THE INFLUENCE OF ENVIRONMENTAL VARIABILITY ON THE CATCH OF CHOKKA, *LOLIGO REYNAUDII*, OFF THE COAST OF SOUTH AFRICA.

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ABSTRACT

Globally, cephalopod fisheries are being relied on more heavily due to the depletion of longer-lived teleost species. The South African chokka squid (*Loligo reynaudii*) fishery is a case in point. Although previously numerous squid were often caught as bycatch, the fishery has officially been in place since 1985. Since the inception of the chokka fishery in South Africa, several studies have investigated the relationship between environmental drivers and annual chokka squid catch, with varying degrees of success. Recently, in 2013, chokka squid catches hit a record low, prompting resurgence in the topic of the squid environment-catch relationship. This study was initiated in an attempt to provide a quantitative relationship between the chokka squid catch and environmental variability, and to build a predictive model that could be used in fisheries management strategies.

Historical data were obtained from various sources and included the mean and standard deviation in ocean bottom temperature; the mean and standard deviation in sea surface temperature; the maximum and minimum as well as the variation in wind speed; the mean, predominant and standard deviation in wind direction; the mean and standard deviation in atmospheric pressure; the mean chlorophyll concentration; the number of upwelling events; the hours of easterly winds blowing per day; and two large variation-in-climate indices, namely, the oceanic Niño index and the Antarctic Oscillation index. The monthly catch data were also provided.

These data were initially analysed for inter-annual and intra-annual cyclic trends and followed by analysis of the delay in response of catch to the environmental variables, anticipating some impact on the different stages of the chokka life cycle. These lagged data were incorporated into a negative binomial generalised linear model, as well as a generalised additive model, which revealed a strong relationship (r^2=0.707) between the catch and environmental variability. The inclusion of all the parameters was necessary; however, the mean bottom temperature and the standard deviation in sea surface temperature were the only parameters that had a significant effect on the catch.

These results were used to build a predictive model that indicated that, although the relationship was strong, the ability of the model to predict catch was weak, particularly from the year 2005 onwards.

Keywords: Catch, Cephalopod, Chokka, Environment, Fisheries, Management, Modelling, Squid.

TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

LIST OF ABBREVIATIONS

AGM	Annual General Meeting
AIC	Akaike's Information Criteria
BT	Bottom Temperature
Chl	Chlorophyll-a Concentration
DAFF	Department of Agriculture, Fisheries and Forestry
DEA	Department of Environmental Affairs
ENSO	El Nino Southern Oscillation
GAM	Generalised Additive Modelling
GLM	Generalised Linear Modelling
MCM	Marine and Coastal Management
MODAPS	MODIS Adaptive Processing System
MODIS	Moderate Resolution Imaging Spectroradiometer
MRSU	Mobile Remote Sensing Unit
NAO	North Atlantic Oscillation
NBGLM	Negative Binomial Generalised Linear Model

ONI	Oceanic Nino Index
P	Atmospheric Pressure
QQ	Quantile-Quantile
SAM	Southern Annular Mode
SASMIA	South African Squid Management and Industrial Association
SAWS	South African Weather Service
SST	Sea Surface Temperature
TAE	Total Allowable Effort
UTR	Underwater Temperature Recorder
WD	Wind Direction
WS	Wind Speed

CHAPTER 1: INTRODUCTION (BACKGROUND AND RESEARCH PROBLEM)

Cephalopod fisheries exist throughout the world and are well known for their high variability in catches. As finfish stocks have become depleted, the dependency on cephalopod fisheries has increased (Pierce and Boyle, 2003), resulting in global catches moving from some 500 000 tons in 1950 to 4 million tons in 2007 (Pierce et al., 2008). The high variability in both biomass and catches over annual and inter-annual time scales makes prediction a major challenge for these fisheries both from a management and an industrial point of view (Pierce et al., 2008).

1.1 Importance of the South African chokka squid fishery

The South African squid fishery is no exception in terms of catch and biomass variability. This fishery comprises one species, *Loligo reynaudii* d'Orbigny, locally referred to as chokka (Roberts and Sauer, 1994), and consequently is often referred to as the 'chokka squid'. Although the species is found on the west coast, at times as far north as southern Namibia (Roberts and Sauer, 1994), the main biomass is located on the Agulhas Bank abutting the province of the Eastern Cape (Figure 1; Cochrane et al. 2014). The fishery relies on foreign income from export of the product to Europe, and as such, is ranked as the fourth-most commercially important marine species in South Africa (Cochrane et al., 2014; Roel et al., 1998). The fishery uses handline-operated jigs to catch the squid from specialized vessels ranging between 11–20 m in length (Cochrane et al., 2014). As a result, this fishery is highly labour intensive, employing around 3 000 fishers (Cochrane et al., 2014) who are paid directly for their individual catch. It is estimated that 27 000 family and extended family members depend on these fishers, some of whom live in the small inland villages of the impoverished Eastern Cape (Cochrane et al., 2014). Income to both the fishery and the fishers tends to be higher during the summer months, November to April, as this is when spawning is most prevalent and catch effort greatest. Fluctuations in catches clearly have socio-economic implications (Agnew et al., 2002).

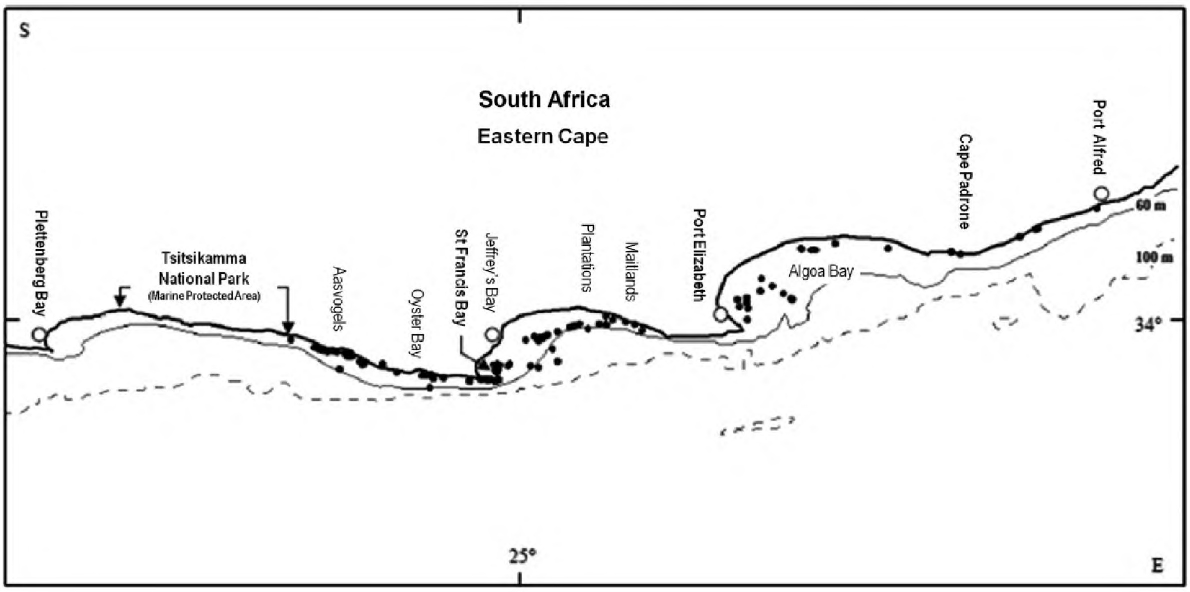

Figure 1: Location of the main fishing grounds of the chokka squid fishery (indicated by black dots), the 60 m contour line (solid line) and the 100 m contour line (dashed line) in South Africa, taken from Cochrane et al. (2014).

1.2 Management, catches and fishery collapse

The chokka fishery first started operating in 1985 using 6–7 m ski-boats, but has since progressed steadily to incorporate larger freezer vessels and ever-improved fishing methods (Cochrane et al., 2014). In 1987, entry into the fishery was closed, but catches increased due to these improvements in efficiency (Roel et al., 1998). Today the fishery consists of 138 freezer boats, each with some 22 fishers. The fleet largely targets inshore spawning aggregations at depths between 20 and 40 m (Figure 1), although in some seasons when spawning occurs, the fishery is located in deeper waters (60m) (Cochrane et al., 2014). As part of the management plan, the squid fishery usually has a closed season of four to six weeks over October and November (Roel et al., 1998; Sauer et al., 2010). In 1998, the first formal stock assessment was conducted, which revealed that the fishery was at high (approximately 90%) risk of collapsing and a reduction in effort of 33% was suggested (Cochrane et al., 2014). However, only a 10% reduction in effort was imposed because of pressure from the industry (Cochrane et al., 2014). In 2008, a new method of estimation indicated that the fishery was actually in a healthier state than previously estimated, and since then, a constant total allowable effort (TAE) has been maintained (Cochrane et al., 2014).

Chokka squid catches vary over daily, monthly and annual time frames (Roberts, 1998), but in general, the fishery is based on an annual catch ranging between 8 000 and 12 000 tons. With the exception of several years of lower catches in 1990, 1992, 1998, 2001 and 2006, the overall catch trend has increased steadily (Figure 2). However, first concerns about a change in this trend were voiced at the 2012 South African Squid Management and Industrial Association (SASMIA) annual general meeting (AGM): catches were 50–60% down from those in 2011 (Moodaley, 2012). Similar sentiments were expressed at subsequent AGMs with 2013 having the lowest catch ever recorded (Moodaley, 2013; Figure 2). In short, the South African chokka squid fishery had crashed. In an emergency response by both management and the industry, a voluntary, additional closed season was implemented in 2014 for the months of April, May and June to allow the stock to rebuild, with dire socio-economic implications for the region. Based on previous knowledge and experience, industry, fishery managers and scientists all felt that the cause of this crash was more likely to have been an environmentally driven event rather than overfishing and that it was imperative to investigate this premise. Ideally, a predictive means would forewarn the fishery of such environmentally driven events, allowing sufficient time to put mitigation measures in place. This thesis is the result of that suggestion and it aims to investigate the hypothesis that the crash in catches was environmentally linked.

