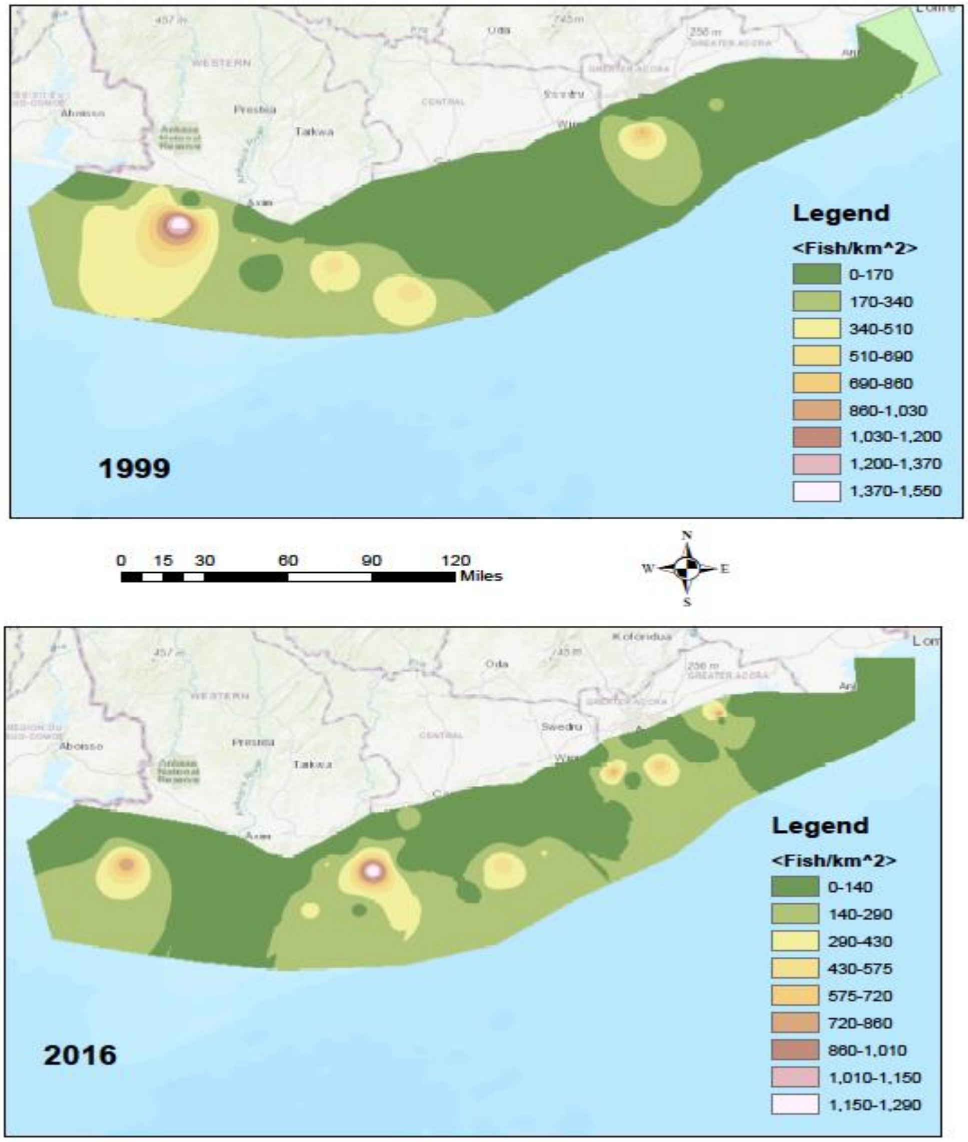
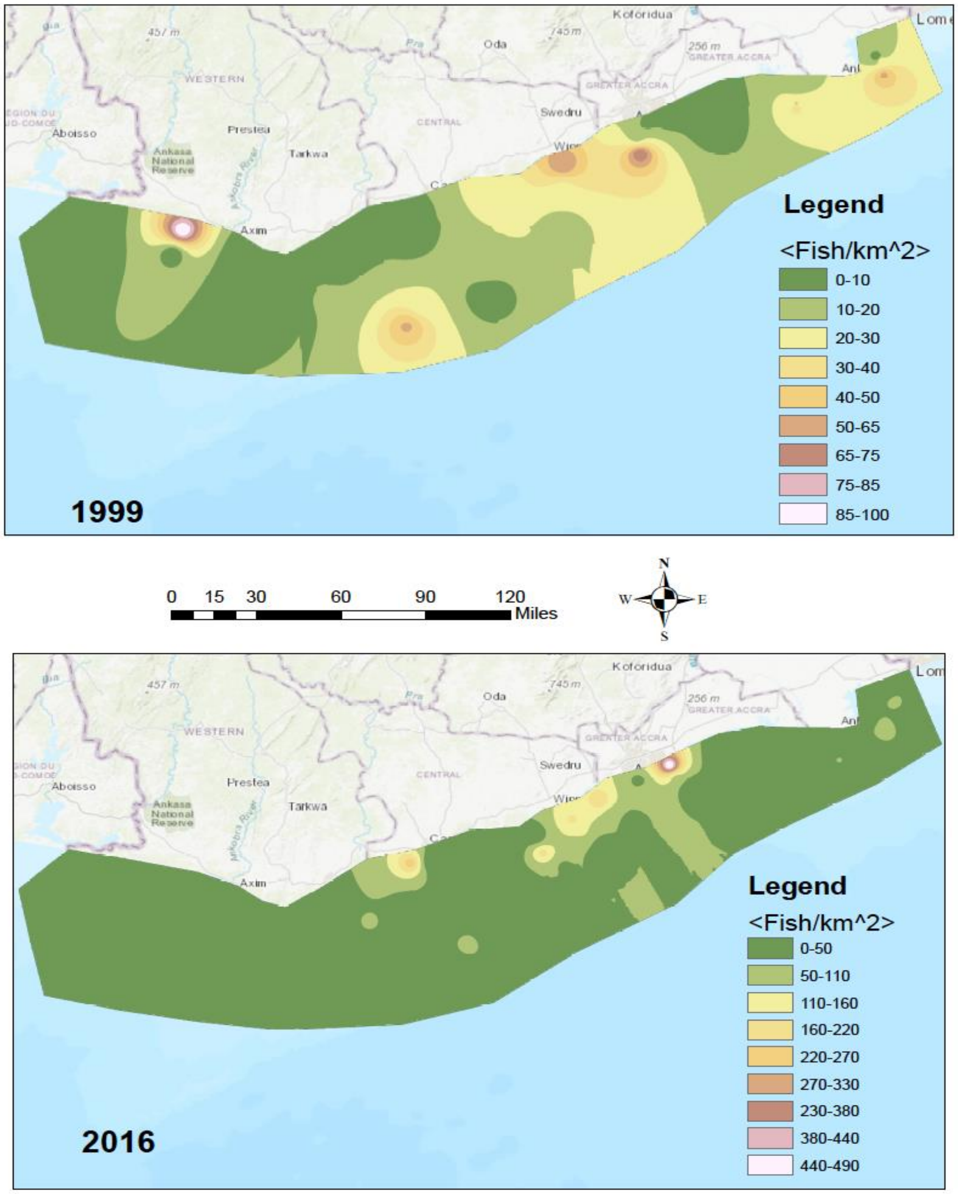


Figure 6: Spatial distribution of red pandora in two representative years. For each year, the brightness of the contours is proportional to fish population density



Koforidua
Oda
WESTERN
CENTRAL
GREATER ACCRA
Swedru
Aboisso
Prestea
Tarkwa
Ankasa National Reserve
Axim
Legend
<Fish/km^2>
0-10
10-20
20-30
30-40
40-50
50-65
65-75
75-85
85-100
1999
0 15 30 60 90 120
Miles
N
W
E
S
Legend
<Fish/km^2>
0-50
50-110
110-160
160-220
220-270
270-330
230-380
380-440
440-490
2016

