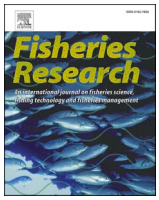
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The influence of environmental variables on the abundance and temporal distribution of *Octopus cyanea* around Mafia Island, Tanzania

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ABSTRACT

Abundance and distribution of short-lived species like *Octopus cyanea* depends on favorable environmental conditions, which are essential for growth and successful recruitment. However, the influence of environmental variables on the abundance and distribution of *O. cyanea* remains unknown, particularly in the Western Indian Ocean (WIO) region, despite its importance as a fishery resource. This study investigated the role of environmental variables (sea surface temperature [SST], chlorophyll-*a* [Chl-*a*], rainfall and wind) on the abundance and temporal distribution of *O. cyanea* around Mafia Island in Tanzania for a period of 60 months (2013–2017). Octopus catch data were obtained from TANPESCA fish processing factory, while environmental data were obtained from the National Aeronautics and Space Administration - NASA satellite (SST and Chl-*a*) and the Tanzania Meteorological Agency - TMA (rainfall and wind). The results for the *O. cyanea* CPUE showed two peaks, between March and October, suggesting successful recruitment and stable environmental conditions during these periods. The additive effect of wind speed and Chl-*a* with a 4-month lag, was the best model for predicting the abundance and temporal distribution of *O. cyanea* around Mafia Island followed by the additive effect of SST, wind and Chl-*a*. Temperature influences octopus growth, while strong wind facilitates the mixing of water, which brings the bottom nutrient rich water to the euphotic zone for increased photosynthesis. In conclusion, the abundance and temporal distribution of *O. cyanea* are influenced by the additive effect of wind, Chl-*a* and SST with time-lagged effect of four months. This study recommends seasonal closure of the octopus fishery between April and July and reopening in March and October for sustainable harvesting of this valuable resource.

1. Introduction

Octopus is an important source of income for the fisheries sector in some African countries including Senegal (Domain et al., 2000), Kenya (Kivengea, 2014), Madagascar (Belazis, 2011; Humber et al., 2006) and Tanzania (Jiddawi and Öhman, 2002). The fishery is a source protein (Msongole, 2018), and employment and income generation (Guard and Mgaya, 2002; Guard, 2009) to people along the Tanzania coast of the Indian Ocean. Local coastal communities along the Tanzanian coast practise artisanal fishing of white-spotted octopus (*Octopus chromatus*), common octopus (*Octopus vulgaris*) and day octopus (*Octopus cyanea*) (Msongole, 2018). Among these, *O. cyanea* is a large omnipresent octopus species associated with coral reefs and extensively distributed throughout the tropical Indian and Pacific Oceans (Norman, 1991). The species is found in a wide range of marine environments from East African coast (Guard and Mgaya, 2002), Madagascar (Benbow et al., 2014) to Hawaii (Herwig et al., 2012). *O. cyanea* is the main species fished by tropical artisanal fishers contributing over 99 % of the catch (Guard and Mgaya, 2002; Guard, 2003). It is the most landed octopus in Tanzania, whose life span takes about 12–15 months (Guard, 2009). *O. cyanea* life cycle entails spawning to hatching (20 days), larval (planktonic) stage (1 month) and post settlement to recruitment (3 months) (Guard and Mgaya, 2002; Guard, 2003). *O. cyanea* is the only commercial octopus fishery in Tanzania due to its rapid growth rate and high prevalence along the shallow coast (Guard and Mgaya, 2002).

Variability in the abundance and distribution of the aquatic organisms can be influenced by both anthropogenic activities and climatic factors (Daskalov, 2003). The abundance and distribution of

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cephalopods, depend much on successive recruitment, which is governed by the availability of favorable environmental conditions (Boyle and Rodhouse, 2005; Pierce et al., 2008). Despite their importance in fisheries, the relationship between abundance and distribution of octopus and environmental factors has been relatively well studied in Senegal for *O. vulgaris* (Caballero-Alfonso et al., 2010; Thiaw et al., 2011; Diankha and Thiaw, 2016). In these studies, the variability of sea surface temperature (SST) controlled the abundance (Caballero-Alfonso et al., 2010) and inter-annual and seasonal stock biomass variability of *O. vulgaris* (Thiaw et al., 2011). Therefore, the knowledge of environmental variables in relation to abundance of *O. vulgaris* can be used to support fisheries management. We hypothesized that, environmental variables also influence the abundance and distribution of *O. cyanea*. Unfortunately, studies on the influence of environmental variables on the abundance and distribution are available only for *O. vulgaris* while *O. cyanea* remains the least studied despite its importance in the fishery.

Traditionally, the octopus fishery in Tanzania was practised by women and children by walking on the intertidal reef flats during low spring tide in order to collect octopus using a wooden stick as a fishing gear (Guard and Mgaya, 2002). Over the years, men got involved in this fishery due to the ban imposed on sea cucumber fishery and the increase in octopus demand for the local and export markets (Guard and Mgaya, 2002; Jiddawi and Öhman, 2002; Chande, 2010). Consequently, men have increased the fishing pressure by fishing in the subtidal inner reef by snorkeling and skin diving, and modified the gear technology from the wooden stick to spear gun. The increased fishing pressure resulted into overfishing in the early 2000s (Ngatunga, 2009). However, a recent study indicated that octopus were landed almost exclusively in Pangani, suggesting potential trophic cascades (Robertson et al., 2018) after years of overexploitation (Zhao, 2018). In order to ensure sustainability of *O. cyanea* fishery, the government of the United Republic of Tanzania in collaboration with the private sector players such as the World Wide Fund for Nature (WWF) initiated seasonal closure of the octopus fishery as a management tool to compliment with the legal size limit and restriction of octopus fishing to spring tide. The few studies conducted in Tanzania on *O. cyanea*, have reported on the variability in the abundance and distribution of this species to the differences in fishing pressure (Guard and Mgaya, 2002). Moreover, octopus catch was also influenced by increased wind and water turbidity (Robertson et al., 2018). However, knowledge on the abundance and distribution of *O. cyanea* in relation to other environmental factors such as SST, chlorophyll-*a* (Chl-*a*), rainfall and wind is currently unavailable.