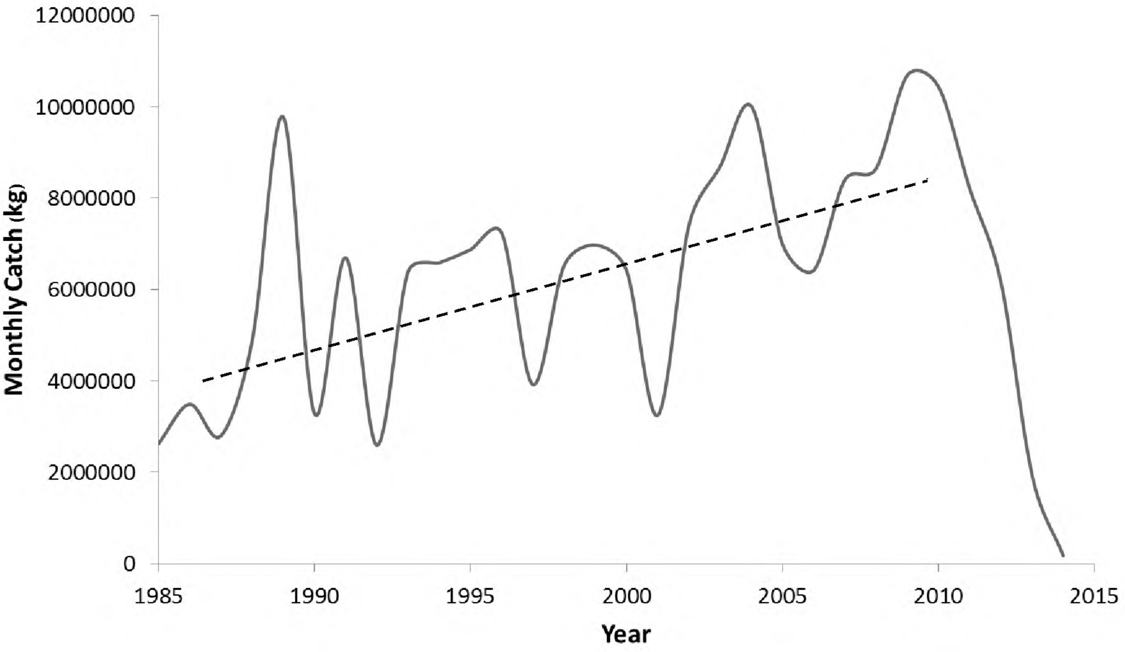

Figure 2: Annual catches of chokka squid observed since the establishment of the hand-jig fishery 1985–2014, displaying a linear average (dotted line) increase in catches from 1985–2010, followed by a rapid decline in catches.

CHAPTER 2: LITERATURE REVIEW

2.1 General view of the environment and fisheries

Numerous factors can affect the abundance of fishery resources, which in turn, create difficulties in managing the resource in a sustainable manner. These factors include, but are not limited to, natural inter-annual cycles, environmental influence on recruitment and the abundance of brood stock, and predator/prey interactions (Christensen, 1996).

It has been globally recognised that the marine environment undergoes cyclical changes in state and observed values (Collie et al., 2008), and these cyclical trends have significant effects on global fisheries catch (Jenkins, 2005; Markaida, 2006). This cyclic trend, together with the highly variable nature of the marine environment, makes it difficult to predict accurately future annual fisheries catch (Christensen, 1996). Furthermore, the ability of an organism to adapt to changes in the environment depends on the life span of the organism and the number of offspring produced (Pierce et al., 2008). Studies on the correlation of the environment with the catches of many commercially important species have been conducted extensively (e.g. Bigelow et al. 1999; Chen & Irvine 2001; Hedger et al. 2004; Zainuddin et al. 2008) with highly varied results, indicating that the relationships are complex and difficult to quantify. One of the main reasons for this difficulty is the high number of environmental factors that may or may not influence different species abundance. In many of these studies, Sea Surface Temperature (SST) is a very important factor in driving the spatial and temporal distribution of species, for example, Blue shark and swordfish (Bigelow et al. 1999). Species' responses to environmental factors have been found to vary over time, as in the case of *Sardinops sagax,* which exhibited a positive response in abundance to SST and a negative response to wind stress prior to the 1980s, but showed opposite responses from 1980 to 1988 (Shannon et al., 1988). Further correlations have been found between SST and several species of hake (*Merluccius* spp., r=-0.475 to -0.774), pilchards (*Sardinops ocellatus*, r=0.546 in Southern Benguela, r=-0.559 in Northern Benguela), anchovy (*Engraulis japonicus*, r=0.798) and Horse Mackerel (*Trachurus capensis*, r=0.335- Shannon et al. 1988). Furthermore, responses of cod, *Gadus morhua*, and haddock, *Melanogrammus aeglefinus,* were found to be strongly correlated (r^2=0.97 and r^2=0.79, respectively) to SST, salinity and depth (Hedger et al., 2004). SST, wind stress, salinity and depth are largely relied on as small-scale or regional indices which result in distributional shifts in species (Daskalov et al., 2003; Hedger et al., 2004). As the correlations vary across species and over time, it is clear that environmental influences on fishery resources are complex and need to be investigated as holistically as possible.

Larger scale, global climate indices, such as pressure cell oscillation indices and wind shifts, also influence the abundance of species and are thus important to consider. These indices indicate global changes in the environment and allow for a more holistic approach. Examples of these indices are the El Niño Southern Oscillation (ENSO) index and the North Atlantic Oscillation (NAO) index. ENSO and zonal westerly winds have been correlated (r=0.428 and r=0.309, respectively) with the King George whiting catches (Jenkins, 2005), indicating the influence of the large-scale environmental indices on the catches of the resource. Similar correlations between the NAO and fishery resource abundances also exist, for example, the positive influence of the NAO on the abundance of several jellyfish species, *Aurelia aurita* (r^2= 0.70), *Cyanea lamarckii* (r^2=0.74), and *Cyanea capillata* (r^2=0.53). The correlations between these indices and fishery catches indicate large-scale causes for fluctuations in the catches. Difficult aspects of modelling these environment-fishery relationships are, firstly, determining which environmental factor to choose, and secondly, linking the influences to different life cycle stages.

The effects of the environment on a fishery can manifest at varying ontogenetic stages, primarily because of the variation in vulnerability of each life stage to environmental stochascity (Pelletier et al., 2007). In marine systems, the variability in abundance of organisms in each cohort is linked to the spawner abundance as well as food availability (Durant et al., 2005). For example, the abundance of the Norwegian spring-spawning herring can be correlated with the variations in the mean annual temperature (Toresen and Østvedt, 2000). Further, the spawning stage in the growth of finfish, such as salmon (*Salmo salar*), is influenced by rising SST (Todd et al., 2008), and thus low abundances of the species can be expected in warmer waters. The larval stage of anchovy has also been negatively correlated with increased water turbulence in the coastal waters of Taiwan (Hsieh et al., 2009); results which were achieved using lagged data. Other studies have also used lagged data to investigate the correlations between the environment on different stages of the life cycle (Daskalov et al., 2003). The cephalopod is one class of organisms that has been thoroughly studied for correlations between the environment and abundances of different age classes.

2.2 Environmental relationships in cephalopod fisheries

Because of a short life cycle, high fecundity rate, high growth rate and high sensitivity to environmental variability, cephalopods are regarded as difficult to manage, but at the same time, good organisms to use to model environmental-abundance relationships (Basson et al., 1996; Pierce et al., 2008; Rodhouse, 2001). In an early review of studies carried out on the biology of cephalopods, Caddy (1983) suggested a possible link between cephalopod survival and the marine environment, prompting a number of studies that were conducted in the early 1990s in Europe and America, and subsequent, extensive studies of such links (see Pierce et al., 2008 for a full review).

Pecl and Jackson (2007) predicted that squid life histories would be flexible because of the link between the squid physiology and the environment. They observed that some *Loliginidae* species responded with increased growth rates in warm waters. They also found that temperature changes led to: (1) changes in productivity as a result of changes in optimal conditions for both predators and prey items; (2) changes in wind patterns and upwelling patterns; and (3) changes in turbidity due to changes in rainfall patterns as a result of higher evaporation rates (Pecl and Jackson, 2007). Cephalopods, like other marine fishery classes, have relationships of varying strengths to varying environmental parameters, and as such, the choice of parameters to be included in the model is key.

2.2.1 Relationships of cephalopod abundance and recruitment to localized parameters

The relationship between cephalopod life histories and temperature (particularly SST) has been regularly explored because temperature data and hypotheses surrounding a general warming climate are accessible (Pierce et al., 2008). Correlations have been found between cephalopod abundance indices and temperature (Agnew et al., 2002; Balguerias et al., 2002; Challier et al., 2005; Chen et al., 2006; Waluda et al., 2001), possibly due to the changes in oxygen affinity of the hemocyanin in the cephalopod's blood, which affects the metabolic rate of the organisms (Zielinski et al., 2001). The influence of temperature on the abundance of cephalopods is varied. For example, temperature displays a positive linear relationship to catches of *Octopus vulgaris* (Balguerias et al., 2002), small *Loligo forbesi* in French waters (Chen et al., 2006) and *Illex coindetti* (Lauria et al., 2016). However, catches of small *L. forbesi* in Scottish waters and *Loligo vulgaris* (Challier et al., 2005; Chen et al., 2006) are negatively correlated with temperature. The relationship also exhibits lagged relationships, attributed to the temperature affecting earlier life history stages of the cephalopod (Challier et al., 2005). This complex relationship is not unique and can be found when investigating other parameters such as wind activity.

Wind activity has been suggested as an important factor to consider when modelling and forecasting fisheries (Bakun and Csirke, 1998; Stergiou and Christou, 1996). Wind appears to be related to the changes in the survival and distribution of the ommastrephid paralarvae (Denis et al., 2002; Rocha et al., 1999) due to changes in the transport patterns of the paralarvae post hatching. Wind intensity also acts as a spawning trigger for *O. vulgaris* (Balguerias et al., 2002). Denis et al. (2002) found that wind speed and direction was a significant environmental parameter to be included when modelling the relationship to Loliginid species in the northeast Atlantic. They found that wind speeds between 2 and 4m.s^{-1} and southerly winds led to increased catches (Denis et al., 2002). Whilst wind has not been as extensively studied as temperature, it has proved to be an important factor to consider when modelling environment-abundance relationships. Wind can result in upwelling that, in turn, is related to cephalopod abundance.