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

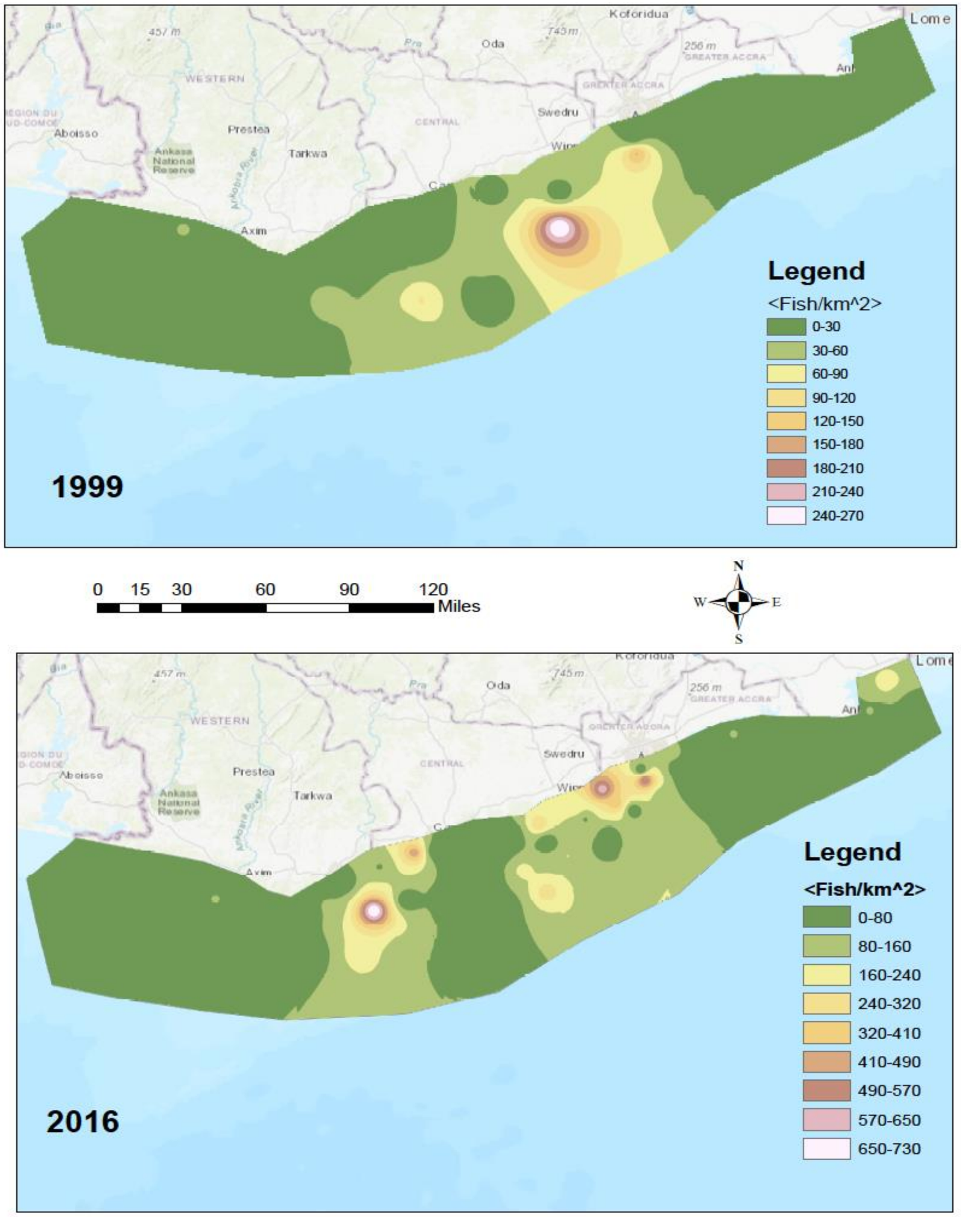


Figure 8: Spatial distribution of goatfish in two representative years. For each year, the brightness of the contours is proportional to fish population density

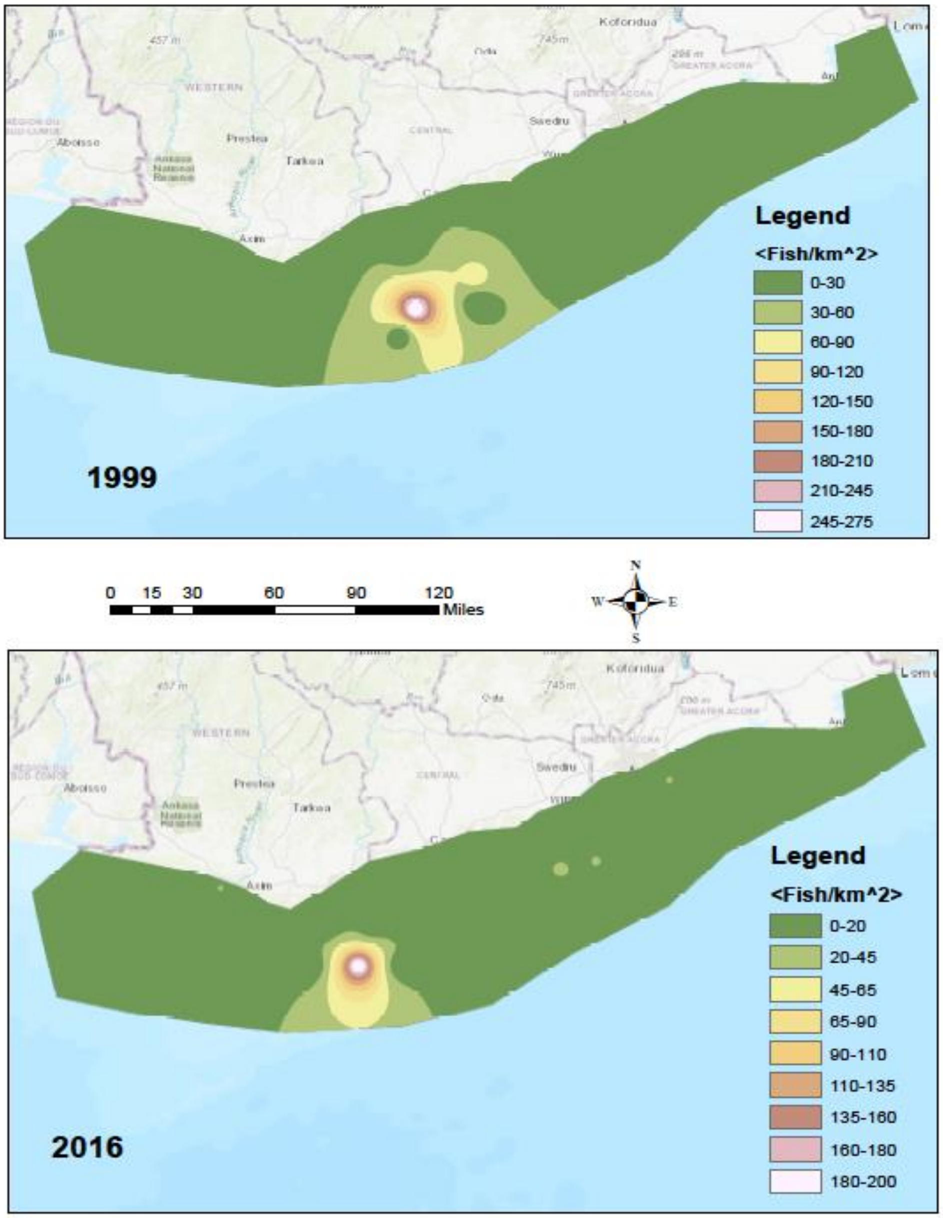


Figure 9: Spatial distribution of flying gurnard in two representative years. For each year, the brightness of the contours is proportional to fish population density

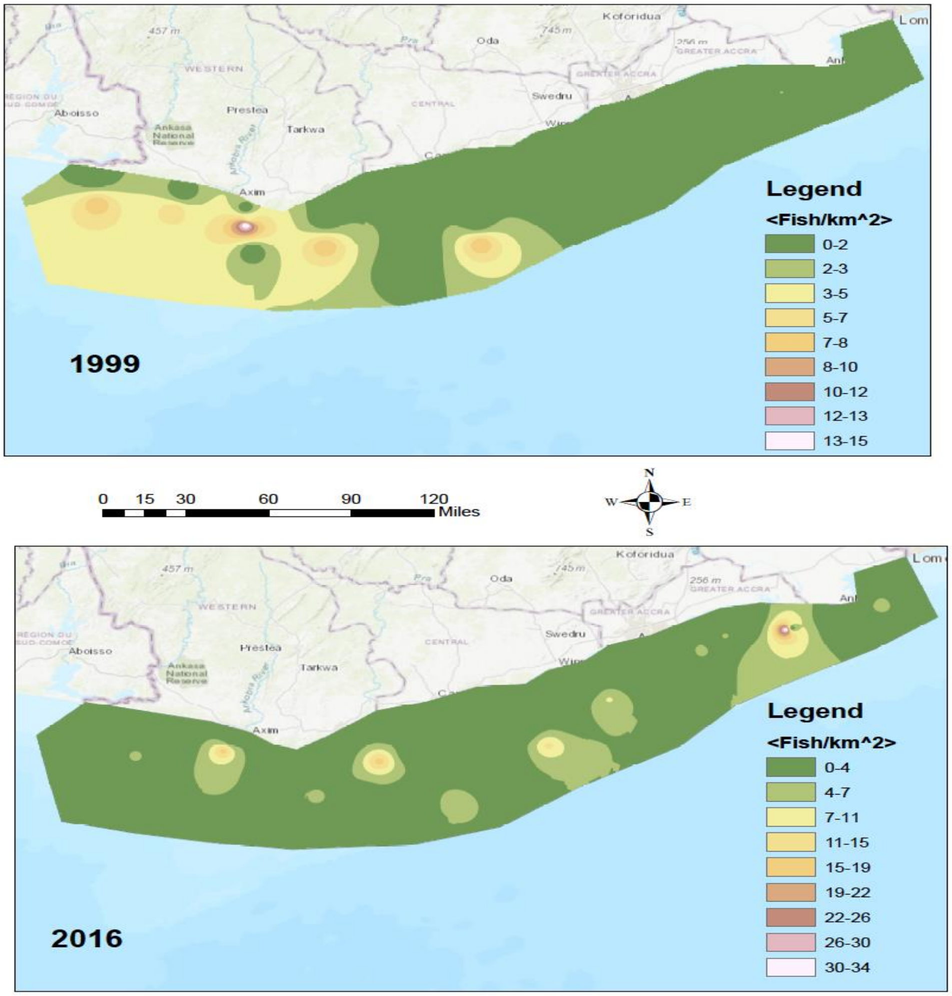


Figure 10: Spatial distribution of brown skate in two representative years. For each year, the brightness of the contours is proportional to fish population density

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 4), which meant distribution and abundance were 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 5).

Table 4: 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 seabream	df	32.4	45.7	34.8	34.4	49.7	50.3	36.9	**55.1**
	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 5: 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**

Red Pandora abundance was negatively affected by fishing effort, whilst upwelling had a positive influence (Table 6). Abundance was higher at depths between 40-60 m, and at temperatures between 21-27 °C and oxygen concentrations < 3 ml l^{-1} (Table 6). 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). 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).