The influence of environmental variables on the abundance and distribution of different species can be predicted through modelling as an alternative to experimental studies. Earliest empirical models such as linear models have been used to explain the relationship between environmental variables and abundance (Pierce et al., 2008 as cited in Fogarty, 1989; Diankha et al., 2013). However, these models rely on simple uni-factorial linear regression or correlation, hence limiting their use for complex interactions of environmental variables on biological processes (Rothschild, 2000; Diankha and Thiaw, 2016). Advances in regression analysis, provided by generalized linear model (GLM) and generalized additive model (GAM), have facilitated increasingly sophisticated approaches, taking into consideration the impact of multivariate combination of environmental variables and their interactions (Guisan et al., 2002). The GAM has been widely used to predict abundance and distribution of different species in relation to environmental variables (Al-Kharusi, 2008; Murase et al., 2009; May-Collado and Forcada, 2012; Drexler and Ainsworth, 2013; Antúnez et al., 2017; Perryman and Babcock, 2017). Accordingly, the GAM is a suitable tool for establishing the relationship between *O. cyanea* abundance and distribution and environmental variables. Therefore, this study investigated the influence of environmental variables (SST, Chl-*a*, rainfall and wind) on the abundance and temporal distribution of *O. cyanea*. To achieve this objective, we used the GAM with time-lagged effects. The knowledge generated enhances our understanding on the influence of environmental variables on abundance and temporal distribution of *O. cyanea* for sustainable harvesting of this valuable resource in the country.

2. Materials and methods

2.1. Study area

This study was conducted in the Mafia archipelago located about 20 km offshore along the coast of Tanzania. The archipelago comprises several islands including, the main Mafia Island, which is about 49 km long and 17 km at its widest part, opposite the Rufiji Delta. Several smaller islands are scattered on the west and south of the island (Fig. 1). Some of the islands are uninhabited but serve as temporary camping sites for the fishers (Mwaipopo, 2008). Fishing is the main economic activity on Mafia Island accelerated by an increase in demand of octopus by fish processing industries for export (Jiddawi and Öhman, 2002; Chande, 2010). The area experiences an average annual rainfall of 2000 mm, with virtually no permanent annual river discharge (Gaspare and Bryceson, 2013). The area is influenced by North East Monsoon (NEM) during the October to March period and South East Monsoon (SEM) between March and October (McClanahan, 1988). The air and SST range from 20 °C–32 °C and 25 °C–31 °C, respectively (Gaspare and Bryceson, 2013).

2.2. Data collection

2.2.1. Octopus cyanea catch and effort data

The monthly total landings data of *O. cyanea*, locally known as *Pweza* in Kiswahili (Fig. 2) for 60 months (2013–2017) used in this study were obtained from TANPESCA fish processing factory based at Kilindoni on Mafia Island. The factory uses agents to collect the catch data from five villages namely; Bwejuu (7.95 °S, 39.52 °E), Kitoni (7.96 °S, 39.61 °E), Changarama (7.99 °S, 39.69 °E), Jibondo (8.06 °S, 39.73 °E) and Nyororo (7.62 °S, 39.69 °E) (Fig. 1). The company has also commissioned boats in each of the villages to transport octopus fishers to their respective fishing grounds. After return from fishing, the agents record the daily total catch in kilograms from the commissioned boats, and report to TANPESCA the total catch collected at each village at the end of each spring tide. The study also used the number of fishers as fishing effort, which was estimated through structured interviews with the TANPESCA agents from the five villages. In each village, one agent was interviewed on the average number of fishers engaged in fishing per day in their commissioned boats. During the study, one agent received 30–100 fishers per fishing season in a month. The catch per unit effort (CPUE) was computed by dividing monthly total catch (kg) with the total number of fishers for a period of 16 fishing days per month. The number of fishing days per month was chosen on the basis of current practice whereby octopus fishery is carried out during spring tides, which occurs twice every month and often lasts for eight days during each period.

2.2.2. Environmental data

This study used monthly mean SST and Chl-*a* data from the Moderate Resolution Imaging Spectroradiometer (MODIS) found in the National Aeronautics and Space Administration (NASA) satellite. The data were obtained from the Sea-Viewing Wide Field-of-View Sensor (SeaWIFS) data centre that archives and distributes satellite data (http://modis.gsfc.nasa.gov). The SST and Chl-*a* data for the 60 months (2013–2017) studied were downloaded in gridded form with horizontal resolution of four kilometres at the Equator. The study also used mean monthly wind speed and total rainfall, which were provided by the Tanzania Meteorological Agency (TMA) for the same period. *In-situ* measurements for SST and fluorescence (an indicator of Chl-*a* concentration) were taken using a conductivity, temperature and depth (CTD) equipment on monthly basis from January to December 2018. A total of 77 stations