Caused by the diversity of currents and predominant winds, upwelling waters occur throughout the oceans (Christensen, 1996). The intensity and frequency of upwelling events can display high levels of inter-annual and inter-temporal variability (Lefkaditou et al., 2008; Robinson et al., 2013). Upwelling systems influence the distribution, food availability and the spawning patterns of cephalopods. The Ommastrephid (also known as oceanic) squid are highly dependent on upwelling systems (Boyle, 1990); however, this dependence is not unique to this family. Jackson and Domeier (2003) found that the mantle length of the male *Loligo Opalescens* had a higher correlation coefficient to upwelling than the females. Similarly, Lefkaditou et al. (2008) found that the mature female *Illex coindetti* converged in areas where upwelling intensity was lower. This demonstrates that environment-abundance relationships are not only species or locality dependent but can also be sex-based. Upwelling is also a known spawning driver for *Octopus vulgaris,* with increased upwelling strength stimulating spawning and the subsequent decrease in upwelling stimulating the hatching (Balguerias et al., 2002). Recent studies conclude that cephalopods display distribution patterns which suggest a preference for upwelling systems (Lauria et al., 2016). It can thus be concluded that upwelling influences the distribution, spawning patterns and catches of cephalopods. Upwelled waters are nutrient rich and thus result in high levels of productivity (Jackson and Domeier, 2003), leading to increased food availability and the potential for increased survival. Furthermore, increased productivity could result in increased growth rates which would likely drive an increase in the cephalopod biomass.

Chlorophyll-*a* concentrations provide an indication of the primary productivity of an area (Keller et al., 2014; Robinson et al., 2013) and the primary productivity of a system provides an indication of the predicted food availability of that system. Therefore, a positive relationship between cephalopods and chlorophyll-*a* concentration is likely, as this will mean increased food availability, which in principle, leads to increased cephalopod abundance. This is evident in the *Dosidicus gigas* fishery (Robinson et al., 2013), the *Todaropsis eblanae* fishery and the *Eledone cirrhosa* fishery (Lauria et al., 2016). A similar trend was seen in the mature *I. coindetii* in the eastern Ionian Sea (Lefkaditou et al., 2008). However, Lauria et al. (2016) found a negative curvilinear relationship for *Eledone moschata,* but Keller et al.

(2014) found and no relationship between *Sepia officinalis* and chlorophyll-*a* concentrations. Although different responses to chlorophyll-*a* concentrations by different cephalopod species have been observed, it has been suggested that these responses are a result of distributional shifts rather than abundance shifts (Puerta et al., 2014). These complex responses highlight the difficulties associated with using small-scale environmental interactions to develop fishery management strategies.

2.2.2 Relationship of cephalopod abundance and recruitment to large-scale indices

All of the previously mentioned investigations into the cephalopod abundance-environment relationships focused on local environmental data such as temperature (Balguerias et al., 2002; Jackson and Domeier, 2003; Leporati et al., 2007), wind direction (Denis et al., 2002) and speed (Stergiou and Christou, 1996). Research has also included large-scale climatic indices such as the El Niño index (Jackson and Domeier, 2003; Markaida, 2006; Zeidberg et al., 2004) and the pressure cell oscillations indices such as the NAO index (Challier et al., 2005; Dawe et al., 2000; Zuur and Pierce, 2004). The incorporation of these indices into the investigation of relationships between cephalopods and environmental parameters is very important (Pierce et al., 2008). These environmental parameters affect different cephalopod species differently because of the difference in biology and ecology of the organisms (Pierce et al., 2008).

The NAO index is one of several changes in the location of pressure cells which was described in the 1920s (Rogers, 1984). It is often used because of its availability and its ability to provide a broad outline of oceanographic conditions in the North East Atlantic (Stenseth et al., 2003). The NAO index (and those oscillation indices located elsewhere) incorporates precipitation, air temperature and wind speed over a large area (Puerta et al., 2014) thus these indices are important to include when modelling environment-abundance relationships. The winter NAO has been positively correlated to the abundance of *L. forbesi* in many studies (Chen et al., 2006; Pierce and Boyle, 2003; Sims et al., 2001); however, in other studies it was found to be unrelated (Challier et al., 2005). The NAO was also found to be unrelated to the abundance of *I. coindetii* and *E. cirrhosa* (Puerta et al., 2014). The importance of including large-scale oscillations in studies of relationships between environmental variability and cephalopods is thus still unclear; including this information should be used as a conservative approach. Other large-scale climatic events that could influence the abundance of cephalopod species are La Niña and El Niño events.

El Niño and La Niña events refer to the respective warming and cooling of the Pacific Ocean (Yu et al., 2011). The El Niño Southern Oscillation (ENSO) is the change in the location of high pressure cells which are linked to the formation of El Niño events (Stenseth et al., 2003). The phenomenon causes global changes in weather and is an important environmental parameter to include in models. Jackson & Domeier (2003) studied the influence of the strong 1997–1998 El Niño and the strong 1998–1999 La Niña events on *Loligo opalescens* growth rates. They found that the species experienced slower growth rates, and thus remained smaller during the El Niño events, than those squid growing during La Niña events (Jackson and Domeier, 2003)due to heightened productivity levels of the ocean during La Niña events (Jackson and Domeier, 2003). In the Gulf of California, Mexico, a large, giant-squid (*Dosidicus gigas*) fishery situated in a region of highly variable upwelling (Robinson et al., 2013) is managed via the total allowable effort (TAE) method, but has no closed season (Robinson et al., 2013). The giant-squid fishery declined from 36 000 tons to 3 000 tons during the 1997–1998 El Niño (Markaida, 2006), believed to be primarily due to a decrease in upwelling events (Robinson et al., 2013). The same trend was observed in the California squid market, *Loligo opalescens*, where the annual fisheries' landings were ten times lower than expected (Ish et al., 2004). It can thus be inferred that El Niño and La Niña events influence the abundance of cephalopods and are important to include in environmental studies.

Studies across the globe have highlighted the complex responses of cephalopods to various environmental parameters. These responses have proved to be gender, species and distribution dependent. As cephalopods live in a dynamic environment, there are other interactions which may interfere with the relationship between environment and species, such as predators, prey abundances and parasite presence (Pierce et al., 2008). The complex relationships found globally have been shown to hold true for the South African chokka.

2.3 Environmental variation and chokka recruitment

Chokka is a short-lived species with a life span ranging between one and two years (Sauer et al., 1997). This short life span results in chokka being highly susceptible to environmental variability (Roberts and Sauer, 1994). Several investigations have attempted to determine correlations between environment parameters and catch with no attempt at explaining the underlying causes for the relationship; this indirect method will henceforth be referred to as the "black box approach" in this thesis, an example of which can be found in Schon et al. (2002). Other studies have tried to find direct correlations between local environmental parameters and a life stage such as hatching (Oosthuizen et al., 2002), and in some cases, changes in spawning behaviour using electronic tagging methods on male and female squid (Downey et al., 2010).

The relationship between several aspects of the chokka life history and the environment has been extensively studied. The key environmental parameters that have been studied for the longest period include SST and bottom temperature. Investigations into the influence of environmental variables on squid populations have been conducted since 1990 (Augustyn, 1990). Augustyn (1990) observed that high squid catches occurred when the water was warmer, although he found some anomalies. This early work was followed by an investigation into the influence of sea temperature and wind on catches of chokka (Sauer et al., 1991) which found that a multiple linear regression analysis indicated that sea temperature and wind direction explained fluctuations in catches convincingly ($p<0.001$ and $p=0.0085$, respectively). However, their data set was small because of the limited number of operative years of the fishery.

Further studies describe increased chokka concentrations in warmer, well-oxygenated waters (Roberts and Sauer, 1994). They also describe low spawning occurrences which coincide with conditions of low visibility (Roberts and Sauer, 1994). The relationship between the successful spawning of the chokka and the water clarity was defined in a study on the squid's "nuptial dance" during which the chokka flash their colours to communicate and attract a mate (Sauer et al., 1997) highlightingthe importance of low turbidity in the spawning season. Similarly, this dependence on low turbidity waters has been observed in global cephalopod species such as *Doryteuthis* (*Loligo*) *pealeii* (Shashar and Hanlon, 2013), *O. vulgaris* and *S. officinalis* (Sobrino et al., 2002).

The first steps towards a quantitative environment-abundance relationship took place in 1998 (Roberts, 1998). This study found that upwelling events correspond to the formation of spawning aggregations (Roberts, 1998); however, the model was not complete and these preliminary studies could lead on to further works. Around the same time, in 1997–1998, an intense El Niño event impacted many regions of the world, leading to an investigation into the influence of this event on squid catches (Roberts, 1999). This study found that the ENSO had little influence on the squid catches due to a SST warming anomaly which disrupted the expected winds (Roberts, 1999), indicating the influence of interactions of parameters. Roberts' study (1999) led on to the first quantified model. Schon (2000) undertook the first holistic approach in quantifying the environment-chokka abundance relationship. Schon (2000) investigated the influence of water temperature, turbidity, salinity, water depth, wind velocity, wind direction, swell height, nature of the seabed, current speed and current direction on chokka catch rates. The study revealed several multiple correlation relationships. Significant negative relationships were found for abundance: depth, first-last-quarter of the lunar cycle, SST, wind speed and turbidity (Schon, 2000). Significant positive relationships for abundance were also found: season, new-full moon and wind direction (Schon, 2000). However, a multiple regression analysis only explained 32% of the variability in abundance and it was not possible to produce a predictive model (Schon, 2000), showing once again the complexity of the investigated relationship.

In studies from 2002 to date, the relationship between environmental variables and the early life stages of the chokka (spawning patterns to hatching to paralarval survival) has been the key focus in South Africa. An initial comparison of the chokka fishery to the anchovy fishery confirmed that chokka are susceptible to the environment and have adapted to spawn large numbers of eggs to buffer these influences (Sauer et al., 2002). A direct investigation was conducted into the influence of temperature on the healthy development and hatching of the chokka paralarvae (Oosthuizen et al., 2002). Eggs incubated in a lab at different temperatures exposed high abnormalities at temperatures below 12°C and above 15°C (Oosthuizen et al., 2002). As this complex relationship was still too refined, further studies were conducted. Roberts and Van Den Berg (2002) investigated a new, potentially influential environmental parameter: current. They found that current was particularly important for the transportation of paralarvae because currents can carry the paralarvae offshore and thus have a very significant influence on chokka abundances (Roberts and Van Den Berg, 2002). Roberts

(2005) explored the relationship between paralarvae abundance and survival, and bottom temperature, dissolved oxygen, chlorophyll and copepod abundance; he showed chokka have a preference for spawning sites where the bottom temperatures and dissolved oxygen had proved to lead to optimal hatching (Roberts, 2005). Further work by Oosthuizen and Roberts (2009) indicated that, although previously the optimal temperature range for spawning had been found to be between 12°C–17°C in laboratory trials, *in situ,* the optimal temperature range for chokka egg development can occur during temperature peaks of 10°C–13°C. Another direct study conducted in 2010 to investigate the effects of temperature on chokka spawning behaviour (Downey et al., 2010) found that, while upwelling acts as a spawning trigger for chokka, gradual temperature changes do not affect spawning aggregations (Downey et al., 2010). Further work published in 2010 focused on the influence of currents on the transport of chokka paralarvae (Hancke, 2010). Hancke (2010) found that the retention of neutrally buoyant particles, which simulated squid paralarvae, depended on where in the current the paralarvae where located: those that were in the eastward-flowing Tsitsikamma current would be swept offshore, suggesting that the position of the currents at the time of hatching is critical to the survival and recruitment into the fishery. This hypothesis was supported by Downey-Breedt et al. (2016) who found that the survival of paralarvae and the subsequent successful recruitment into the fishery depended on the timing and location of hatching. These studies highlight the importance of current, dissolved oxygen, temperature and upwelling in the early stages of the squid life cycle.