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). 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). 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). 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 $^{\circ}$C and salinities between 34.5-35.5 psu (Table 6). 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). 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), with the effects of temperature and oxygen have the strongest influences (Table 8).

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

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 suggested 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, the 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

Generally, 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, Maravelias, Katsanevakis, Karageorgis, & Papaconstantinou, 2010). These results were consistent with other findings on distribution of demersal species in other parts of the world (Grüss, Yemane, & Fairweather, 2016; Parra et al., 2016; Russell et al., 2014). 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, 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 (Anderson, Gurarie, Bracis, Burke, & Laidre, 2013; Anderson & Millar, 2004; Araújo et al., 2006; Harman, Harvey, & Kendrick, 2003; Recsetar et al., 2012; Simpson et al., 2011). In addition to the above, the 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, spatial conflicts that exist between artisanal and industrial fishers (Ameyaw, 2017) by reason of fishing areas and target species could be managed. Again 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 & Pauly, 2004; Ministry of Fisheries and Aquaculture Development, 2015) and the use of unsustainable fishing practices like light fishing (Ameyaw, Asare, Mutimukuru-maravanyika, Laryea, Sabah, & Mills, 2012). There is also a vibrant market for some bycatch species, especially in the central region of Ghana, which makes classifying them as bycatch inaccurate (Nunoo, Boateng, Ahulu, Agyekum, & Sumaila, 2009). It is recommended that these bycatch species be no longer classified as a bycatch for the demersal fishery but rather added to the species that are routinely assessed and monitored.

To conclude, the study demonstrated that both environmental variability and fishing effort were 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 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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The Influence of Environmental Factors and Fishing Effort on Demersal Fish Species in Ghanaian Waters

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ABSTRACT

Disentangling the effects of fishing and the environment on fish abundance and distribution is essential for informing future fisheries management measures. Fishery-independent trawl survey data (6 years data between 1999 and 2016) were examined 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 influenced year-to-year variability in the abundance of 6 species negatively and 2 species positively, with 1 species unaffected. All species showed significant spatio-temporal associations with temperature, salinity and oxygen levels within the region. We observed some interannual consistency in fish spatial distributions given climatic variables' correlation; however, some variability appeared to reflect tracking of year-to-year shifts in climatic variables, such as inshore-offshore shifts in goatfish, red pandora and red cornetfish associated with thermal and oxygen shifts. While the habitat models did not entirely explain the variability in these spatiotemporal patterns, overall, both commercially targeted and non-targeted demersal species appeared to be impacted by fishing and the species also track spatial and temporal changes in environmental conditions from year-to-year. Future fisheries management regulations in the region should incorporate spatially resolved measures of fishing effort alongside measures of environmental variables.

Keywords: spatial distribution, environmental variables, Ghana, marine ecosystems, anthropogenic pressures

INTRODUCTION

Numerous studies around the world have revealed how the dynamics of the marine demersal fish communities are linked with oceanographic and climatic variability (Araújo, Guimarães, & Costa, 2006; Collie, Wood, & Jeffries, 2008) and also to anthropogenic pressures, such as fishing (Bartolino, Ciannelli, Spencer, Wilderbuer, & Chan, 2012; Kendall, Bauer, & Jeffrey, 2008; Stelzenmüller, Rogers, & Mills, 2008). With fish species adapted to specific ranges of environmental variations, significant alterations in these preferred ranges can be stressful or fatal (Recsetar, Zeigler, Ward, Bonar, & Caldwell, 2012; Simpson et al., 2011). An effect of changing environment on fish populations was illustrated by fish species changing their distribution to new depths and latitudes due to increasing water temperatures (Nye, Link, Hare, & Overholtz, 2009). Pihl, Baden, and Diaz (1991) also highlighted the importance of oxygen for fish, demonstrating the effect of low oxygen on three demersal fish species in York River, Chesapeake Bay, USA, and observing these fish migrating from deeper to shallower water when the oxygen levels were low and returning to the deeper waters when the levels of oxygen improved.

Apart from the effects of environmental variability, fish populations have historically been affected by high fishing pressure. The effect of fishing has led to a worldwide decrease, or even collapse of many fish species (Myers & Worm, 2003). Beyond individual species abundances, fishing has been noted to 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 (Genner et al., 2010; Jennings, Greenstreet, & Reynolds, 1999; Pauly, Christensen, Dalsgaard, Froese, & Torres, 1998). Often the effects of changes in environmental factors and fishing activities develop simultaneously and may interact, thereby complicating their relative effects (Bartolino et al., 2012; Perry et al., 2010; ter Hofstede & Rijnsdorp, 2011). 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 it caused a primarily eastward shift (Engelhard, Righton, & Pinnegar, 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 (Planque, Loots, Petitgas, Lindstrøm, & Vaz, 2011; Walters & Collie, 1988). Despite the vast evidence of these influences, tropical and sub-tropical regions are underrepresented in such analyses (Cheung et al., 2009).

Understanding the impacts of environmental and harvest pressure on fish populations is particularly important for regions where commercial fisheries are vital for the economy and sustenance of coastal communities. The demersal fishery in Ghana serves important roles for food security, income generation and employment (Ministry of Fisheries and Aquaculture Development, 2015). Demersal species of high economic value, such as grouper (*Epinephelus aeneus*), seabream (*Pagellus bellottii*), cephalopods (*Sepia sp*.) and soles, make up about 23% of the total annual catch from the marine sector (Ministry of Fisheries and Aquaculture Development, unpublished report). Several fishing gears are employed by small-scale (or artisanal), semi-industrial (or inshore), and industrial vessels to target these demersal species (Aheto et al., 2012; Asiedu & 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 approximately 15000 mt in 2016 (Toresen, Olsen, Asante, Carocci, & Psomadakis, 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 (Ministry of Fisheries and Aquaculture Development, 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. Further complicating the sustainable management for these species is whether there are spatiotemporal changes in species abundance and distribution in response to changing conditions.

In this study, we evaluated the environmental and fishing pressure influence on the distribution of demersal fish populations in the shallow sub-tropical waters off the coast of Ghana. The objective of the study was to explore the influence of fishing and environmental factors on the abundance and distribution of demersal fish populations in Ghana using statistical models. 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.

Materials and Methods

Study Area

We examined the coastal zone of Ghana, which is 550 km long, defined as the region between 3° 06' W and 1° 10' E latitude and between longitude 4° 30' and 6° 6' N (Mensah & Koranteng, 1988). The area traditionally experiences four hydrographic regimes; a major upwelling (long cold season) from July to September, a minor upwelling (a short cold season) from December to January, a long warm season (February to June) and a short warm season (October to November).

The upwelling periods are characterized by low sea surface temperature, low dissolved oxygen, high salinity and high biological productivity (Wiafe, Yaqub, Mensah, & Frid, 2008).

Fish Survey

Fisheries-independent data were obtained from demersal trawl surveys conducted in 1999, 2000, 2002, 2004, 2005, 2006, 2007 and 2016 by the collaborative effort of the Government of Ghana, the Institute of Marine Research (IMR) and the Food and Agriculture Organisation (FAO) of the United Nations (UN). These surveys are conducted to assess the status of fish stocks within Ghana's exclusive economic zone (EEZ). The 1999, 2004, 2006, 2007 and 2016 surveys were conducted between February to June and in September for the 2000 and 2002 surveys.

The trawl surveys were conducted by the R/V "Dr. Fridtjof Nansen" research vessel. Trawling was done using the Gisund super bottom trawl equipped with a 20-mm mesh in the cod-end, 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 trawl locations differed among years (Figure 1). 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 approximately 30 minutes. All fish collected were identified to the nearest discernible taxon (Carpenter & De Angelis, 2002), counted and weighed to the nearest kilogram. Also, the length measurements of selected commercially significant species were taken to the nearest 1cm. Further details of sampling can be found in country reports on Dr. Fridtjof Nansen Surveys for Ghana (eg. Toresen, Olsen, Asante, Carocci, & Psomadakis, 2016). Fish abundance was standardized as the number of individuals per unit area of seabed swept by the trawl (fish km^{-2}). The area swept is equivalent to (trawl distance (NM) * trawl width (NM)), where trawl distance is from trawl start (gear on the bottom) to trawl stop (gear off the bottom), and the trawl width is estimated. In Ghana this is estimated at 21m (or 0,011327 NM) (Krakstad, Oddgeir, & Zaera, 2008).

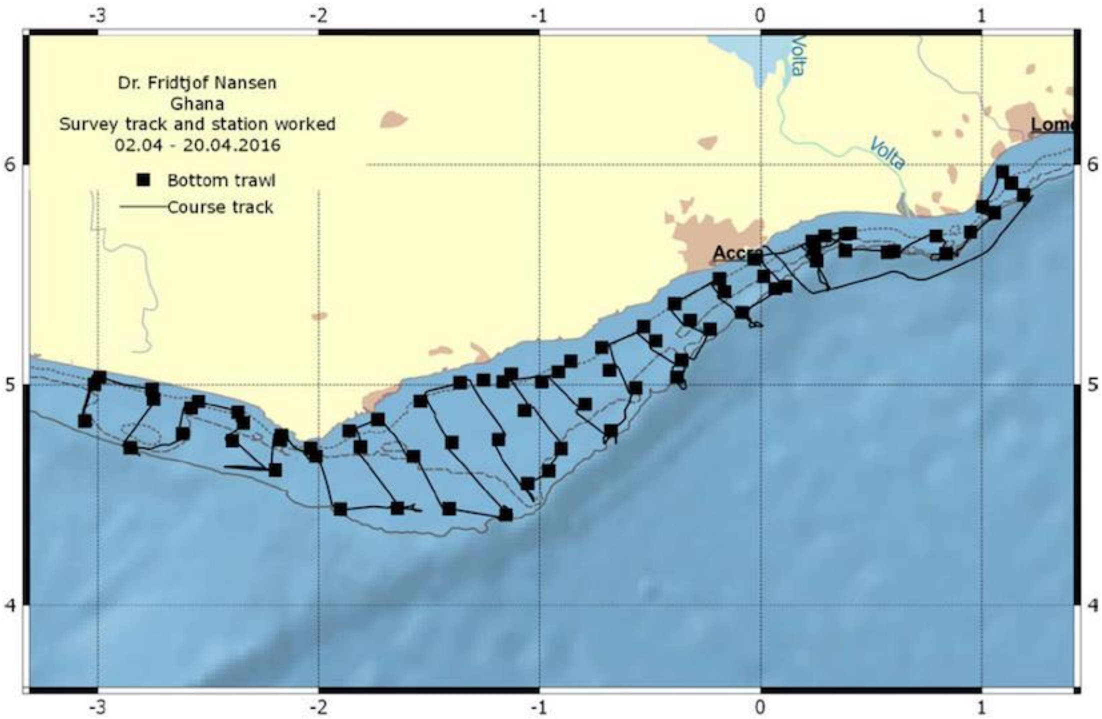

Figure 1: Coastal map of Ghana, showing trawl stations of 2016 survey. Source: (Toresen, Olsen, Asante, Carocci, & Psomadakis, 2016).