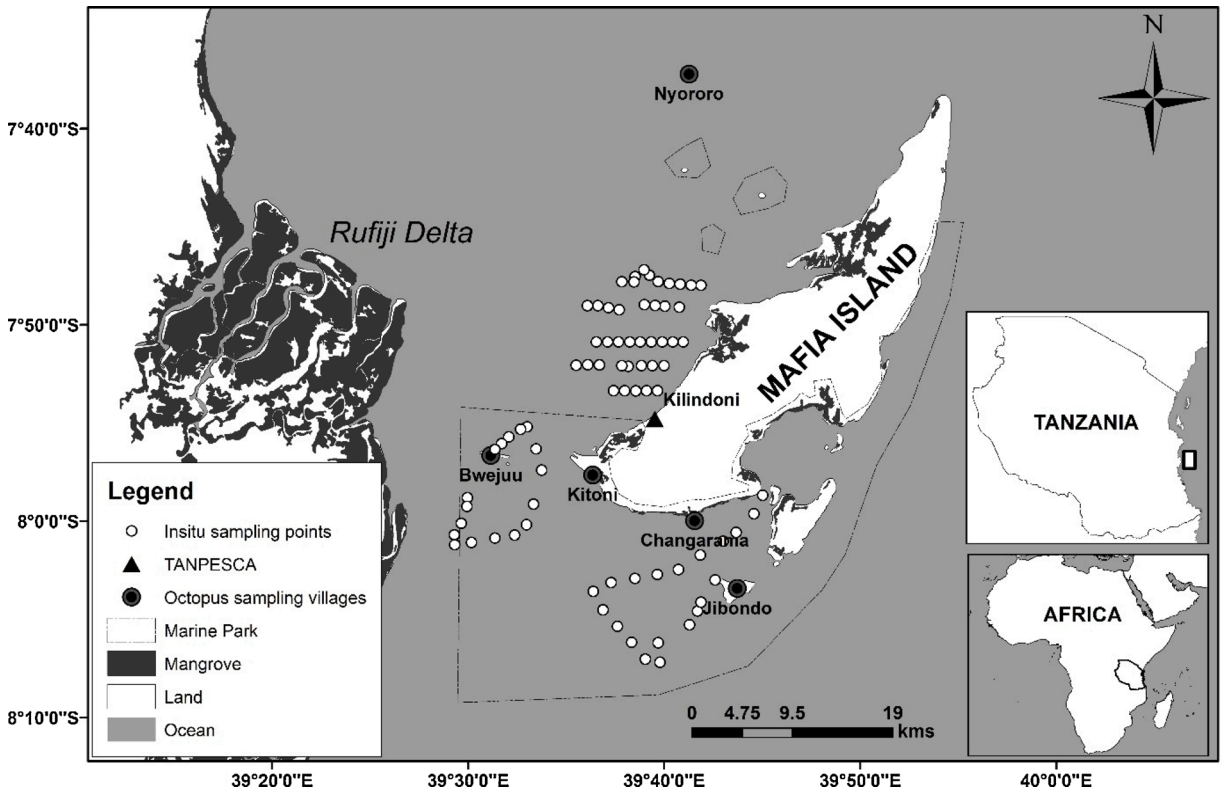


Fig. 1. A map showing study area. The inset maps show position of the study area in Tanzania and its location in Africa.

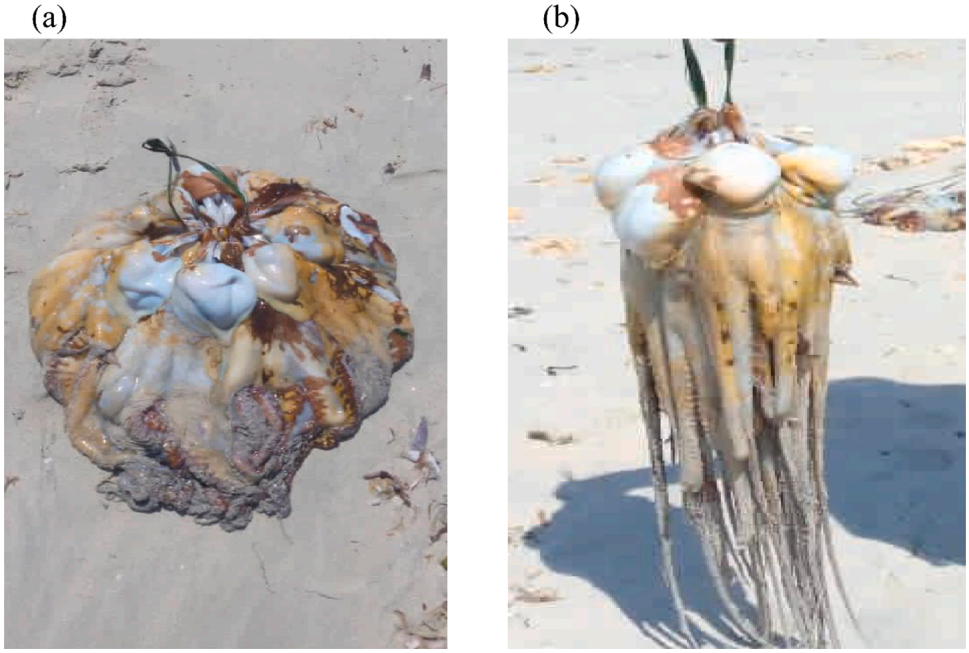


Fig. 2. A representative photograph of the *Octopus cyanea* (locally known as *Pweza* in Kiswahili) used in this study. (a) *O. cyanea* individuals in a bunch placed on the sand, and (b) A stretched bunch to show the full length. Source: Anthony Mbega.

located about 300 m apart in 11 transects were chosen for sampling (Fig. 1). In this study, we selected the CTD measurements for the mean SST and fluorescence from the uppermost 25 cm of the water column for validation with the satellite data extracted from the same locations and time. We did this because the satellite measures SST and Chl-*a* at the uppermost layer of the water column and the CTD takes the profile of the measured environmental variables.

2.3. Data processing and analyses

The SST and Chl-*a* values from the satellite data were averaged from latitude 7°37′ to 8°08′ S and longitude 39°28′ to 39°58′ E using ArcGIS Version 10.2.2 (ESRI GIS Mapping Software). The SST and Chl-*a* data were stored in spreadsheet alongside the *O. cyanea* CPUE, wind speed and rainfall data. The data obtained were analyzed by using R statistical

software (R-Core-Team, 2017). Both satellite and *in-situ* measurements of SST and Chl-*a* were cleaned and checked for normality using Shapiro-test and homoscedasticity by using Levene's test. The data were not normally distributed and had variations in variances even after log transformation. Therefore, the relationship between *in-situ* and satellite SST and Chl-*a* data were estimated by using a non-parametric, Spearman rank correlation test (Zar, 2005).

The GAMs were used in the analysis of the possible relationship between *O. cyanea* CPUE and environmental variables. The models were determined by using *gam()* function in the *mgcv* R package (Wood, 2017). The models assume non-parametric and non-linearity regression (Beck and Jackman, 1998; Andersen, 2009). The model fits were validated by examining the residual plots. For the adequate model fits, the residuals should be randomly distributed around the lower single digits of the y-axis (e.g., 0.5 or 1.5). The best model was selected based on the lowest Akaike information criterion (AIC) (López-Rocha et al., 2012). The alternative models were selected based on the criterion suggested by Burnham and Anderson (2002), whereby, if the difference in AIC values between the best and other alternative models is < 2, the alternative model can be considered to be an important choice with statistical support. Moreover, if $4 <$ AIC difference > 7, then alternative models can be considered important but with weak statistical support; and if the difference in AIC values between the best and other alternative models is >10, the alternative models are considered to have no statistical support and hence are not useful for predicting the abundance of *O. cyanea*.