The relationship between chokka abundance and various environmental parameters has thus been extensively studied from 1990 to 2016 and the studies continuously highlight and contribute evidence to the complexity of the relationship. Although plenty of evidence exists, and many different statistical techniques have been employed, a conclusive quantitative model has yet to be defined.

2.4 Modelling approach

There are two critical steps in modelling the relationship between environmental parameters and fishery abundance: firstly, select the correct parameters; secondly, select the correct modelling approach. Since the earliest studies, statistical models have evolved from establishing and defining a linear relationship between individual parameters, to multivariate linear models which allow for non-normality in the predictor variables, such as generalised linear models (GLM) (Bellido et al., 2001). These have further evolved to use non-linear models which allow for non-normality, non-linearity and heteroscedasticity of the predictor variables, such as Generalised Additive Models (GAM) (Bellido et al., 2001). These complex models have been further used to attempt to construct models from which future catches can be predicted (predictor models) (Agnew et al., 2002). The aims of the predictor models are to use environmental data to predict future catches, enabling more sustainable fisheries. Many of the earlier studies with smaller datasets found a strong linear correlation between environmental parameters and cephalopod population abundances (Agnew et al., 2002). These relationships are expected to deteriorate with an increased data set size caused by increased observation error due to observations being estimations based on a sample (Solow, 1998). Initial use of GAM provided important information on the non-linearity of the relationship between SST and the landing of *L. forbesi* (Bellido et al., 2001). This study saw the potential use of GAM as a predictive tool for fishery catches based on SST (Bellido et al., 2001). Further work used GAM to define the relationship between the abundance of *O. vulgaris* and the spatial and temporal distribution and the SST (Balguerias et al., 2002). This study once again highlighted the necessity of including more environmental parameters (Balguerias et al., 2002). GAM has been used extensively and has proved successful numerous times. In Japan, a GAM-based analysis displayed the strength of the GAM in accounting for distributional changes in abundance to environmental parameters of krill, Japanese anchovy, and sand lance (Murase et al., 2009). However, Murase et al. (2009) highlights the need for an improved GAM model (by selecting alternative or additional environmental drivers) to predict biomass (Murase et al., 2009).

2.5 Research problem

The above-mentioned South African studies have mostly investigated the short-term (daily and monthly) influence of the environment on chokka squid reproduction, spawning and distribution. However, there have been limited studies that have looked at the long-term (over 10 years) correlations between environmental drivers and the variability of chokka squid. While both the direct and the indirect approaches used in South Africa provide encouraging evidence of the role of the environment on chokka squid catch, there is presently no model that can be used to either forecast or explain poor catch. Producing a quantitative model of the role of the environment in catch would assist management strategies in the future.

This study investigates the influence of ocean and atmospheric environmental variability on chokka squid biomass as measured by the fishery recorded catches. The environmental variables used in the study include: bottom temperature (BT), sea surface temperature (SST), wind speed (WS), wind direction (WD), atmospheric pressure, climatic variables, the number of upwelling events and chlorophyll-*a* concentration. These variables were incorporated into the study because of universal evidence of changes in cephalopod abundance due to temperature, upwelling (Sauer et al., 2010), turbidity (Roberts, 1998), food availability (Robinson et al., 2013), and climate events (Markaida, 2006; Roberts, 1999).

The overall key questions are:

Is there evidence of a natural cyclic trend in the catch variability?

Is there a lagged effect on the monthly catch of each environmental variable?

Is there a strong correlation between catch and ocean bottom temperature, sea surface temperature, wind speed and direction, atmospheric pressure, Oceanic Niño Index, Antarctic Oscillation Index, the number of upwelling events and the chlorophyll-*a* concentration?

Can a predictive model be constructed in order to provide better future management plans?

Can the results explain the recent decline in chokka catch?

CHAPTER 3: DESCRIPTION OF THE STUDY AREA, METHODS AND MATERIALS

3.1 Study area

3.1.1 Spawning grounds

Much research has been conducted on the biology and reproduction of chokka squid (Augustyn and Roel, 1998; Downey et al., 2010; Melo and Sauer, 1999; Roberts and Sauer, 1994; Sauer et al., 1991; Schon et al., 2002). These studies report that the spawning grounds of chokka squid are primarily located off the southern coast of South Africa along the inshore waters found on the Agulhas Bank at depths of 18 to 50 m (Figure 3, and also Roberts & Sauer, 1994). Spawning extends from the Tsitsikamma Coastal National Park (TCNP) to Port

Alfred (Augustyn and Roel, 1998) and coincides with upwelling sites along this part of the coast (Roberts and Sauer, 1994).

TCNP is a pristine environment and is South Africa's oldest Marine Protected Area (MPA), influenced by highly varied currents that are particularly important for the distribution of the chokka squid paralarvae (Hancke, 2010).

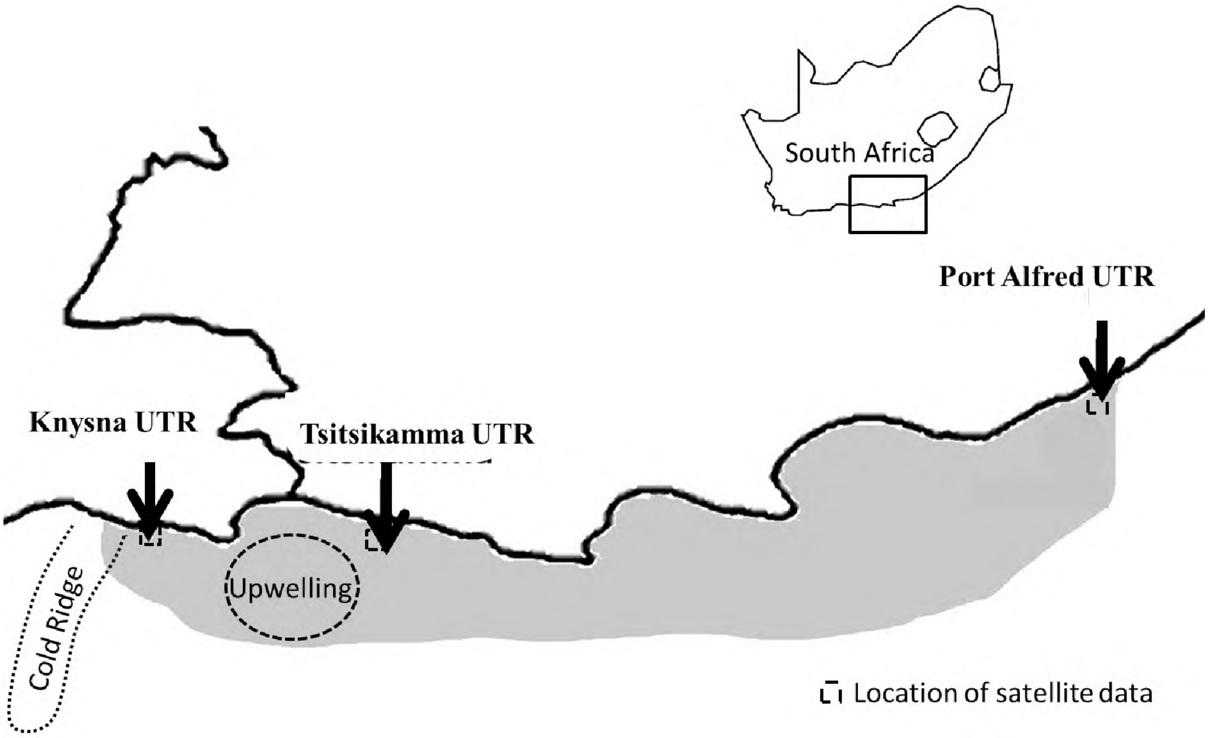

Figure 3: Location of the inshore spawning grounds of the chokka squid (grey area), and the locations from which Underwater Temperature Recorder data (indicated by black arrows) and satellite data (indicated by dashed squares) were collected. The location of the Tsitsikamma upwelling cell and the cold ridge are also indicated.

3.1.2 Oceanography of study area

The Agulhas Bank region is influenced by the fast-flowing, warm Agulhas Current on the eastern and southern sides, and the slower, cooler Benguela Current on the Atlantic Ocean slope (Hancke, 2010). At the southernmost tip of the Agulhas Bank, the Agulhas Current undergoes retroflection. Shoreward boundary phenomena such as meanders and the iconic

Natal Pulse cause warm filaments and plumes of the Agulhas Current to regularly sweep the Eastern Agulhas Bank, adding to the high variability of the environment here (Hancke, 2010). The TCNP has been observed to be affected by a narrow, largely eastward flowing jet current that is vital for the distribution of larvae and paralarvae of numerous marine species (Hancke, 2010). This current, locally referred to as the Tsitsikamma Jet, has been observed to flow both in an eastward and westward direction, with the westward current being the most beneficial for transporting chokka squid paralarvae as this is the direction of a cold ridge, an upward doming of the thermocline on the central part of the Agulhas Bank where planktonic food is most abundant (Hancke, 2010). Wind-driven intermittent coastal upwelling occurs between Knysna and Tsitsikamma and is most active during summer (Location on Figure 3). This upwelling supports high densities of copepods (paralarval food) (Augustyn et al., 1992; Roberts & Van Den Berg, 2002), as does the cold ridge which is shown to support the highest concentrations of zooplankton (Roberts, 2005).

3.2 Catch data

The South African Department of Agriculture, Forestry and Fisheries (DAFF) provided the total monthly chokka squid catch data from January 1972 to March 2014 across the entire spawning grounds. The catch consists of the commercial trawl bycatch and the hand-held jig catch. The jig catch data span January 1985 to March 2014. This study incorporated only the targeted jig fishery data as the trawl data was incomplete at the time of data collection. Although DAFF is the official repository for fisheries catch data in South Africa, Bergh (2013) revealed numerous irregularities and discrepancies between fisheries catch data and values recorded by the Marine and Coastal Management (MCM) data for research purposes. The MCM data were inherited by DAFF when MCM was dissolved. The biomass model outputs have since been calibrated and corrected using an updated Bayesian assessment model (Bergh, 2013). This study assumed that the catch represents the abundance of squid.