The species for the analyses were chosen based on their commercial importance (target and bycatch) and data availability (Table 1). The target species were red pandora, bluespotted seabream, cuttlefish, goatfish and canary dentex, while the bycatch species were brown skate, red cornetfish and flying gurnard. These two groups were selected to test for the relative effects of fishing and climate. It was assumed that 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 therefore help to separate effects of climate from those of fishing.

Table 1: Summary of the demersal survey data collected from 1999 to 2016 and used in the study. A total of 335 demersal survey tows were considered.

Species	Common Name	Number of non-zero abundance Estimates	Percentage (%) of non-zero abundance Estimates	Ratio of mean and variance of non-zero abundance Estimates
Pseudupeneus prayensis	Goatfish	224	63.10	3.8687×10^{-3}
Dentex canariensis	Canary dentex	176	49.58	2.9783×10^{-3}
Pagellus bellottii	Red pandora	255	71.83	4.7972×10^{-4}
Pagrus caeruleostictus	Bluespotted seabream	241	67.89	8.5374×10^{-3}
Sepia hierredda	Cuttlefish	240	67.61	2.0681×10^{-3}
Raja miraletus	Brown skate	124	34.93	5.6440×10^{-2}
Dactylopterus volitans	Flying Gurnard	134	37.75	7.9973×10^{-3}
Fistularia petimba	Red cornetfish	228	64.23	1.8896×10^{-2}

Environmental data and other predictors

The explanatory variables used in the models were selected based on their importance to fish abundance and distribution (Koranteng, 2001). Data on bottom temperature, salinity and oxygen were collected contemporaneously during the trawl survey. Vertical profiles of these measurements were collected with a Seabird 911 Conductivity Temperature Depth, the mean value measured along the defined depth were captured and used in the analysis. Though the bottom depth, temperature, salinity and oxygen were the only variables found to be correlated

(Table 2), all the variables were included in the model since there was no prior knowledge of which variables were important for the studied species.

Table 2: Correlation (Pearson's r) of mean values between explanatory variables used to predict fish distributions

	Abundance	Bottom Depth	Bottom temperature	Salinity	Oxygen	Upwelling Index	Fishing Effort
Abundance	1.00	0.04	-0.04	0.06	-0.03	0.00	-0.02
Depth		1.00	**-0.68**	0.29	-0.58	-0.07	0.03
Bottom temperature			1.00	-0.54	**0.90**	0.11	-0.04
Salinity				1.00	-0.43	0.02	0.07
Oxygen					1.00	0.08	-0.06
Upwelling Index						1.00	-0.40
Fishing Effort							1.00

An upwelling index was also assessed in the species distribution models given the known effects of coastal upwelling on fish communities. Annual data on sea surface temperature (SST) recorded from eight stations (Keta, Tema, Winneba, Elmina, Takoradi, Axim, Half Assini) along the coast of Ghana were obtained from the database of the Fisheries Scientific Survey Division in Ghana for the upwelling calculations. The annual upwelling index (UI) was estimated by subtracting annual mean SST from 25°C. Below this threshold, upwelling is considered to be occurring (Bakun, 1978).

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 before use in the analysis (following Stamatopoulos and Abdallah, 2015). Standardization of effort was needed given the different classes of fishing vessels vary greatly in size, speed, and gears used, and thus differ in relative fishing effort (Robson, 1966). Fishing effort was included in the model to test the relative effect of fishing on the abundance and distribution of the species. Since appreciable time lags may be involved in the response of the fish abundance to fishing effort (Daan, Gislason, Pope, & Rice, 2005), the mean effort for the four lagged years prior to the year of survey were used in the analysis. The time lag relationship between abundance and fishing effort was examined using the cross-correlation function in R (Figure 2).

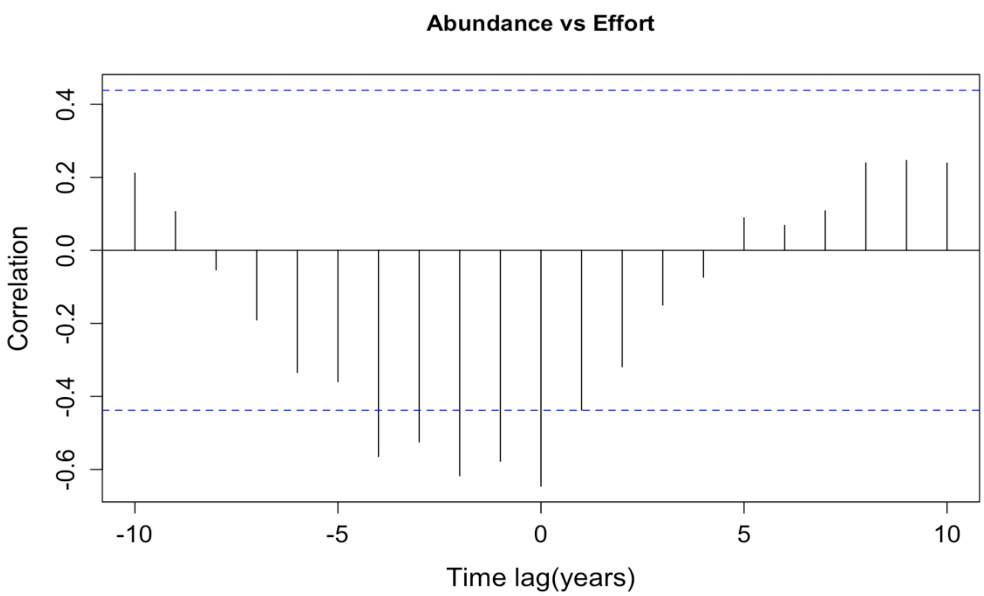

Figure 2: Cross correlation function between species abundance and fishing effort. The dotted lines represent significance limit at 5% level.

Annual spatial distribution depictions of the environmental parameters and the study fish species were constructed using the inverse distance weighting (IDW) interpolations with ArcGIS software. Raster size was maintained across variables, and IDW was conducted using a smoothing power of 2. Survey data collected during the thermally stratified period were used for the fish distribution plots. These years were examined because the surveys consistently sampled the thermally stratified period, allowing for consistent temporal comparisons across years (Mensah & Koranteng, 1988).

Data analysis

Generalized additive models (GAM) were used to assess the relationships between fish distribution and the selected explanatory variables (Venables & 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 (Dingsør, Ciannelli, Chan, Ottersen, & Stenseth, 2007; Hedger et al., 2004). The fish abundance data used for the analysis had a high percentage of zero observations and the data were also over-dispersed, hence a two-stage modelling approach was used (Guisan & Zimmermann, 2000; Maunder & Punt, 2004). We sued the Zero Inflated Poissson location scale model (using the ‘ziplss’ function in the ‘mgcv’ R package), a two stage zero inflated Poisson model with two components. Potential presence was modelled with one linear predictor and the second linear predictor modelled the Poisson mean abundance given potential presence (Wood, Pya, & Säfken, 2016). Abundance and presence/absence were modelled as:

$$Abundance\ or\ presence/absence$$
$$= s(Latitude, Longitude) + s(Depth) + s(Bottom\ temperature) + s(Salinity)$$
$$+ s(Oxygen) + Fishing\ Effort + Upwelling\ Index$$

Several candidate models were constructed to reflect 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) assumed that the presence and abundance of fish is described simply by location (latitude and longitude) and depth. Due to the potential for spatial autocorrelation, which would violate the assumption that data are independent, location was included as a smoothing term to account for spatial autocorrelation (Wood, 2017). 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 included individual or combined effects of annual, non-spatial predictors. Model 5 included only the spatially-resolved environmental variables collected during the trawl surveys (temperature, oxygen and salinity). Models 6 and 7 included combinations of both spatial and non-spatial predictor variables. Lastly, all predictor variables were included in a final model variant (Model 8).

Table 3: 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

Candidate models were compared 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. The relative importance of each variable included in the final model was assessed by excluding each variable individually from the best fit model and examining the change in both AIC and DE. Response plots were generated for each variable that had a significant influence ($p < 0.05$) on species distribution or abundance. To reduce model overfitting and the risk of generating ecologically unrealistic responses (Lehamnn, Overton, & Leathwick, 2002), a smooth term (k) maximum was set at 5 for all predictor variables and 15 for the interaction between latitude and longitude. 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 et al., 2007).