A principal component analysis (PCA) technique was used to assess the influence of environmental variables on the variation of *O. cyanea* abundance. The *Factoextra* package was used to analyze the environmental variables and their influence on *O. cyanea* abundance (Kassambara and Mundt, 2017). Inter-annual and monthly climatological trends of *O. cyanea* CPUE, SST, Chl-*a*, wind and rainfall were analyzed based on the grammar of graphics by using *ggplot2* package (Wickham et al., 2018). A cross-correlation test was used to detect lagged time that takes into consideration the influence of environmental variables on the abundance of octopus (Vaughan, 2017). The time lags in days for the influence of environmental variables on the variation of *O. cyanea* abundance are reported with the highest significant *p*-values in the cross correlation analysis. Shifted (lagged) catch was termed as 'proxy catch', which represents octopus larval abundance.

3. Results

3.1. Validation of the satellite data

The Spearman rank correlation model showed significant relationship between the *in-situ* and satellite data for both SST ($R^2 = 0.84$; $p < 0.05$) and Chl-*a* ($R^2 = 0.82$; $p < 0.05$; Fig. 3). The correlation model used satellite SST and Chl-*a* data acquired during January to December 2018, corresponding with the time when *in-situ* measurements were taken. Therefore, satellite data used in this study explained the real conditions in field.

3.2. Variability of O. cyanea CPUE and environmental variables

The results for the trends of *O. cyanea* CPUE and environmental variables are shown in Figs. 4 and 5. The monthly mean CPUE ranged from 0.2 to 15 kg/fisher/day with two clear peaks in March and October, while the lowest CPUE occurred around May. The monthly mean SST ranged between 26 °C and 30 °C, increasing gradually during the transition period between September and October, and then increasing rapidly during the NEM season from October to March. Thereafter, SST decreased between March and July and became relatively low and stable during the SEM season between July and September. The monthly mean Chl-*a* ranged between 0.3 and 0.7 mg/L. It increased rapidly from November to January, then decreased between January and April, and thereafter became relatively low and stable between April and November.

During the study period, the monthly total amount of rainfall received in Mafia Island ranged between 0 and 400 mm. The island experienced periods of heavy rains between March and April and a prolonged period of dry season from July to around October. Short rains were experienced between November and January (Fig. 5). Moreover, Mafia Island experienced wind speeds ranging from 4 to 9 knots. The island experienced periods of strong winds between April and October (SEM) and calm wind between November and March (NEM). However, the strongest wind prevailed between July and August, while the calmest wind was experienced in March.

3.3. Relationship between O. cyanea CPUE and environmental variables

A PCA showed no clear relationship between *O. cyanea* CPUE and

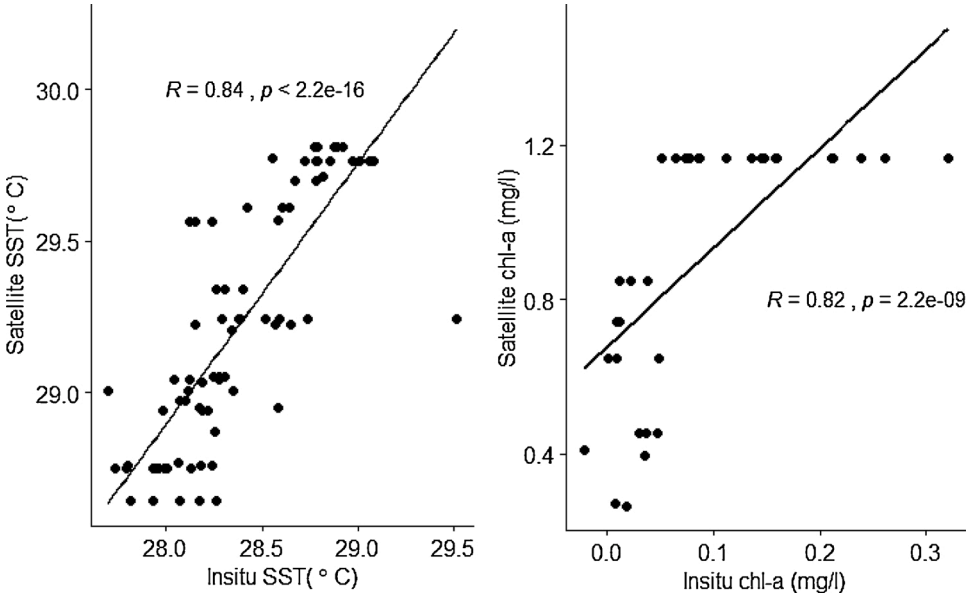


Fig. 3. The relationship between *in-situ* and sea surface temperature (SST) and chlorophyll-*a* (Chl-*a*) satellite data around Mafia Island.

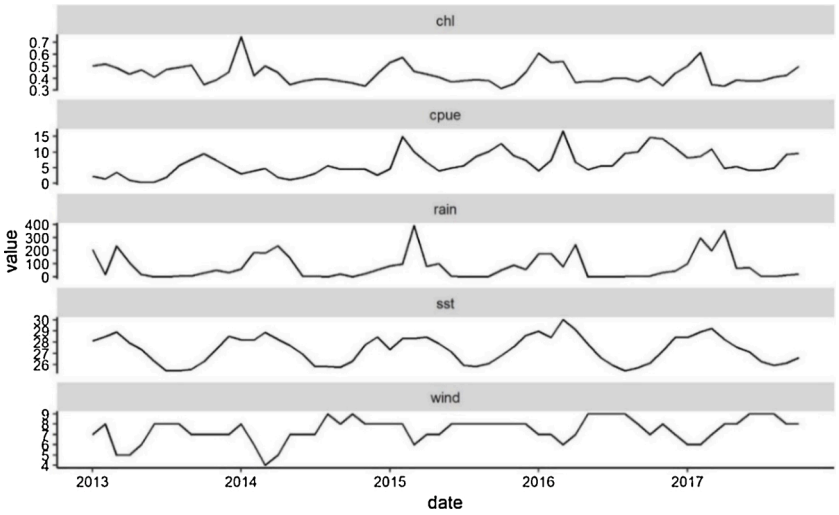


Fig. 4. Inter-annual trends of chlorophyll-*a* (Chl-*a*; mg/L), *Octopus cyanea* catch per unit effort (CPUE; kg/fisher/day), rainfall (mm), sea surface temperature (SST; °C), and wind speed (knots) for five years (2013–2017).