3.3 Environmental data

The environmental parameters considered in this study were *ocean bottom temperature* (BT), *atmospheric pressure* (P), *wind speed* (WS), *wind direction* (WD), *sea surface temperature* (SST) and *chlorophyll-a* concentration (Chl). A monthly mean standard deviation was used in several of the parameters (BT, P, WS, WD, and SST) as this provides information about the monthly variability of the weather. Variability is potentially important as it provides a more accurate description of change in the environment and is shown to have a profound effect on the relationship between environmental and biological communities (Katz and Brown, 1992). Environmental variables used in this study were collected at Port Alfred, Tsitsikamma and the Knysna lagoon (Figure 3). These daily values from each location were averaged over 30 days to reflect general patterns across habitats of the chokka squid distribution range over a month.

3.3.1 Ocean bottom temperature data

Bottom temperature data were obtained from the Department of Environmental Affairs (DEA) based on *Starmon* underwater temperature recorders (UTR). These temperature loggers are situated at depths ranging between 2 m and 10 m and are attached to concrete mooring blocks. The data were taken from UTRs positioned in three different localities (Knysna, Tsitsikamma and Port Alfred, Figure 3) that have been recording data for varying time periods since 1991. Knysna has *in situ* data available since 1985, whilst Tsitsikamma has data available since June 1991, and Port Alfred data is available since October 1995. The Knysna *in situ* data were collected using a bucket and a mercury thermometer, but this method was replaced with a UTR deployed in March 1995. UTR's have a 10-year battery life, during which they can record 350 000 measurements at an accuracy of 0.05°C across a range of temperatures from -2°C to 40°C. The UTR recorders have a time accuracy of one min/month, and the data can be retained for 25 years. These data recorders were set to take hourly temperature measurements.

Monthly mean temperatures were calculated from the available hourly data. Comparison of early Knysna temperature recordings to those obtained from UTR recordings showed negligible differences for periods where these data overlapped (Roberts, pers. comm.).

The bottom temperature data display high variability in the summer months (October-April) and low variability in winter months (May- September), as shown for example, in Figure 4. Sudden drops in temperature — seen in January, February and March — indicate upwelling events. For this study a difference of 2°C in mean temperature between two days was taken as an upwelling event (from start to finish). The monthly average number of upwelling events across the three localities was used because the chokka catch data had a low spatial resolution. This lack of high-resolution spatial data meant that the chokka biomass could have been correlated to any of the three localities.

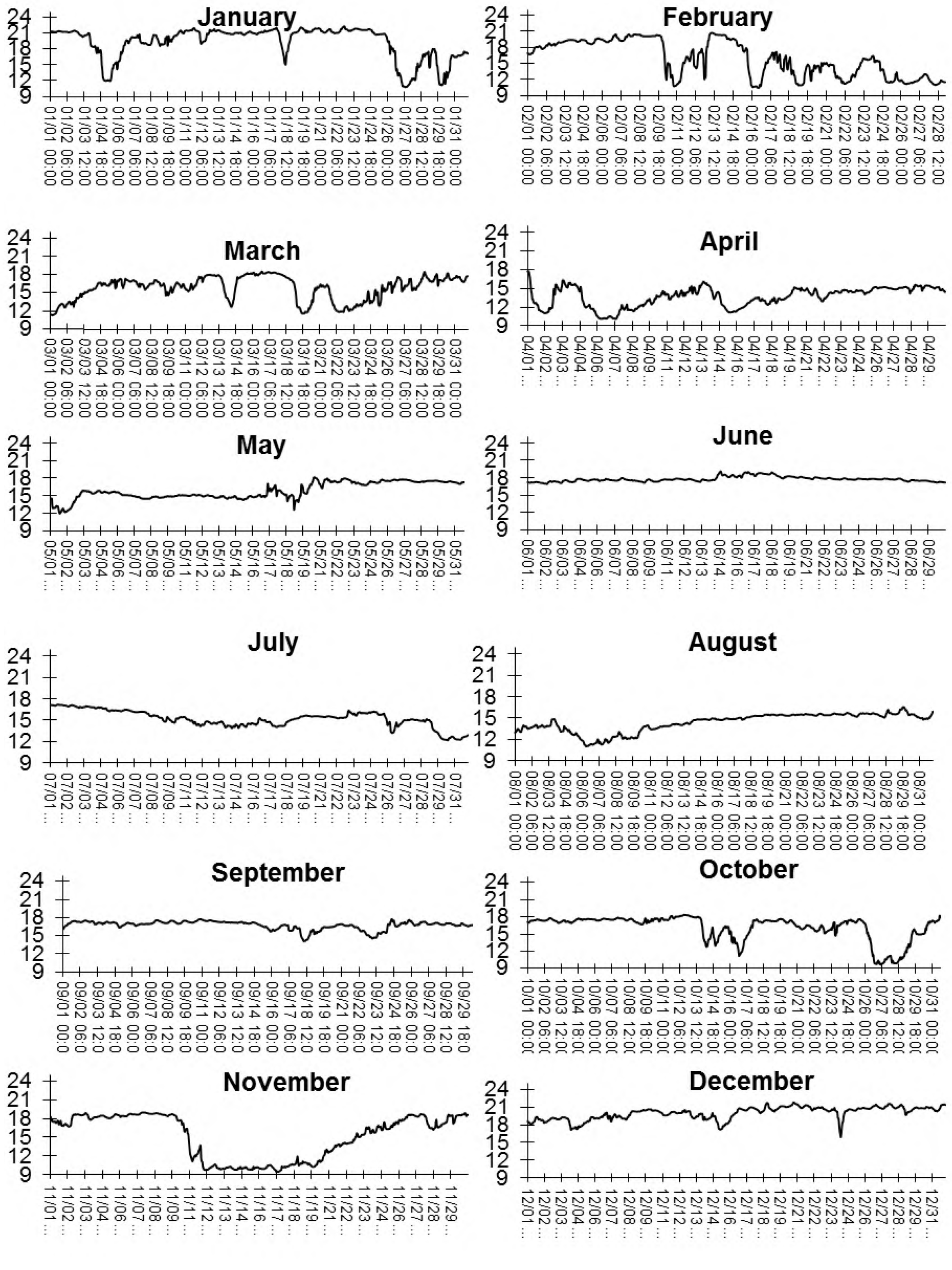

Figure 4: Hourly temperature data from Underwater Temperature Recorders (UTR) deployed in the Tsitsikamma Coastal Marine Park in 2001. Note the stability of the data in winter months (May-September).

3.3.2 Wind and atmospheric pressure data

Although Denis et al. (2002) did not find that wind speed and direction had a significant effect on squid abundance, these variables, together with atmospheric pressure data, were included in the analysis because they were considered to be a significant driver of upwelling events in other studies (Downey et al., 2010). Hourly wind speed, wind direction and atmospheric pressure data were obtained from the South African Weather Service (SAWS), and were all collated into mean monthly data. Data were available from 1972 for both Port Elizabeth and Cape St Francis weather stations, and from 1996 for the Knysna weather station. These three locations were used to provide environmental parameters that span the south coast of South Africa.

Daily maximum and minimum wind speed were calculated into monthly means for each location. For each location, daily mode of wind direction was calculated by selecting the wind direction that occurred most often and the monthly mean of the daily modes was calculated to provide the predominant monthly wind direction. The mean monthly total easterlies per hour were also calculated for each location.

3.3.3 Climate variables

3.3.3.1 Oceanic Niño Index

The Oceanic Niño Index (ONI) is the daily anomaly from mean SST (NOAA 2015). These data, which were obtained from www.cpc.ncep.noaa.gov, provide information on the occurrences of El Niño and La Niña events. These data are based on 30-year means from which five-year deviations are estimated in order to minimise the effects of inter-annual ENSO events (NOAA 2015). This allows El Niño and La Niña events to be compared to current climate instead of historical climates. ENSO data, in the form of ONI data, were used, based on the need to include a broader analysis of environmental variability, previously found to have effects on fisheries worldwide (Stenseth et al., 2003). An El Niño event is signified by a mean temperature higher than 0.5°C for five months (Yu et al., 2011). The data in Figure 5 include the threshold of ONI that signifies the occurrence of an El Niño event.

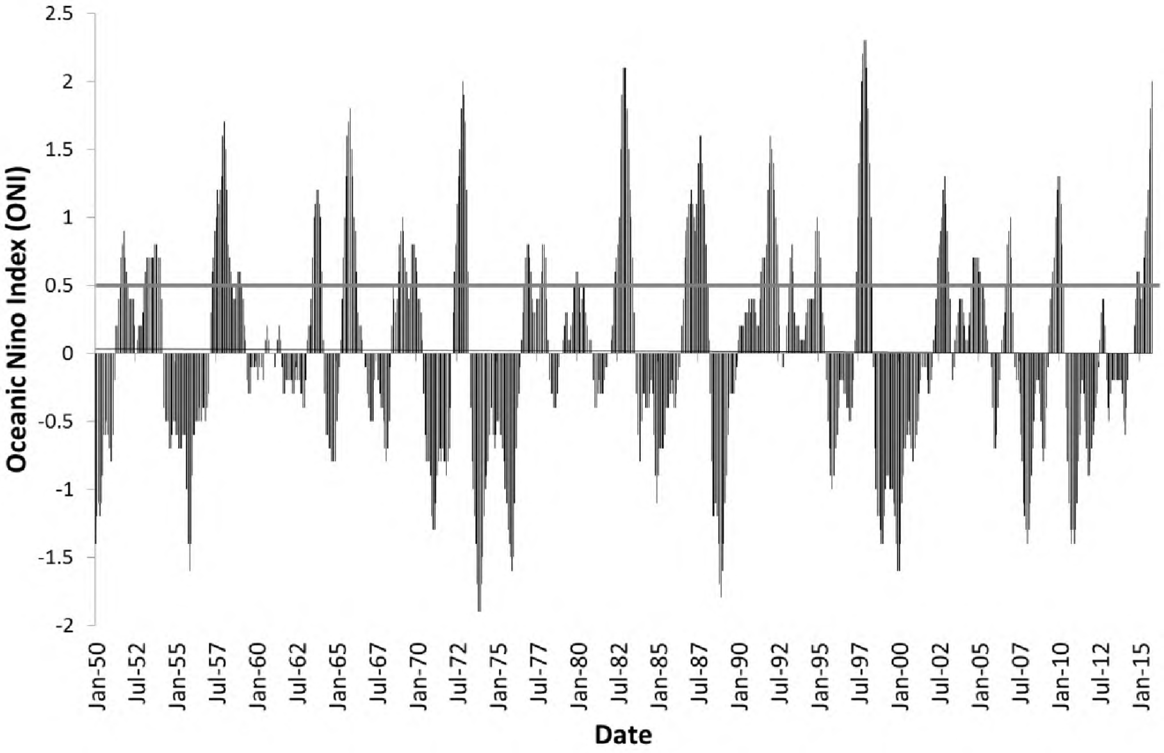

Figure 5: The Oceanic Niño Index (ONI) 1950 to October 2015; the grey line depicts the threshold above which the ONI needs to be for five months in order for an El Niño event to be declared.