RESULTS

Environmental Variables

The study area spanned the shallow waters (sampled depths ranged from 17.5-115.5 m) of the relatively narrow Ghanaian continental shelf (30-90 km wide), and included 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°C on average) were the coolest. 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. 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°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 2). Oxygen concentrations were generally higher in the year 1999 than in 2016, though the bottom temperature seemed to have been higher in that former year than the latter year. The higher oxygen concentrations were also observed in relatively shallower depths along the coast, and 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 2).

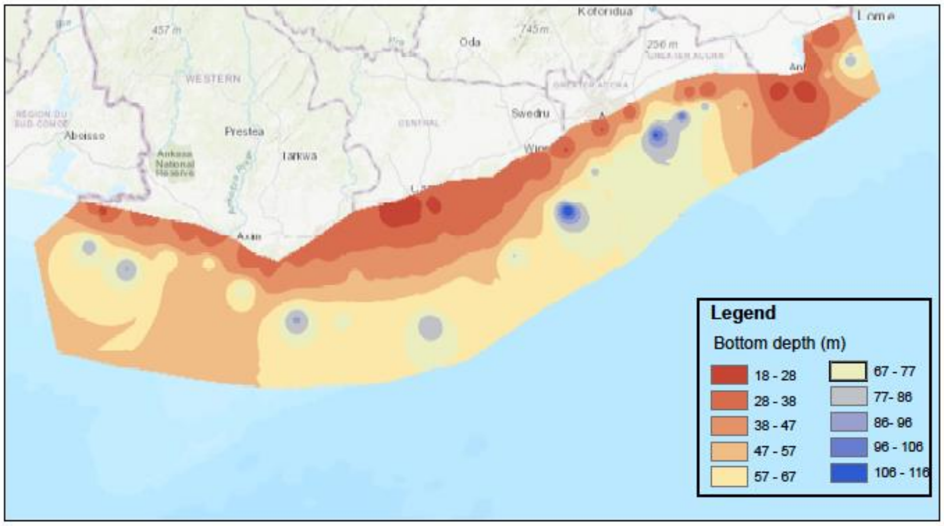

Figure 3: Spatial representation of bottom depth averaged across years on the continental shelf.

Note: the shaded area is the area surveyed

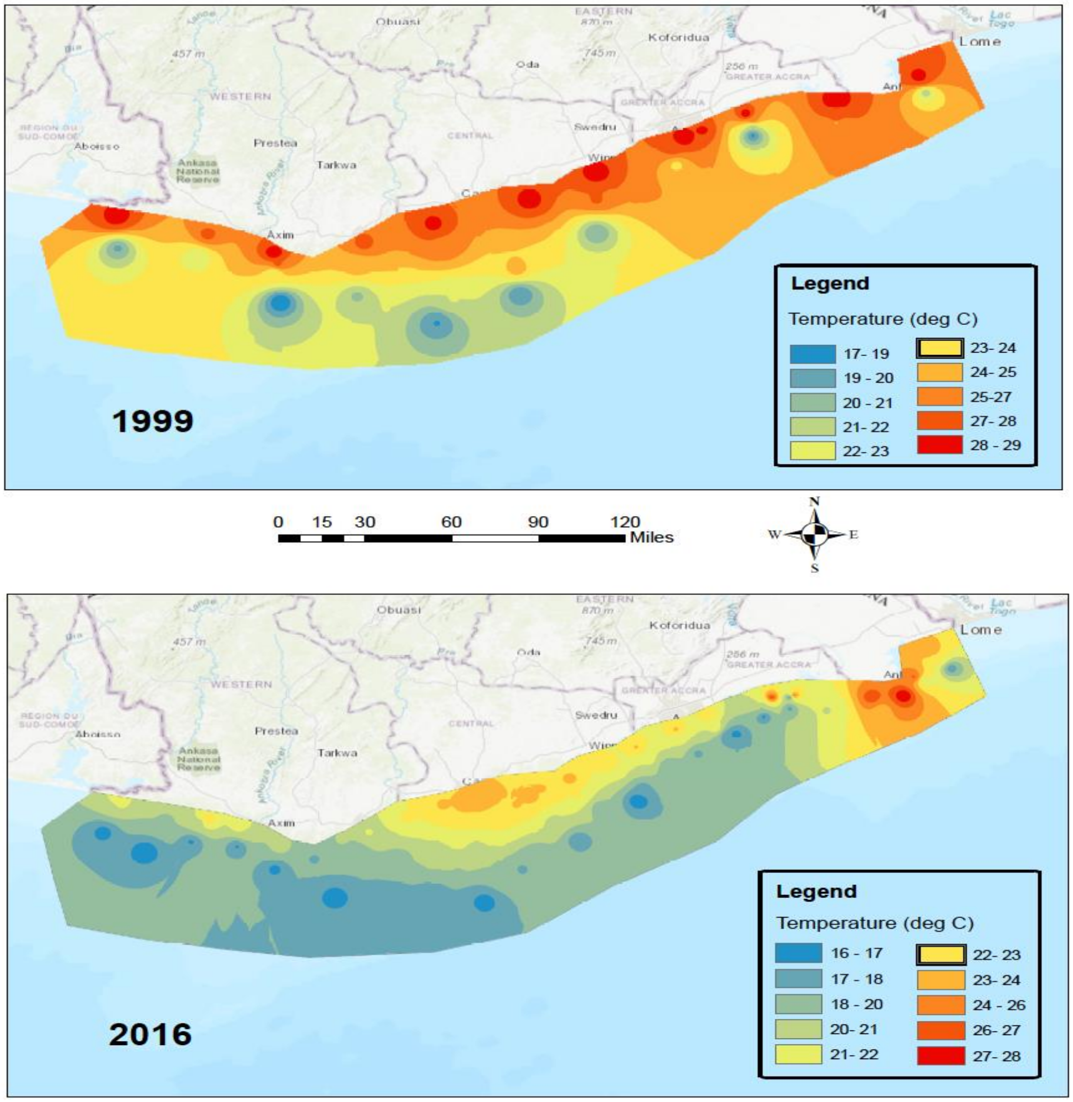

Figure 4: Spatial distribution of bottom temperatures on the continental shelf in two representative years.

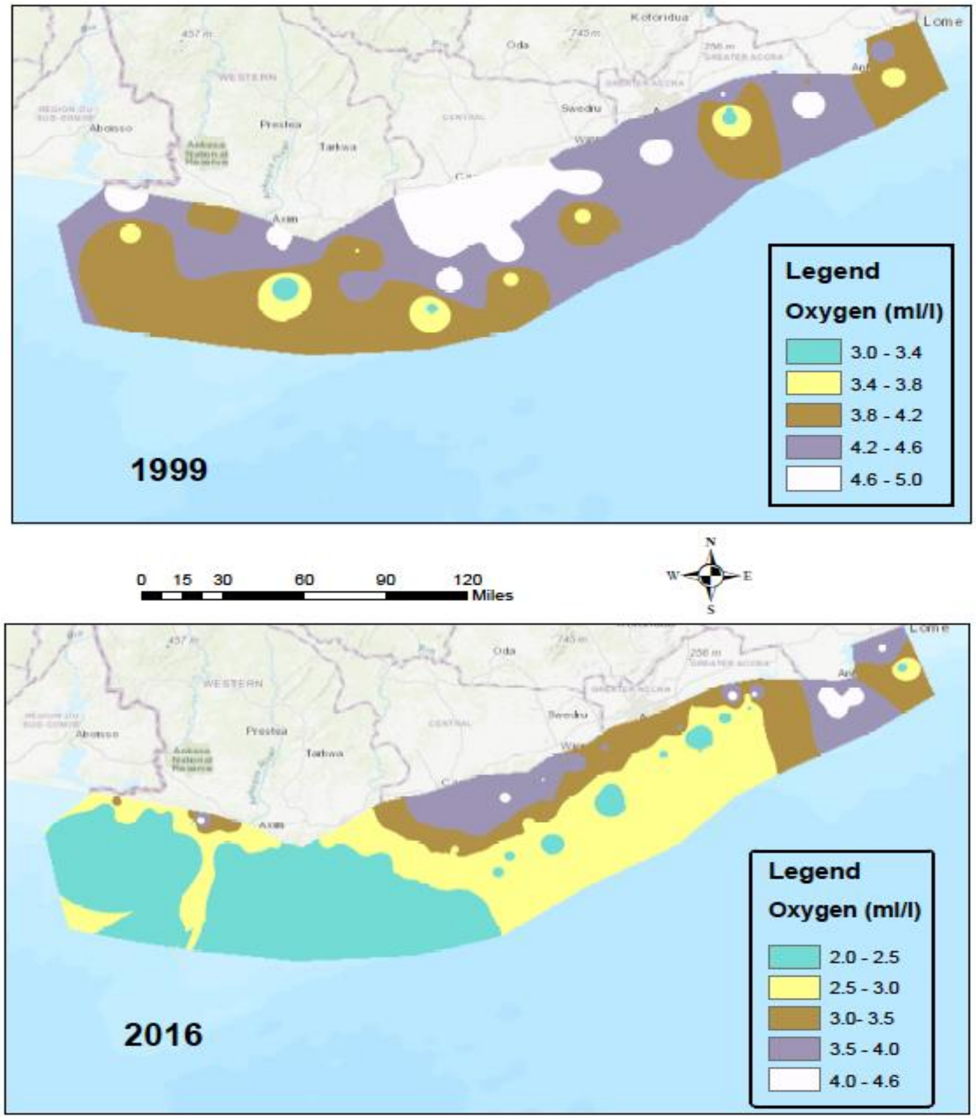

Figure 5: Spatial distribution of oxygen concentrations on the continental shelf in two representative years. For each year, the spatial distribution of oxygen concentration within the study area is indicated by the brightness of the contours