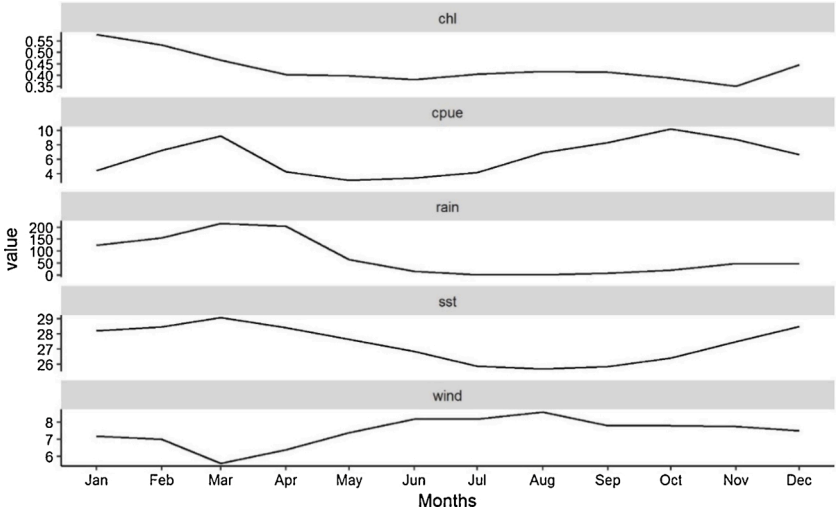


Fig. 5. Monthly climatological trends of *Octopus cyanea* catch per unit effort (CPUE; kg/fisher/day), chlorophyll-*a* (Chl-*a*; mg/L), rainfall (mm), sea surface temperature (SST; °C), and wind speed (knots) for the year 2018.

environmental variables based on both dimension 1 (Dim 1) and dimension 2 (Dim 2) before incorporating time-lagged effects (Fig. 6). Cross-correlation results showed a clear relationship between *O. cyanea* CPUE and all environmental variables with a 60-day (2 months) to 120-day (4 months) lag (Fig. 7). The CPUE decreased as Chl-*a* and rain, but increased with SST and wind for a time lag of four months.

The GAMs with a 4-month lag showed the lowest AIC values as compared to 2- and 3-month lags (Table 1), implying that, GAMs with a 4-month lag explain better the relationship between *O. cyanea* CPUE and environmental variables. This was also revealed by the PCA with a 4-month lag in CPUE, which showed that, *O. cyanea* CPUE had a negative linear relationship with Chl-*a*, SST and rain, while wind showed positive correlation. This variability was explained by Dim 1 for 55.2 % (Fig. 8). This study revealed two spawning peaks of *O. cyanea* in June and July and the other one in November based on the 4-month lagged catch, which represents larval abundance (proxy catch) (Fig. 9).

The AIC values of the univariate GAMs, showed that, wind was the dominant environmental factor, which influenced the abundance and temporal distribution of *O. cyanea* followed by other environmental variables (Table 1). Based on the AIC, GAMs showed the additive effect of wind and Chl-*a* with a 4-month lag, as the best model for predicting the abundance and distribution of *O. cyanea* around Mafia Island followed by the additive effect of wind, Chl-*a* and SST. This is because the difference in the estimated AIC values between the two models was less than 2 units (i.e. 1.1898) and was significant different.

However, the abundance of *O. cyanea* increased with an increase in wind speed and decrease in Chl-*a* concentration. A positive influence on the abundance and temporal distribution of *O. cyanea* was observed at the wind speed ranging between 8 and 9 knots and Chl-*a* concentration ranging between 0.3 and 0.45 mg/L (Fig. 10). The alternative model, which involved the additive effect of wind, Chl-*a* and SST added the impact of SST, which showed that the abundance of *O. cyanea* increased with an increase in SST up to an optimum temperature of 27 °C, beyond which the abundance decreased (Fig. 11).

4. Discussion

The variability of environmental parameters at different life cycle stages of cephalopods including octopus, may have an influence on their abundance and distribution (Pierce et al., 2008). Important life cycle stages of octopus include spawning, hatching, larvae, recruitment, and movements to and from the breeding sites. The absence of clear

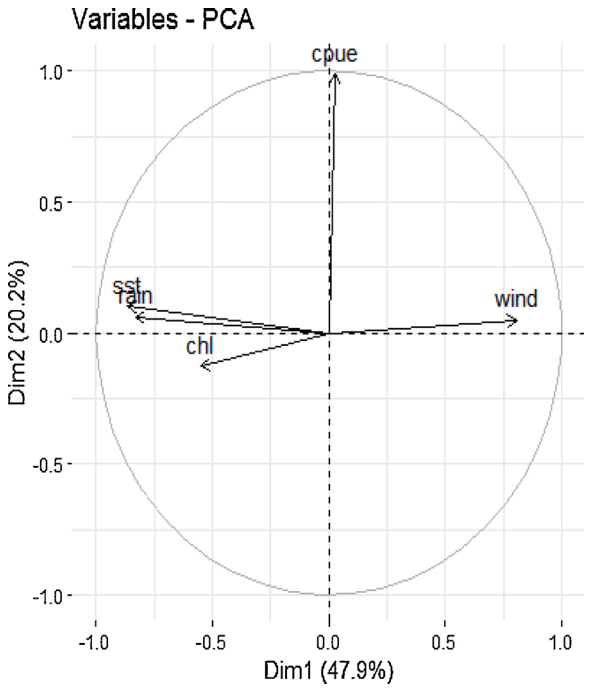


Fig. 6. Biplot showing the relationship between *Octopus cyanea* catch per unit effort (cpue), monthly mean sea surface temperature (sst), chlorophyll-*a* (chl), rainfall (rain) and wind speed (wind) before incorporating time-lagged effects.

relationship between *O. cyanea* CPUE and environmental variables from the PCA results before time lag analysis suggests that, the influence of changes in environmental variables on the octopus abundance is not urgent. This indicated that, the CPUE is not felt immediately; rather it takes time before the octopus responds to the changes in environmental condition by adjusting their distribution and abundance. Octopus exists in planktonic stage during its larval stage for about one month, before settling down to live a benthic life as octopus. It has been established that, the time between post settlement and recruitment is about three months (Guard and Mgaya, 2002; Humber et al., 2006). The para-larvae possess substantial potential for recruitment and dispersal of octopus provided that, optimum environmental conditions and food availability prevail. This stage is considered critical for the octopus life cycle (Villanueva and Norman, 2008). Thus, the time lag before the octopus fishery responded to the changes in environmental variables represents the extended period between octopus larval stage and recruitment. These results corroborate those of Chédia et al. (2010), who found the time lag of four to six months before *O. vulgaris* stock responded to the changes in SST in Tunisian marine waters.