3.3.3.2 Antarctic Oscillation Index

The Antarctic Oscillation Index (AAO), also known as the Southern Annular Mode (SAM), refers to the variability in circulation in the southern hemisphere (Marshall, 2003; Stenseth et al., 2003). The AAO indicates a large-scale latitudinal shift in a high-pressure cell between the mid-latitude and high-latitude surface pressures (Gong and Wang, 1999). Furthermore, the AAO and is correlated with precipitation (Gong and Wang, 1999). These data were obtained from http://www.cpc.ncep.noaa.gov and are calculated by taking the mean daily 700 mb height anomalies poleward of 20°S. These data were standardised in order to compensate for the high variability in the cold season (NOAA 2005). The data show a fluctuation in the AAO, indicating a regular change between negative and positive values (Figure 6). A positive SAM index results in the westerly belt of winds shifting southwards and a decrease in rainfall (Marshall, 2003), whereas a negative sign indicates a northward shift in the belt of westerly winds (Stenseth et al., 2003).

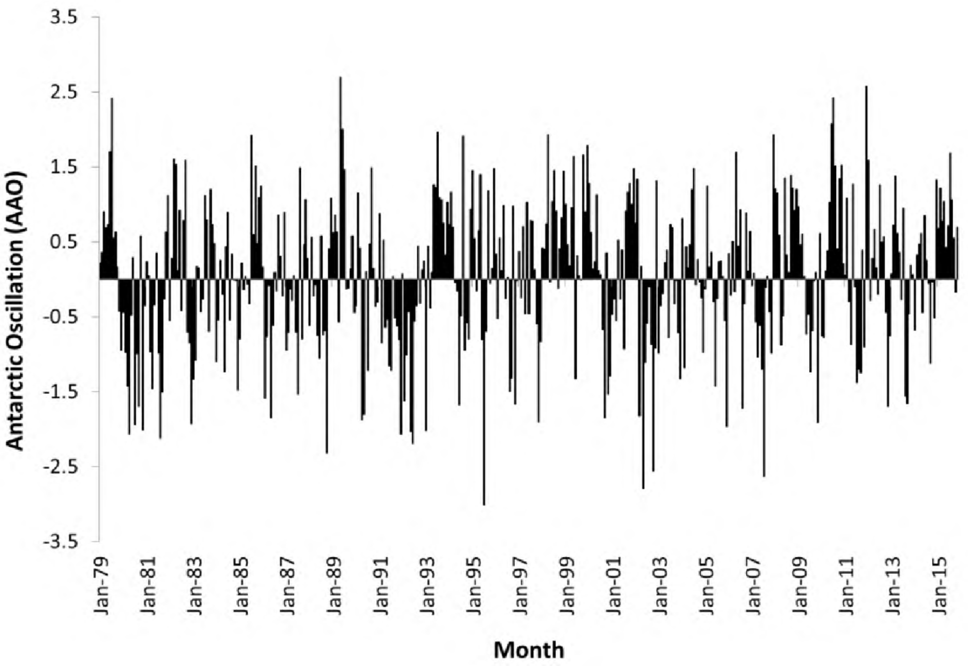

Figure 6: The monthly observed Antarctic Oscillation from January 1979 to November 2015.

3.3.4 Satellite data

The sea surface temperature (SST) and chlorophyll-*a* data were obtained from the Marine Remote Sensing Unit (MRSU- www.afro-sea.org.za), which provides marine remote sensing data for Africa. The SST and chlorophyll-*a* data used in this study were for the southern region of South Africa with the coordinate grid running from 27°S, 27°E to 37°S, 40°E.

3.3.4.1 Sea surface temperature (SST)

The SST data were based on infrared readings from the Moderate Resolution Imaging Spectroradiometer (MODIS) satellite ocean data. These data were pre-processed by NASA to a Level 2 product to remove the effects of absorption by the atmosphere using the MODIS Adaptive Processing System (MODAPS).

Daily SST data were taken for three locations (Figure 3): Knysna (-34.09, 23.06), Tsitsikamma (-34.02, 23.9) and Port Alfred (-33.6, 26.9). For each location, the monthly mean and standard deviation of these data were computed, and the mean of these means and deviations were taken across all three locations.

3.3.4.2 Sub-surface Chlorophyll-a concentration

Chlorophyll data provide information on productivity, and have been used in analytical models in order to facilitate management decisions in many freshwater bodies (Pierce and Guerra, 1994). The chlorophyll data were obtained using MODIS. The MODIS Chlorophyll-*a* Pigment Concentration data are based on a coefficient of absorption by phytoplankton at 675 nm (NASA, 2014). The daily Chlorophyll-*a* data were obtained from three locations (Figure 3): Knysna (-34.09, 23.06), Tsitsikamma (-34.02, 23.9), and Port Alfred (-33.6, 26.9), and were averaged to obtain monthly means.

3.4 Modelling approach

All statistical analyses and modelling approaches were conducted using the statistical program *R* (R Core Team, 2015), using the packages *mgcv* (Wood, 2011, 2004, 2000), *ggplot2* (Wickham, 2009), *car* (Fox and Weisberg, 2010), *lattice* (Sarkar, 2008), *nlme* (Pinheiro et al., 2015), *gstat* (Pebesma, 2004), *MASS* (Venables and Ripley, 2002), and *MuMIn* (Bartón, 2015). The statistical and modelling methods outlined in this thesis followed Clark (2013) for Generalised Additive Models in *R*. It was assumed that the reported squid catch was directly correlated to the abundance of squid in the coastal areas. Preliminary analysis of the data was carried out using a simple histogram, which indicated a Poisson distribution in catch data.

3.4.1 Monthly and annual trends in catch.

Temporal patterns in catch were investigated using a GLM with Poisson distribution. Due to over-dispersion, negative binomial GLMs were used. A box and whisker plot identified outliers. GAMs were used to explore the predictive trends of the catch over time and GAM plots with a smoother trend line were used to visualise the trends. Chi-squared (χ^2) goodness-of-fit tests were conducted in order to test the validity of using GAMs with splines, GAMs without splines, and GLMs.

GAMs are useful statistical tools because they have few assumptions compared to linear parametric tests (Guisan et al., 2002). A GAM analysis describes the relationship between the mean of the dependent variable and a "smoothed" function of the independent variable(s) (Guisan et al., 2002). An advantage of GAM analyses is the ability to investigate the data for relationships rather than force the data to fit a predetermined model (Guisan et al., 2002). This means that these models can accommodate data which is non-linear and explain relationships overlooked by linear models (Guisan et al., 2002).

3.4.2 Description of environmental parameter data

The environment is dynamic and daily trends are unpredictable. However, annual trends in the data can provide information of general changes in the weather patterns. To describe these trends, each environmental parameter was plotted against year using a GAM smoother.

3.4.3 Parameter selection

A negative binomial generalised linear model (NBGLM) was conducted on the complete data set in order to identify the set of environmental factors that have significant $(P<0.05)$ relationships with the total monthly squid catch. A full model was constructed using the following formula:

$$\begin{aligned} &glm.nb(Catch \sim AveBT + StdDevBT + StdDevWS + AveWD + StdDevWD \\ &+ AveP + StdDevP + ONI + MaxWS + MinWS + ModeWD + AAO \\ &+ Chl + AveSST + StdDevSST + EpH + upw), \end{aligned}$$

where *Ave* represents the mean, *StdDev* represents the standard deviation, *BT* represents ocean bottom temperature, *WS* represents the wind speed, *WD* symbolises the wind direction, *P* is the atmospheric pressure, *ONI* is the oceanic Niño Index, *Max* is the maximum, *Min* is the minimum, *ModeWD* is the predominant Wind Direction, *AAO* is the Antarctic Oscillation Index, *Chl* is the mean chlorophyll content, *SST* is the sea surface temperature, *EpH* is the monthly mean hours of easterly winds blowing, and *upw* is the number of upwelling events per month.

The most optimal model was selected from the full model using multi-model inference criteria based on the lowest AIC values (Burnham and Anderson, 2003). Selected variables from the parsimonious model were then plotted against the monthly catch.

3.4.4 The effects of monthly lags on catch

Each of the environmental data set was modified to indicate a lag ranging from no lag to a lag of 13 months. In this study, a lag is defined as a delayed response of the catch to the environmental variable. This is important, as each environmental parameter may not affect the specific catch within that month. These lags provide information about the effects of environmental parameters at different stages of the squid life cycle, with shorter lags (0 to 1 and 13 months) indicating the effects of the environmental parameters on the timing of spawning; mid-length lags (2 months to 3 months) indicating the effects of the parameters on the survival of paralarval stages, and longer lags (4 months to 12 months) indicating the effects of these parameters on earlier life stages. Each environmental parameter was shifted month-by-month (0–13 months) to correlate with a future catch. These lags were then incorporated into several negative binomial GLMs that were used to analyse the correlation between the environmental parameters and the catch. Multi-model inference was conducted, and the model with the lowest Akaike's Information Criteria (AIC) was considered the best fit. The best-fit lag data for each environmental variable were then incorporated into a complete data set, which was used for all further studies. The purpose of these lags was to examine the associations of environmental parameters with spawning events and earlier life history stages.

The AIC was developed in order to select predictor variables that lead to parsimonious models (Akaike, 1987). This method is based on the approximation of a scatter and is measured according to the anticipated log-likelihood of the model which is produced by the results of the test (Akaike, 1987). The AIC is calculated according to the formula $AIC = (-2)\ln g(x \mid \theta(x)) + 2m$, where $g(x \mid \theta(x))$ the true distribution of factor g, and m is is the expected distribution of x. When several factor gs are being compared to each other, the model with the lowest AIC is found to be the best fit model (Akaike, 1987).