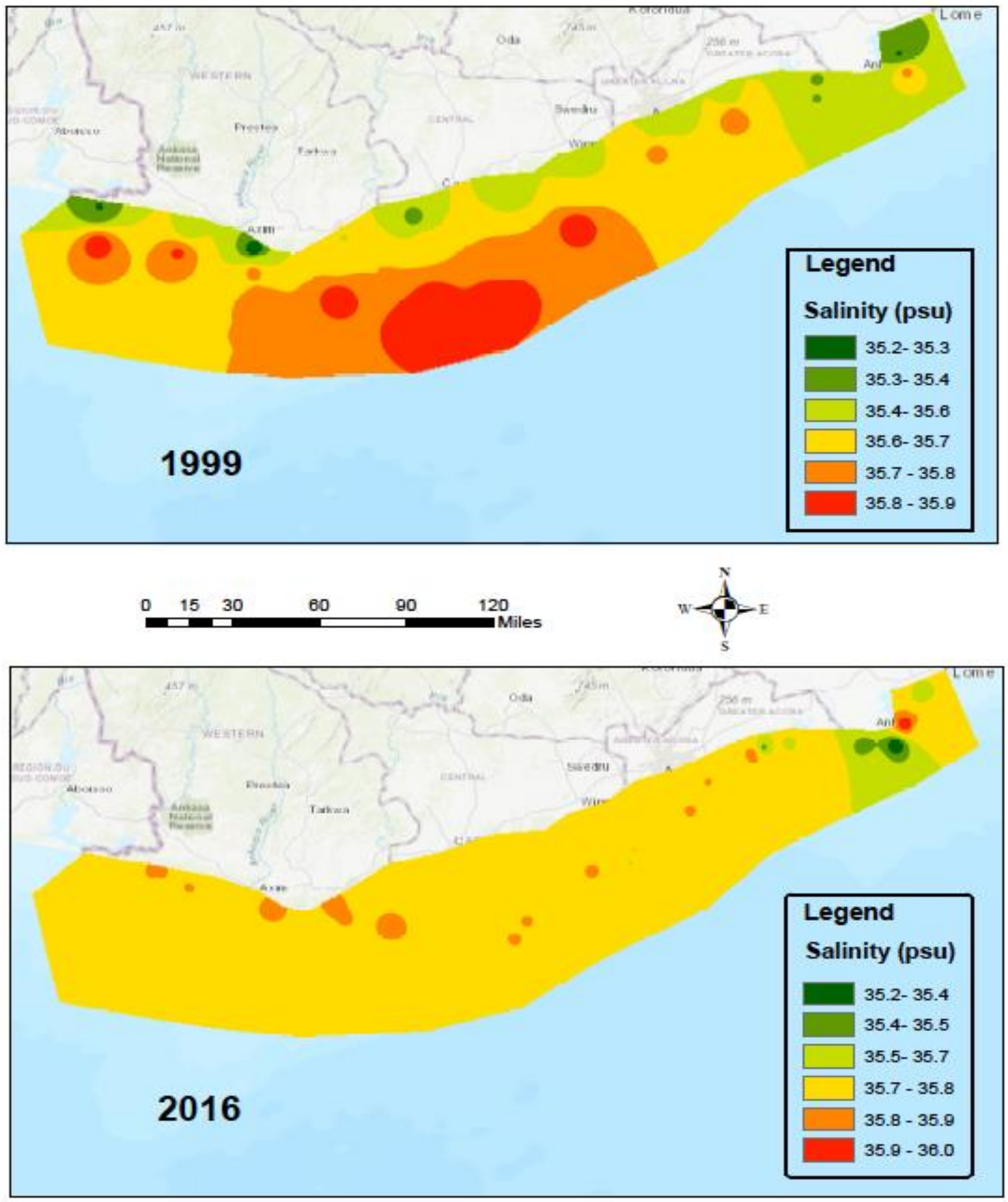

Figure 6: Spatial distribution of salinity on the continental shelf in two representative years. For each year, the spatial distribution of salinity within the study area is indicated by the brightness of the contours.

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. 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 (Figure 6). Other species, like bluespotted seabream (Figure 7), goatfish (both target species) (Figure 8) 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 (Figure 9), on the other hand, displayed less consistent changes in their distribution from year to year.

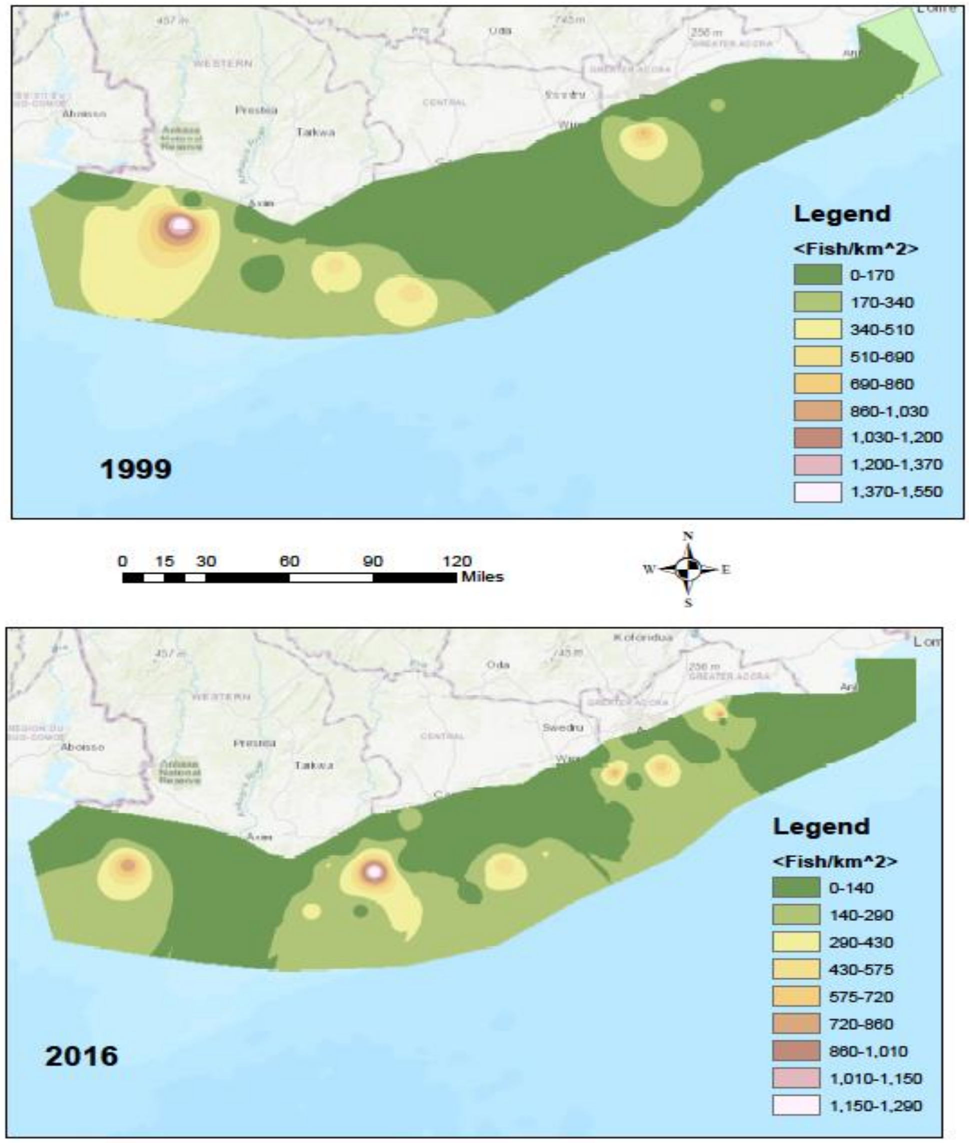

Figure 7: Spatial distribution of red pandora in two representative years. For each year, the brightness of the contours is proportional to fish population density