This study found two spawning peaks based on the larval abundance data (proxy catch) (Fig. 9) in agreement with Guard (2003), who also obtained two spawning peaks between June and July and another peak in October and November based on gonadosomatic indexes and recruitment observations. The peak of *O. cyanea* CPUE in October was probably attributed to successful recruitment of the octopus spawned earlier in June and July, while the peak observed in March was probably because of the successful recruitment of the octopus spawned during another spawning peak in November. These peaks were the result of stable and conducive environmental variables, including strong and stable wind (Mahongo et al., 2011), cooler temperature and a decrease in Chl-*a* concentration (indication of the increase in zooplankton abundance) (Fig. 9). This enabled high primary production to take place and provide food to the octopus larvae. It has been shown that, *O. cyanea* larvae feed on zooplankton including larval stages of crabs and shrimps (Van-Heukelem, 1976). Therefore, Chl-*a* serves as the source of food for the prey of *O. cyanea* larvae. Evidently, the present study revealed that, the increase in the population of *O. cyanea* larvae was attained after the growth of zooplankton population, which consumed the phytoplankton, resulting in the decrease of available Chl-*a* concentration. This is corroborated by the obtained negative correlations between *O. cyanea* 'proxy catch' (4-month lagged CPUE) and Chl-*a* (Figs. 7, 10 and 11). This is in agreement with Otero et al. (2009), who found a significant increase in octopus larval abundance and biomass with the decrease in nitrate, ammonium and Chl-*a* concentrations.

The present study showed that wind was the dominant environmental factor, which influenced the abundance and temporal distribution of *O. cyanea* followed by other environmental variables (Table 1). This is reasonable because strong wind acts as the key factor for octopus larval abundance and distribution. Strong wind affects abundance and distribution of octopus because it facilitates the mixing of water, which brings the bottom nutrient rich water to the euphotic zone where photosynthesis takes place. It also guarantees octopus larval dispersal. Strong wind also creates cooler environmental condition, which favours biological production, thereby increasing the availability of more prey and high growth rate (Chédia et al., 2010), consequently affecting the abundance and distribution of octopus. Otero et al. (2008) reported that wind-driven turbulence also affected the early life phase of *O. vulgaris* in

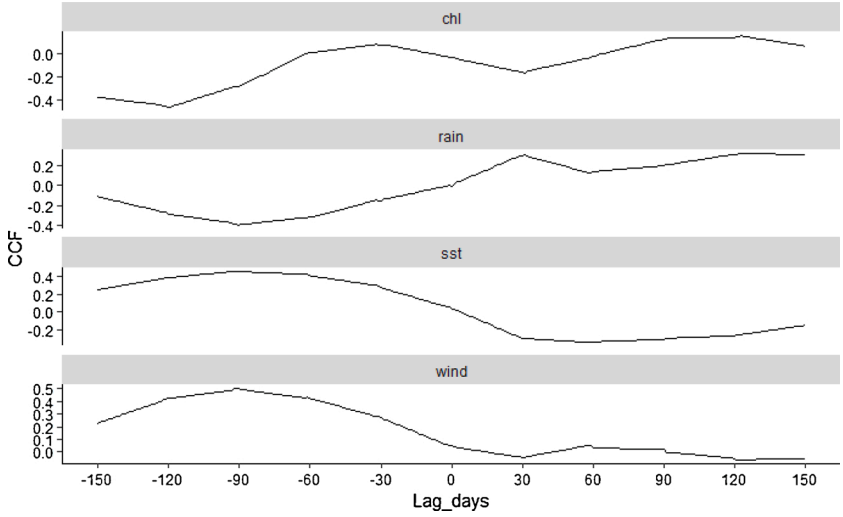


Fig. 7. Cross correlation between *Octopus cyanea* catch per unit effort (CPUE) and environmental variables (chlorophyll-*a*; Chl-*a*, rain, sea surface temperature; sst and wind).

Table 1
The generalized additive models (GAMs) for prediction of abundance and temporal distribution of *Octopus cyanea*.

Time lag = 2 months		Time lag = 3 months		Time lag = 4 months	
Covariance	AIC	Covariance	AIC	Covariance	AIC
SST, Rainfall, Wind* and Chl-*a*	311.899	SST, Rainfall, Wind* and Chl-*a*	302.7457	SST, Rainfall, Wind* and Chl-*a**	299.748
SST, Rainfall and Wind*	311.4542	SST, Rainfall and Wind*	306.4818	SST, Rainfall and Wind*	304.5112
SST, Rainfall and Chl-*a*	316.8708	SST, Rainfall* and Chl-*a*	313.5631	SST, Rainfall and Chl-*a**	308.243
SST, Wind* and Chl-*a*	310.0455	SST, Wind* and Chl-*a*	303.0107	SST, Wind* and Chl-*a**	297.8695
Rainfall, Wind* and Chl-*a*	314.1214	Rainfall, Wind* and Chl-*a*	301.5177	Rainfall, Wind* and Chl-*a**	298.4683
SST and Rainfall	316.7716	SST and Rainfall*	313.8328	SST and Rainfall	314.069
SST and Wind*	309.7483	SST and Wind*	306.0516	SST and Wind*	302.5793
SST* and Chl-*a*	317.4855	SST* and Chl-*a*	318.1608	SST and Chl-*a**	307.7092
Rainfall* and Chl-*a*	319.3794	Rainfall* and Chl-*a*	311.9448	Rainfall* and Chl-*a**	306.2438
Rainfall and wind*	314.1979	Rainfall and wind*	304.5504	Rainfall and wind*	306.8238
Wind* and Chl-*a*	313.144	Wind* and Chl-*a*	301.2176	Wind* and Chl-*a**	296.6797
SST*	316.5595	SST*	318.2512	SST*	312.4606
Rainfall*	318.7849	Rainfall*	312.0119	Rainfall*	317.0526
Wind*	313.2991	Wind*	304.3267	Wind*	305.1678
Chl-*a**	326.7027	Chl-*a**	320.8222	Chl-*a**	308.4407

Bolded AIC shows the best fit, SST = Sea Surface Temperature, Chl-*a* = chlorophyll-*a*. The asterisk * represents significant influence.