3.4.4 Model selection

To complement the GLM analysis, a stepwise GAM was conducted in order to provide a flexible predictive perspective of the catch and environmental factor relationships. The GAM model was constructed using the following formula:

$$gam(Catch \sim AveBT + StdDevBT + StdDevWS + AveWD + StdDevWD \\ + AveP + StdDevP + ONI + MaxWS + MinWS + ModeWD + AAO \\ + Chl + AveSST + StdDevSST + EpH + upw)$$

The best-fit model was selected based on the lowest AIC value, which would be used in further analyses. This model was given by the formula:

$$gam(Catch \sim s(AveBT, k = 4) + s(StdDevBT, k = 4) + s(AveSST, k = 4) + \\ s(StdDevSST, k = 4) + s(StdDevWS, k = 4) + s(AveWD, k = 4) + \\ s(StdDevWD, k = 4) + s(AveP, k = 4) + s(StdDevP, k = 4) + \\ s(ONI, k = 4) + s(Chl, k = 4) + s(MaxWS, k = 4) + s(MinWS, k = 4) + \\ s(ModeWD, k = 4) + s(EpH, k = 4) + s(AAO, k = 4) + s(upw, k = 4).$$

Where k=4 sets the upper limit of the degrees of freedom in the model because, if this is not included, the models which include the full dataset do not reach a solution. The *s* is a function used by *R* to incorporate spline smoothers into the model. The model defined by this formula is referred to as the “full model”.

3.4.5 Analysis of relationship between catch and environmental variables

Each of the environmental variables was analysed individually in order to determine the strength (based on R^2 values) of each relationship with the catch. The correlation of each of the environmental variables and the observed change from the mean of the total monthly catch were then plotted individually and described according to the plots. Positive catch response values indicate increased catches whilst negative responses imply decreased catches.

3.4.6 Building a predictive model based on relationships

The fitted values from the GAM were plotted against time, to indicate the likely catch trend based on the data. A descriptive predictive model was constructed for the full model in order to ascertain whether this model could be used in future predictions of catch. This was followed by a predictive model for each individual variable that had a $R^2 > 0.1$ in order to understand the interaction between the environmental factor and the total catch. These descriptive models were visualisations of the relationships between the catch and the environmental variables and indicated the predicted catch according to the parameters.

3.4.7 Analysis of assumptions

The assumptions for GLMs include that the predictor variable data are independent, the residuals are normally distributed, and the variance are homoscedastic (McCullagh and Nelder, 1989). The distribution of the catch data was analysed using a histogram.

Poisson-distributed GLMs are often confounded by over-dispersion. Over-dispersion is a phenomenon in which the observed variance is greater than the expected variance in a model (Hinde and Demetrio, 1998). Generally, in GLM, observed variance is expected to be approximately equal to the observed mean. Over-dispersion is caused by high variability in the individual experimental units, some correlation between responses, cluster sampling, compound distributions and variables which were not recorded (Hinde and Demetrio, 1998). If the model is confounded by over-dispersion, the model standard errors may be incorrect, which may result in flawed interpretation of regression parameter estimates (Hinde and Demetrio, 1998). Over-dispersion was observed using preliminary Poisson-distributed GLM models in this study, which then prompted the use of negative binomial GLM.

Cook's distance can be used to investigate the influence each observation has on the final model by identifying the outliers (Sheehan et al., 2003). These outliers are found to have a Cook's distance with a value of greater than or equal to one (Sheehan et al., 2003), although other studies suggest using a threshold of 4/n or 4/(n-k-1) where n is sample size and k is the number of individual variables (Zou and Lee, 2008). An analysis of Cook's distance was performed in order to identify outliers in the data that could influence the outcome of the project.

In order to test for normality of the residuals, a Shapiro-Wilk test was conducted, as well as an analysis of Quantile-Quantile (QQ) plots. The need for both tests is because of the high sensitivity of the Shapiro-Wilk test when the sample size is bigger than 50 (D'Agostino et al., 1990) and as a result, an observation of the distribution was conducted in order to analyse whether the residuals were normally distributed.

The residuals were plotted against the observed values in order to determine whether they were independent, and plotted against the fitted values in order to test for homogeneity of the data. These analyses are in Appendix 1.

CHAPTER 4: RESULTS

4.1 Monthly and annual catch trend

A negative binomial GLM analysis of monthly chokka squid catch recorded since 1985 in South Africa showed that there was one peak in catches every year (Figure 7): in summer (end of October to mid-January). The monthly catch ranged from 2 826 kg in March 1987 to 2 849 906 kg in December 2003. A GAM with a Poisson showed a mid-strength relationship (r^2=0.423) between catch and month, with 43.5% of the deviance explained by the model, indicating a temporal trend in catch.

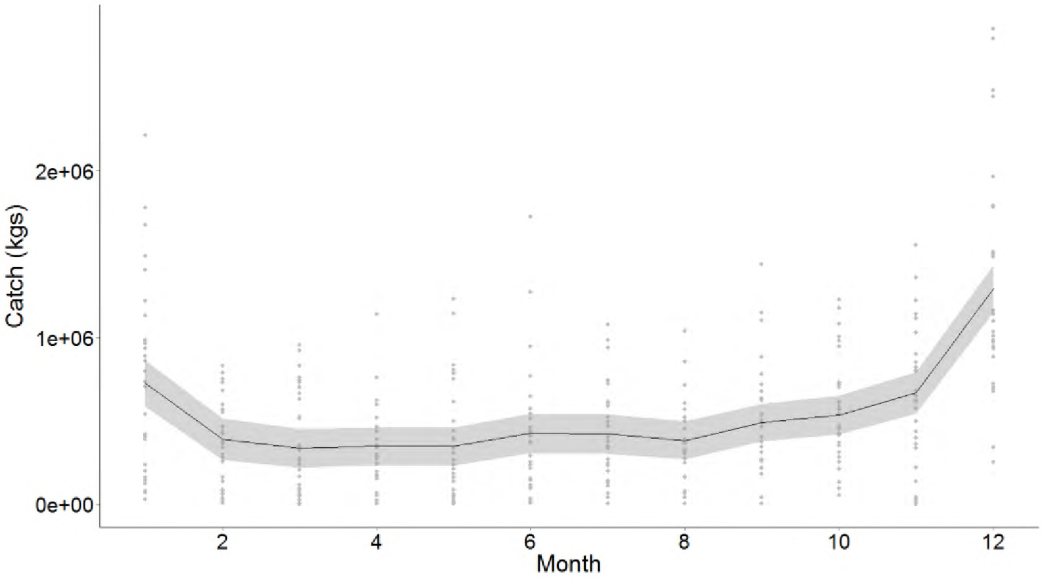

Figure 7: The GAM predicted trend in total monthly chokka squid catch off the coast of South Africa, observed over the years 1985–2014. Data points indicate observed monthly values (1985–2014), with a 95% confidence interval (shaded area).

The annual catch trend (Figure 8) indicated an increase in catch from 250 000 kg to around 500 000 kg from 1985 to 1986, which was followed by a gradual increase from 500 000 kg to below 750 000 kg in catch from the end of the 1980s until mid-2009, when there was a major decline in catch to 250 000 kg in 2013 (Figure 8). A GAM with a Poisson distribution showed a weak relationship (r^2= 0.105) between catch and year, with 14.9% of the deviance explained by the model, providing evidence of no inter-annual cycle in chokka catch.

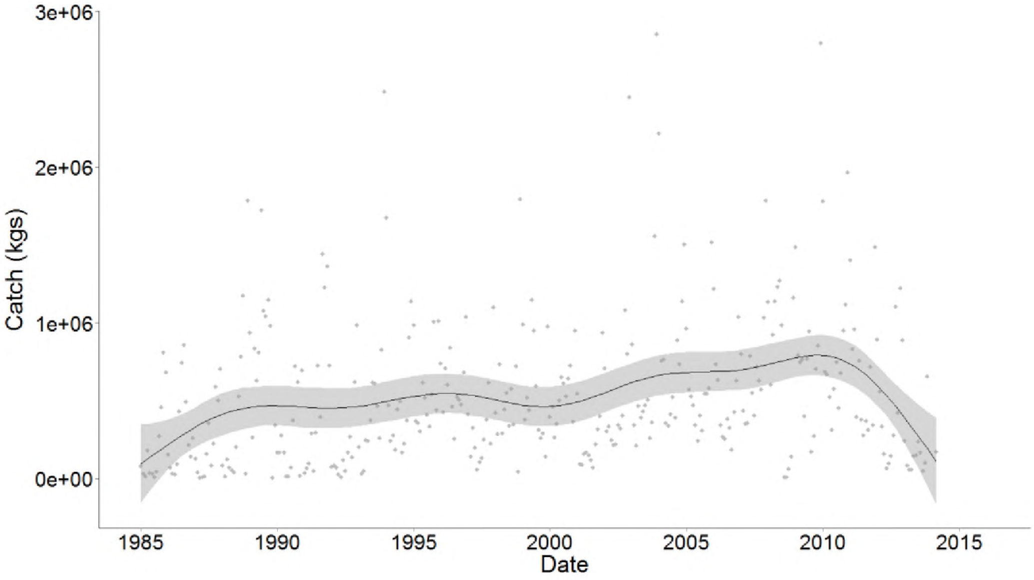

Figure 8: The monthly catch per annum (dots) of chokka squid off the coast of South Africa, 1985–2014, with the GAM trend in annual catch (black line) with a 95% confidence interval (shaded area).

4.2 Annual trends in environmental variables

4.2.1 Ocean bottom temperature (UTR)

Since 1985, the mean annual ocean BT has displayed a fluctuating trend (Figure 9, $p<0.001$). A mean decrease of approximately 0.5°C in temperature was observed in 1988, 1995 and 2010 (Figure 9). The highest mean annual temperature of 17.5°C was recorded in 1992 and 2003–2006 (Figure 9). The annual trend in standard deviation in bottom temperature (indicating the variability in ocean bottom temperature) displays a very slight linear increase from 1.22°C to 1.31°C ($p<0.001$, Figure 10), which matches other ocean warming areas, showing that the annual stability of the ocean bottom temperature has steadily decreased.