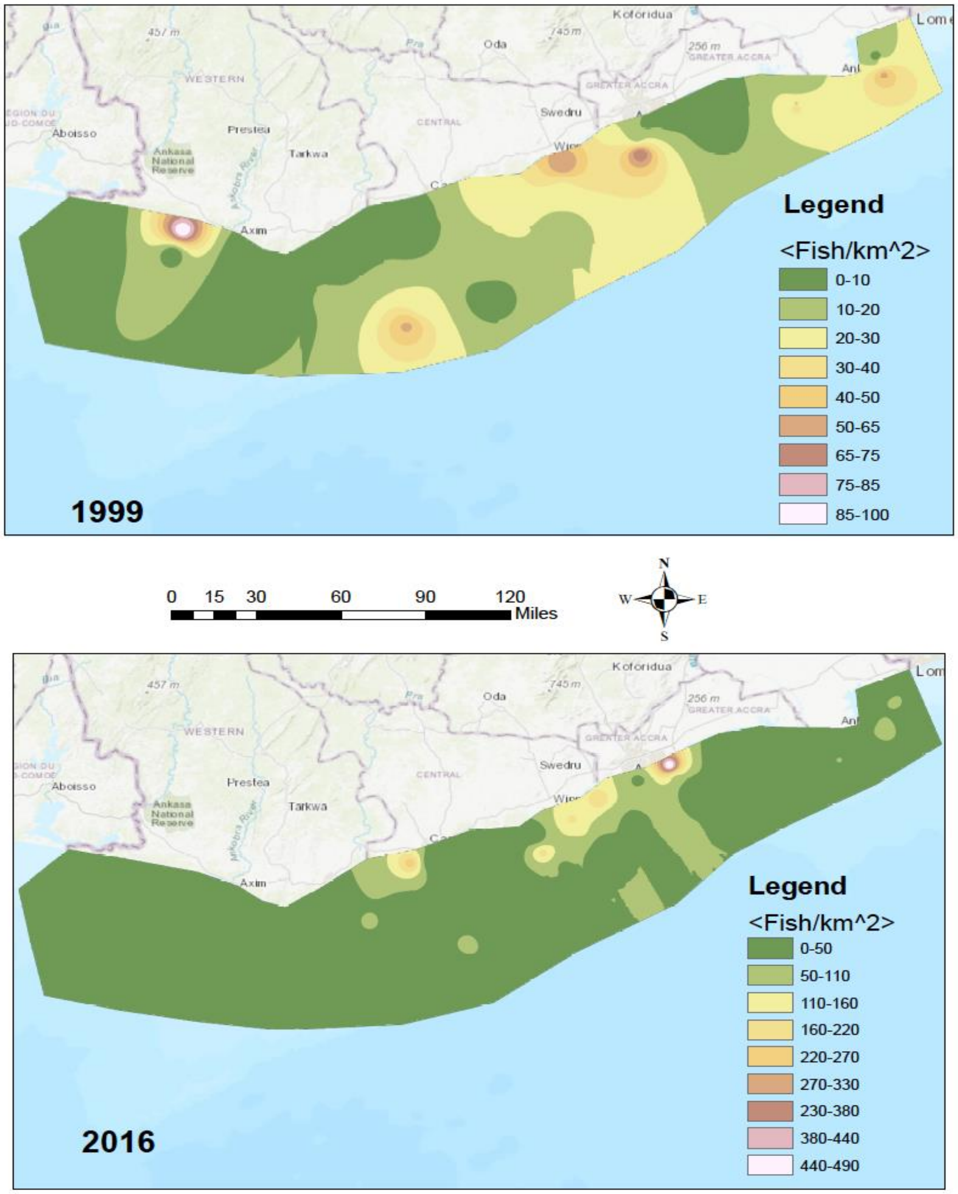

Figure 8: Spatial distribution of bluespotted seabream in two representative years. For each year, the brightness of the contours is proportional to fish population density

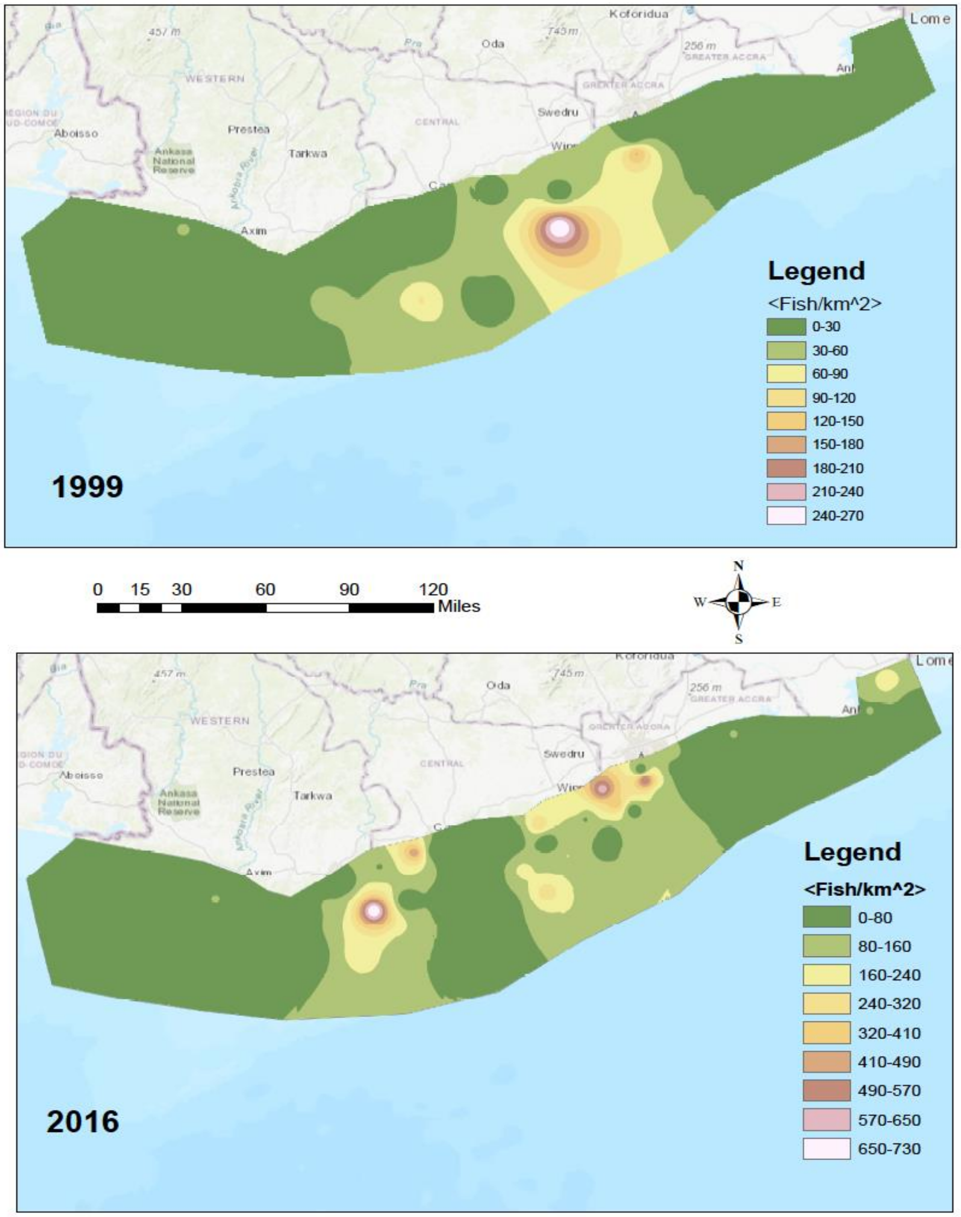

Figure 9: Spatial distribution of goatfish in two representative years. For each year, the brightness of the contours is proportional to fish population density

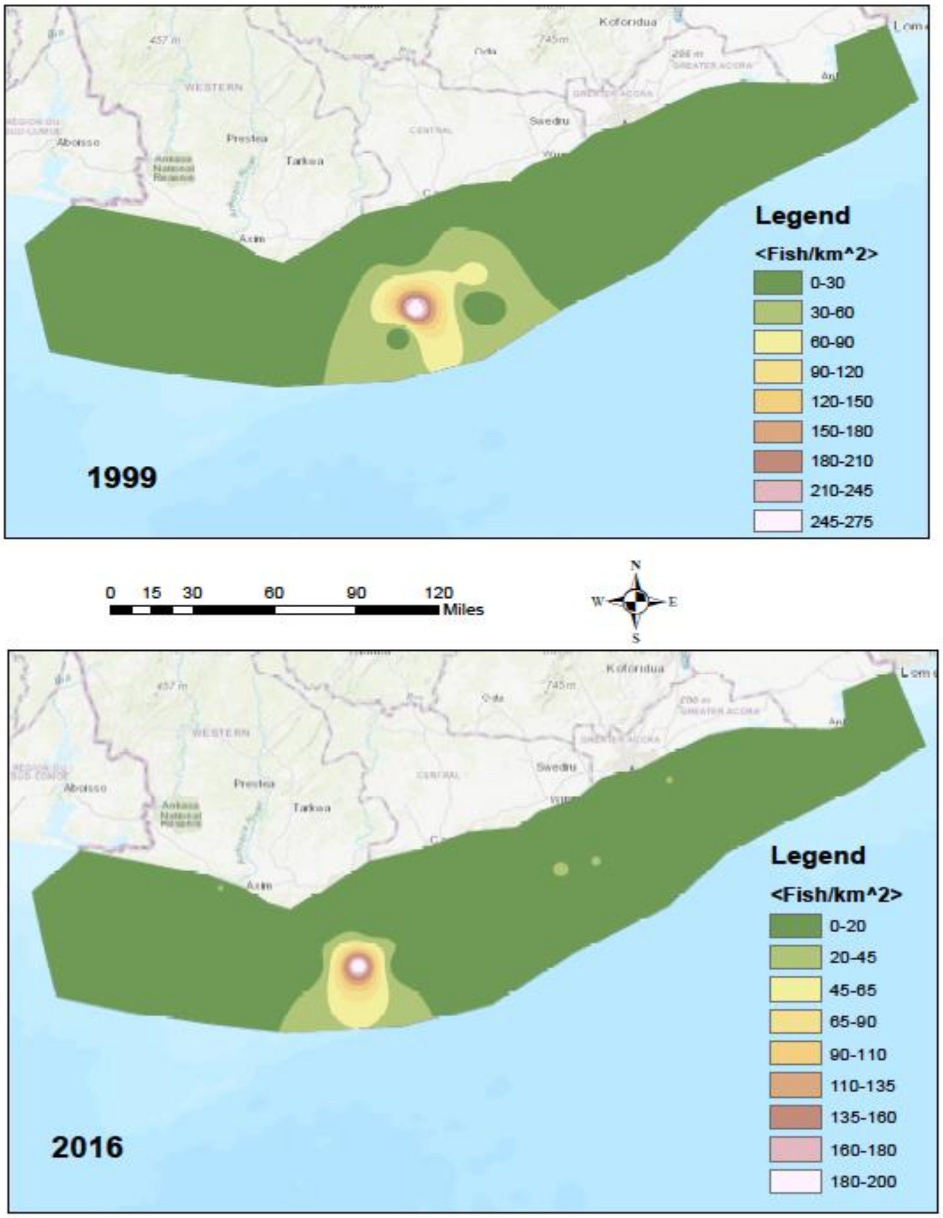

Figure 10: Spatial distribution of flying gurnard in two representative years. For each year, the brightness of the contours is proportional to fish population density