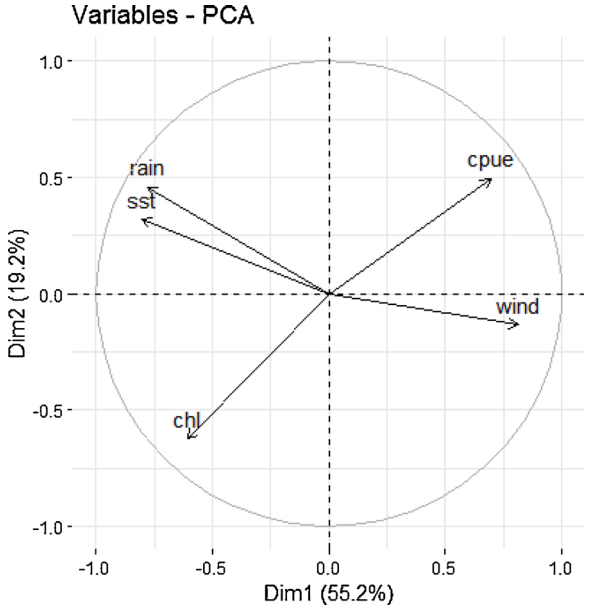


Fig. 8. Biplot showing the relationship between 4-month lagged *Octopus cyanea* catch per unit effort (cpue), monthly mean sea surface temperature (sst), chlorophyll-*a* (chl), rainfall (rain) and wind speed (wind).

the Galician upwelling system, northeast Atlantic Ocean, and contributed 85 % of the annual variability of the adult catch.

The abundance of *O. cyanea* increased with an increase in SST up to an optimum temperature of 27 °C, beyond which the abundance decreased. This affirms the great influence of temperature on octopus growth at different life cycle stages (Hernández-Garcıa et al., 2002). This study modelled optimum temperature for the growth of *O. cyanea* larvae and juveniles at around 27 °C. This agreed with the laboratory work by Van-Heukelem (1976), who also observed *O. cyanea* to grow exponentially for the first third of its benthic life at the temperature ranging between 22 and 27 °C. Van-Heukelem (1976) also reported maximum oxygen consumption for *O. cyanea* juveniles at 24.5–27.5 °C. In addition, Yarnall (1969) found fast growth rate of about 32.4 g/day at the temperature ranging between 26 and 28 °C for *O. cyanea* kept in captivity. Moreover, the optimum temperature for the recruitment of *O. vulgaris* in Senegalese waters was recorded at 24 °C (Diankha and Thiaw, 2016). The modelled optimum temperature is within the range for the SST reported in the studied Mafia Island (Gaspare and Bryceson, 2013). The results obtained in the present study indicate the significant role of temperature on octopus abundance and distribution by influencing feeding and metabolic rate (García-Fernández et al., 2019).

The rainfall was found to correlate weakly with octopus CPUE based on AIC values. Therefore, the inclusion of rainfall in the model had weak statistical support (Table 1). This corresponds to results from previous studies, which indicated that, rainfall itself does not influence the biological processes of octopus, but river discharge may be correlated with octopus landings by affecting primary production (Lloret et al., 2001; Sobrino et al., 2002; Chédia et al., 2010). The sediments brought to the sea during rainy season through river discharge might be the reason for the lowest octopus CPUE in May (Fig. 5). The sediments possibly limited primary production and concealed the octopus from skin divers and filled octopus dens, making them inaccessible by foot fishers (Muhaji Chande, Personal communication with octopus fishers). This is a plausible explanation because Mafia Island has no permanent river discharge, save for small surface water streams during the rainy season. Therefore, based on the results of this study, it is reasonable to suggest that, rainfall does not have a direct influence on the octopus CPUE, but affects indirectly through its influence on river discharge.

In conclusion, our study demonstrated that, *O. cyanea* at the study area has two CPUE peaks in March and October. The abundance and temporal distribution of *O. cyanea* are influenced by the additive effect of wind, Chl-*a* and SST with time-lagged effect of four months. The studied *O. cyanea* prefers habitats with wind speed ranging between 8 and 9 knots, Chl-*a* concentration ranging between 0.3 and 0.45 mg/L and an optimum temperature of around 27 °C. These environmental conditions favour biological production and guarantee octopus larval dispersal. Future studies should target the use of local fisher knowledge and GIS layer as a model layer to further understand the seasonal variation of octopus abundance and distribution to ensure sustainable utilization.

Seasonal closure of octopus fishery is practised in some areas in Tanzania, including Songosongo and Somanga villages in Kilwa District, Jojo village in Mafia district and Kukuu and Kisiwa Panza villages in Mkoani district, Pemba, among others. This management practice aims to improve octopus catches by giving the stock enough time to recover from fishing by completely closing the fishery at a particular place for three months. Based on the findings of this study, we suggest closure of the fishery between April and July because of the unsuccessful recruitment and also June and July fall in the spawning peak. On the other hand, opening of the fishery can be carried out in March and October in order to allow octopus spawned during the two spawning peaks to be recruited and grow to bigger sizes for sustainable harvesting of this valuable resource.