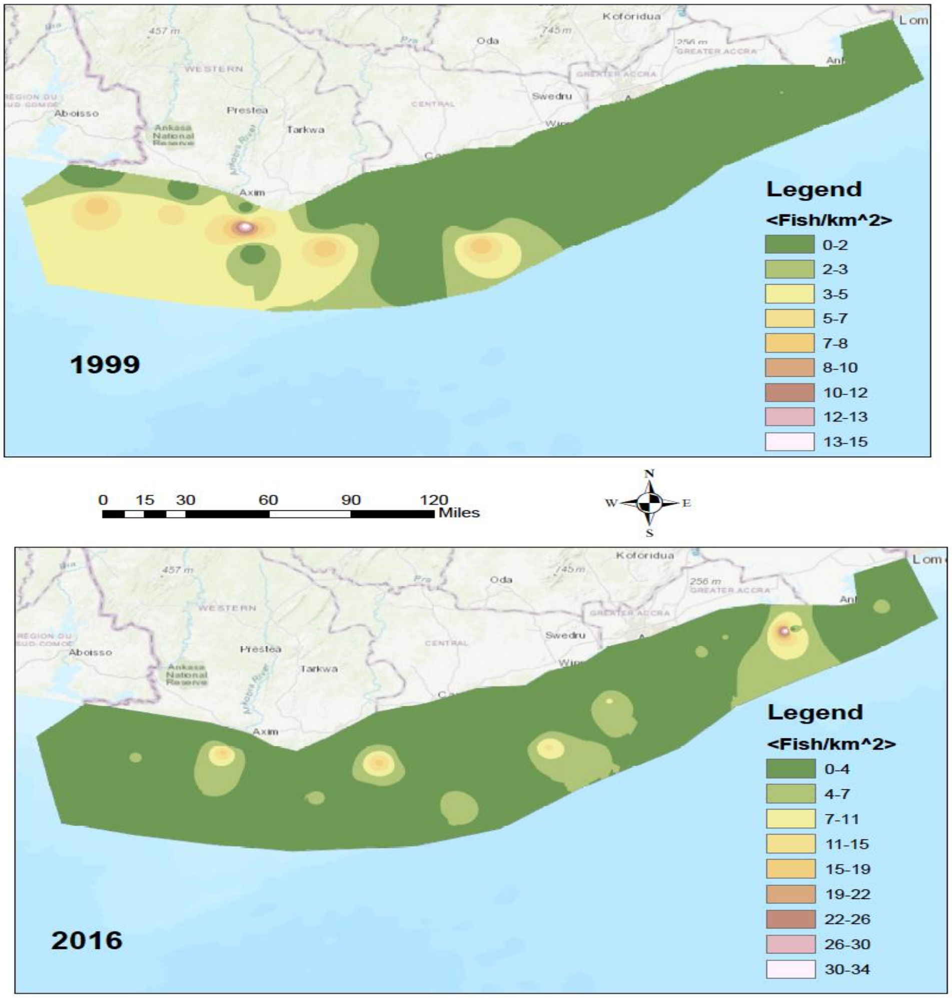

Figure 11: Spatial distribution of brown skate in two representative years. For each year, the brightness of the contours is proportional to fish population density

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 4), indicating presence and abundance were 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 42.4% for brown skate to 71% for Canary dentex, suggesting that the models have adequate power and predictability (Table 5a and b).

Table 4: 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	35.73	51.99	37.76	37.73	56.11	56.13	39.78	**70.64**
	AIC	183751.60	161798.80	171066.10	183684.40	149878.90	160546.40	169342.40	**128441.90**
Bluespotted seabream	df	34.80	50.31	36.86	36.81	55.41	55.73	38.84	**72.14**
	AIC	12897.11	11285.28	12783.31	12878.14	11238.49	11164.78	12787.00	**10022.10**
Cuttlefish	df	30.15	46.69	32.14	32.16	49.68	49.21	34.20	**61.49**
	AIC	14305.64	11402.00	13994.05	13605.76	11243.80	11364.68	13599.19	**10191.06**
Goatfish	df	33.89	50.07	36.12	36.34	53.68	53.75	38.32	**67.74**
	AIC	23334.96	20324.20	22244.98	22310.08	19290.51	19924.40	21853.53	**17774.73**
Canary dentex	df	33.70	46.79	35.75	35.69	52.00	51.89	37.89	**67.46**
	AIC	7077.45	6414.52	6993.77	6976.41	6278.38	6061.28	6937.61	**4289.83**
Brown skate	df	28.31897	43.40653	31.71055	30.42419	46.31257	45.44502	33.71826	**57.20339**
	AIC	1787.295	1390.129	1767.201	1781.229	1381.127	1388.667	1755.287	**1308.318**
Red cornetfish	df	34.60083	48.38495	36.40323	36.57779	51.72825	51.86429	38.37236	**64.74422**
	AIC	7338.654	5818.595	6668.614	7143.591	5379.597	5723.584	6664.031	**5090.256**
Flying gurnard	df	34.73254	49.72557	37.00131	36.74207	55.09551	54.60345	39.0914	**67.13665**
	AIC	4401.847	2676.962	4330.216	4347.508	2558.663	2548.102	4181.18	**1977.821**

Table 5: 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	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 (%)		68.5	59.5	56.2	44	58

Table 1b: 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**	-0.001
	Upwelling Index		-0.001	-0.001
Presence/Absence	Location	0.378	0.001	0.001
	Bottom depth	0.73	0.001	0.001
	Temperature	0.192	0.335	0.018
	Oxygen	0.428	0.203	0.054
	salinity	0.697	0.151	0.03
	Fishing effort		**-0.001**	0.001
	Upwelling Index		-0.038	0.09
DE (%)		42.4	47	71

Red Pandora abundance was negatively affected by fishing effort, whilst upwelling had a positive influence (Table 6). Abundance was higher at depths between 40-100 m, and at temperatures between 19-26 ˚C and oxygen concentrations < 1.5-3ml (Table 6). The strongest effects on red pandora abundance were those of temperature, salinity and fishing (Table 6).

Bluespotted seabream presence and abundance was positively associated with depths between 30-70 m (Table 6). There were strong negative effects of fishing and upwelling on abundance (Tables 6 and 7), and effects of oxygen, temperature and fishing were of greater magnitude (Tables 6 and 7). Abundance was higher at temperatures between 17-22.5 ˚C and at salinities greater than 35.3 psu (Table 6).

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). Fishing effort had a positive influence on abundance and upwelling had a negative effect (Table 6). The strongest effects on abundance were those of fishing effort, salinity 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). 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). 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). 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 was negative and influence of upwelling was not significant (Table 6).

The brown skate was most abundant at depths between 40-115 m, at temperatures between 16-24 °C, salinities between 34.8-35.6 psu and oxygen concentrations between 2.5-3.2 ml l^{-1} (Table 6).

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), with the effects of temperature and oxygen have the strongest influences (Table 8).

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	40-100	19-26	35.25-35.75	1.5-3	-	+
Bluespotted seabream	30-70	17-22.5	>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	?	3-5	-	+
BYCATCH SPECIES						
Brown skate	40-115	16-25	34.8-35.6	?		
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	3474	1.7	214	3.4	94	0.5	874	3	59	0.6
Salinity	3494	3	66	0.5	264	1.4	391	1.5	436	2.8
Bottom temperature	1478	4.7	235	1.4	360	1.9	808	2.8	309	3.5
Fishing effort	195	2.2	11	1.3	124	0.7	675	2.4	241	2.6
Upwelling Index	130	0	55.8	0.3	19	1.2	41	0.4	243	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	17	1.5	350	4.3	309	4.7
Salinity	215	12.9	340	4.4	73	1.2
Bottom temperature	31	2.3	345	9.8	926	12.6
Fishing Effort			800	4.2	42	0.7
Upwelling Index			15	0	53	0

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 suggested 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 species than upwelling (Tables 7 and 8). Surprisingly, the 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 environmental predictors temperature, oxygen and salinity (Tables 7 and 8).

DISCUSSION

Generally, 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. 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, Maravelias, Katsanevakis, Karageorgis, & Papaconstantinou, 2010). These results were consistent with other findings on distribution of demersal species in other parts of the world (Grüss, Yemane, & Fairweather, 2016; Parra et al., 2016; Russell et al., 2014). 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, 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 (Anderson, Gurarie, Bracis, Burke, & Laidre, 2013; Anderson & Millar, 2004; Araújo et al., 2006; Harman, Harvey, & Kendrick, 2003; Recsetar et al., 2012; Simpson et al., 2011). In addition to the above, the 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, spatial conflicts that exist between artisanal and industrial fishers (Ameyaw, 2017) by reason of fishing areas and target species could be managed. 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 & Pauly, 2004; Ministry of Fisheries and Aquaculture Development, 2015) and the use of unsustainable fishing practices like light fishing (Ameyaw, Asare, Mutimukuru-maravanyika, Laryea, Sabah, & Mills, 2012). There is also a vibrant market for some bycatch species, especially in the central region of Ghana, which makes classifying them as bycatch inaccurate (Nunoo, Boateng, Ahulu, Agyekum, & Sumaila, 2009). It is recommended that these bycatch species be no longer classified as a bycatch for the demersal fishery but rather added to the species that are routinely assessed and monitored.

This study demonstrated that both environmental variability and fishing effort were 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 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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CONFLICT OF INTEREST

There is no conflict of interest.

CRediT Authors Statement

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