CRediT authorship contribution statement

Muhaji A. Chande: Conceptualization, Methodology, Investigation, Writing - original draft, Formal analysis. **Yunus D. Mgaya:** Supervision, Formal analysis, Methodology, Writing - review & editing. **Lusato B.**

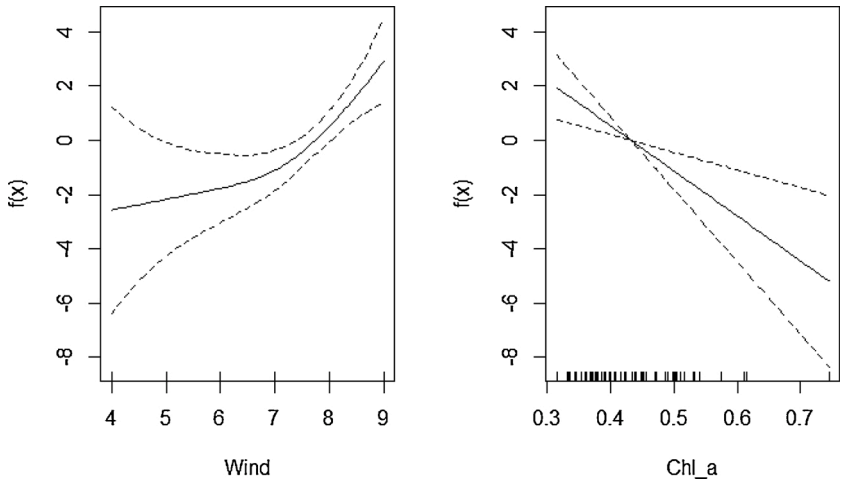


Fig. 9. Monthly climatological trends of 4-month lagged *Octopus cyanea* catch per unit effort (CPUE; Proxy catch, kg/fisher/day), (chlorophyll-*a*; Chl-*a*, mg/L), rainfall (mm), sea surface temperature (SST; °C), and wind speed (knots) for five years (2013-2017).

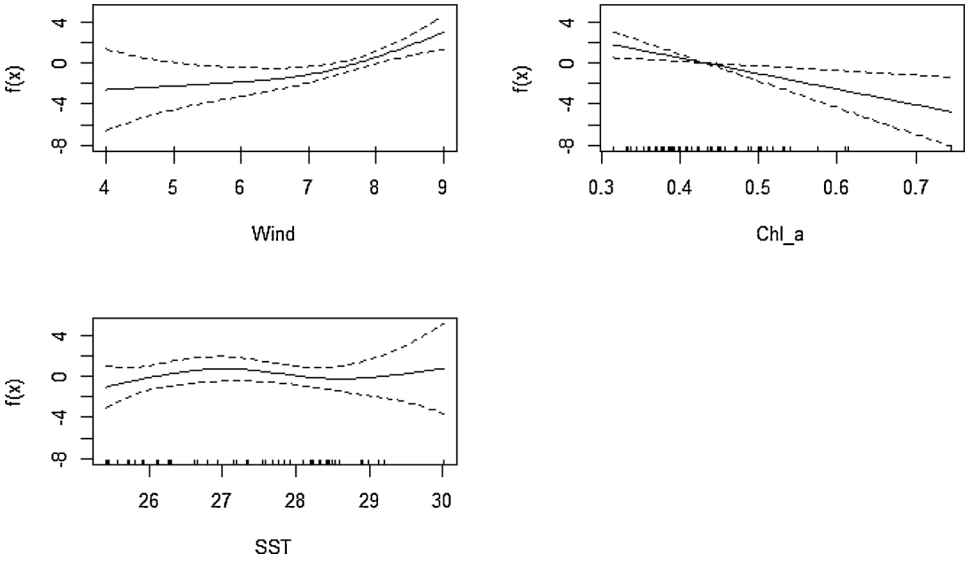


Fig. 10. The generalized additive model (GAM) derived effect of the best model predictor (wind and Chl-*a*). Dotted lines indicate the 95 % confidence intervals. The narrow confidence limits indicate high relevance and wide confidence limits indicate low relevance ranges of distribution. The relative density of data points is shown by the rug plot on the x-axis. The y-axis represents the spline function. Values of a predictor variable showing a positive effect on *Octopus cyanea* distribution were represented by all values above the zero-axis of the fitted GAM function.

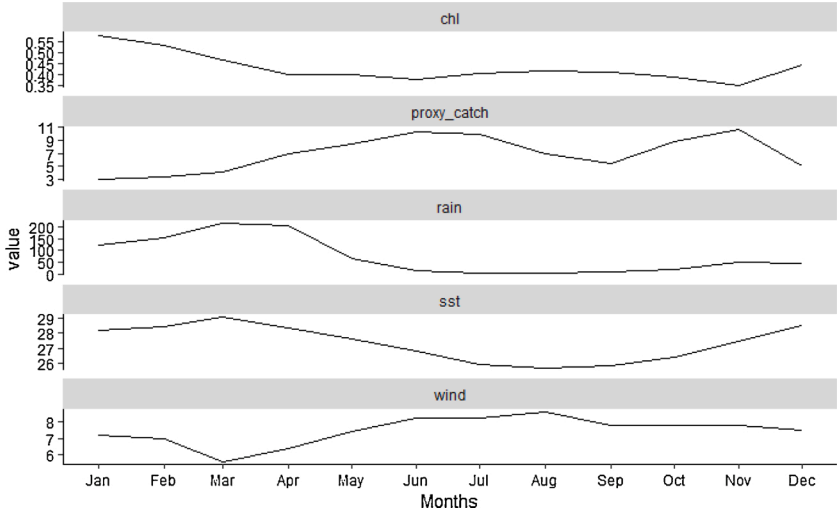


Fig. 11. The generalized additive model (GAM) derived effect of the alternative model predictor (wind, Chl-*a* and sea surface temperature; SST). Dotted lines indicate the 95 % confidence intervals. The narrow confidence limits indicate high relevance and wide confidence limits indicate low relevance ranges of distribution. The relative density of data points is shown by the rug plot on the x-axis. The y-axis represents the spline function. Values of a predictor variable showing a positive effect on *Octopus cyanea* distribution are represented by all values above the zero-axis of the fitted GAM function.

Benno: Supervision, Formal analysis, Methodology, Writing - review & editing. **Samwel M. Limbu:** Data curation, Writing - review & editing.

Declaration of Competing Interest

The authors declare that there are no conflicts of interest.

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