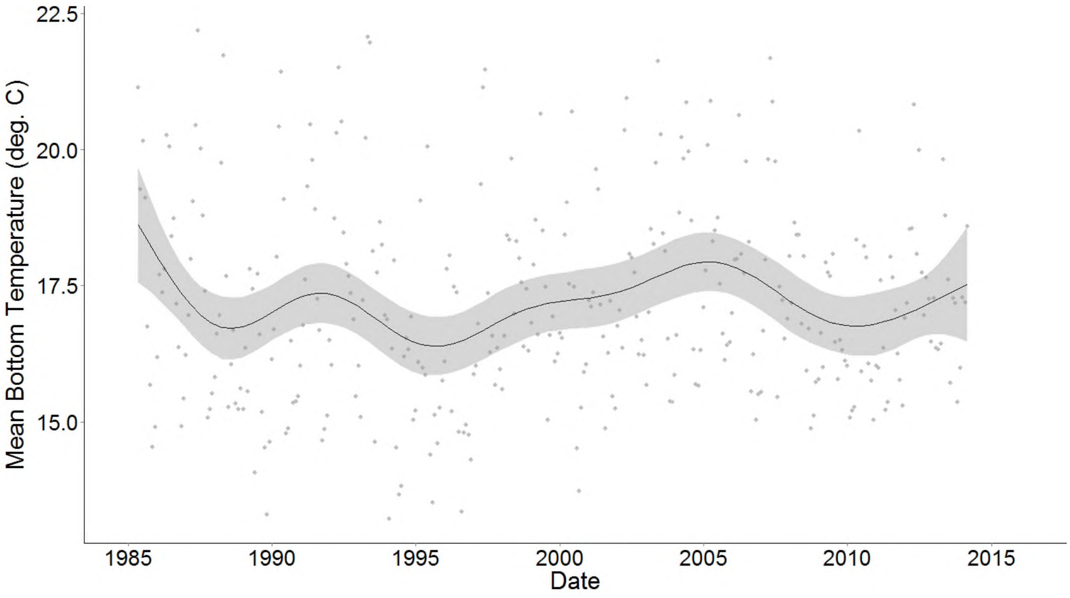

Figure 9: The predicted GAM trend (black line) in annual mean ocean bottom temperature based on observed monthly mean temperatures off the coast of South Africa from 1985 to 2014 (dots), with a 95% confidence interval (shaded area).

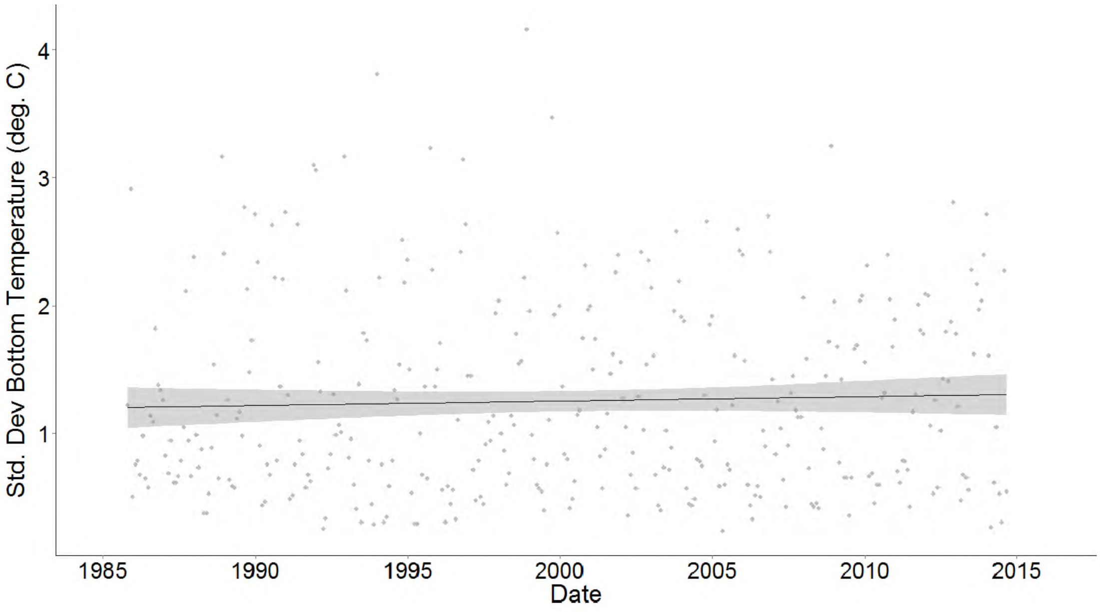

Figure 10: The predicted GAM trend (black line) in annual standard deviation in ocean bottom temperature based on observed monthly standard deviations in temperatures off the coast of South Africa from 1985 to 2014 (dots), with a 95% confidence interval (shaded area).

4.2.2 Sea surface temperature (Satellite)

There are no SST data prior to 2003, thus historical inferences cannot be made here. The annual trend in SST shows large fluctuations in temperatures from 20.81°C in 2003 to 19.31°C in 2005 ($p<0.001$, Figure 11). A decrease in SST occurred again from 20.58°C in 2009 to 18.28°C in 2011 after which it increased to 19.87°C in 2014 (Figure 11). The annual trend in the standard deviation in SST was measured from 2003 to 2014. A general increasing trend from 0.92°C in 2003 to 1.58°C in 2014 ($p<0.001$, Figure 12) was evident. This increasing trend once again provides evidence of a decrease in the stability of the ocean temperatures.

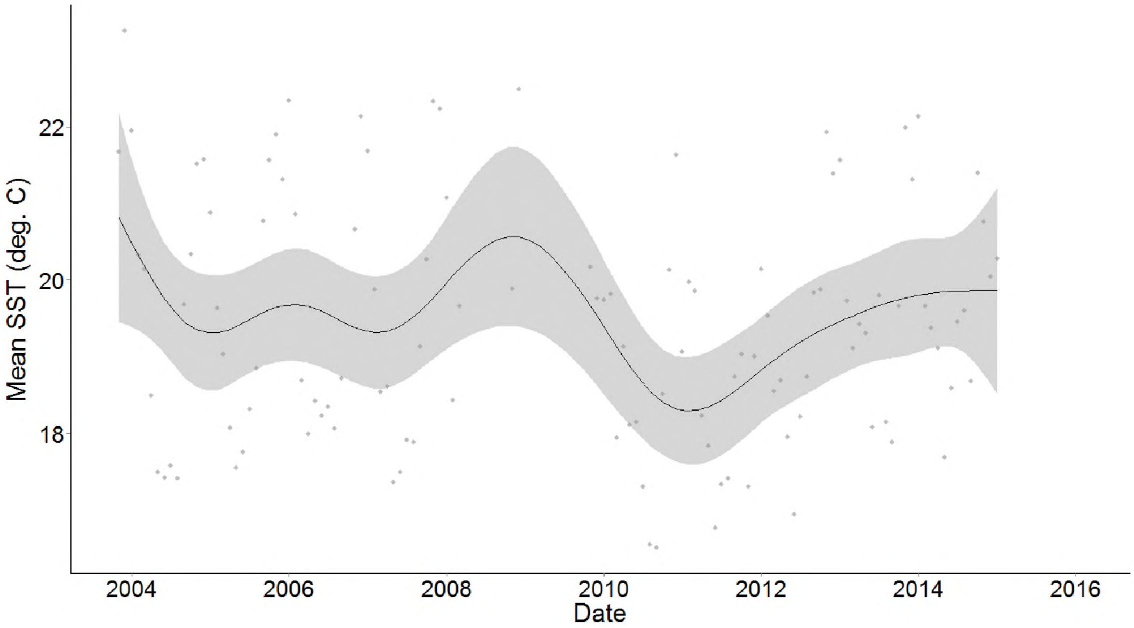

Figure 11: The predicted GAM trend (black line) in annual mean ocean sea surface temperature based on observed monthly mean in temperatures off the coast of South Africa from 2003–2014 (dots) with a 95% confidence interval (shaded area).

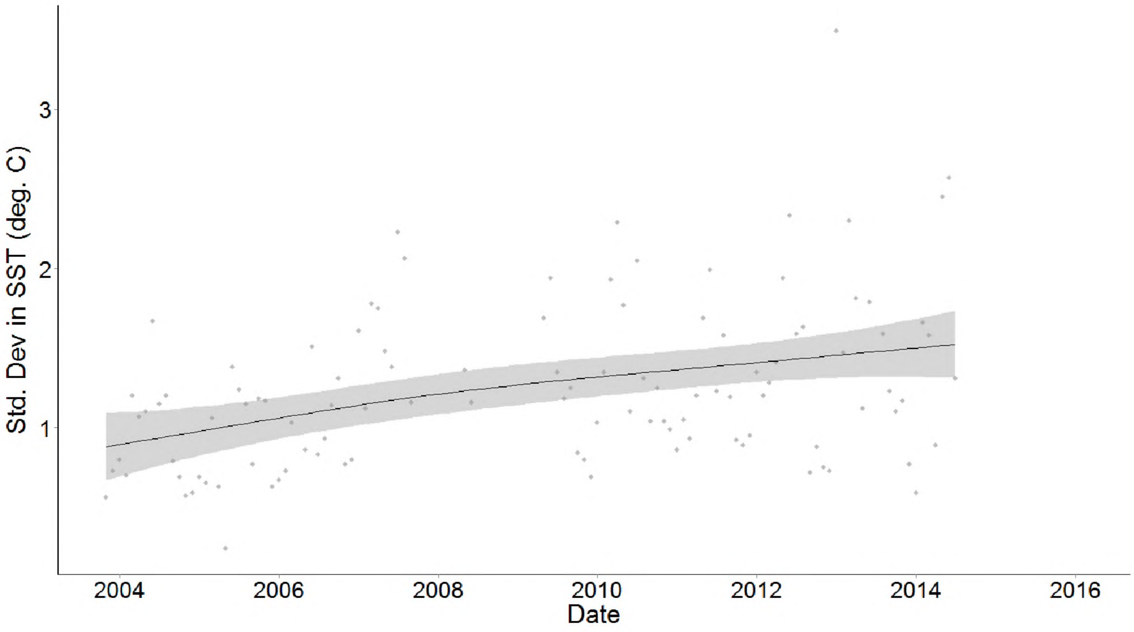

Figure 12: The predicted GAM trend (black line) in annual standard deviation in ocean sea surface temperature based on observed monthly standard deviation in temperatures off the coast of South Africa from 1985–2014 (dots) with a 95% confidence interval (shaded area).

4.2.3 Wind speed

The trend in the standard deviation in wind speed from 1985–2014 displayed a gradual decrease in variability from 3.86 $m.s^{-1}$ in 1988 to 2.65 $m.s^{-1}$ in 2006 ($p=0.00834$, Figure 13). In addition, the maximum wind speeds appear to have decreased from 8.81 $m.s^{-1}$ in 1994 to 7.16 $m.s^{-1}$ in 2006 ($p<0.001$, Figure 14). The minimum wind speeds have also shown a decreasing trend from a peak of 2.75 $m.s^{-1}$ in 1994 to 1.38 $m.s^{-1}$ in 2009 ($p<0.001$, Figure 15). Wind speed has dropped since 1994 and has become more stable (less variable).

Figure 13: The predicted GAM trend (black line) in annual standard deviation in wind speed based on observed monthly standard deviation in wind speeds off the coast of South Africa, 1985–2014 (dots), with a 95% confidence interval (shaded area).

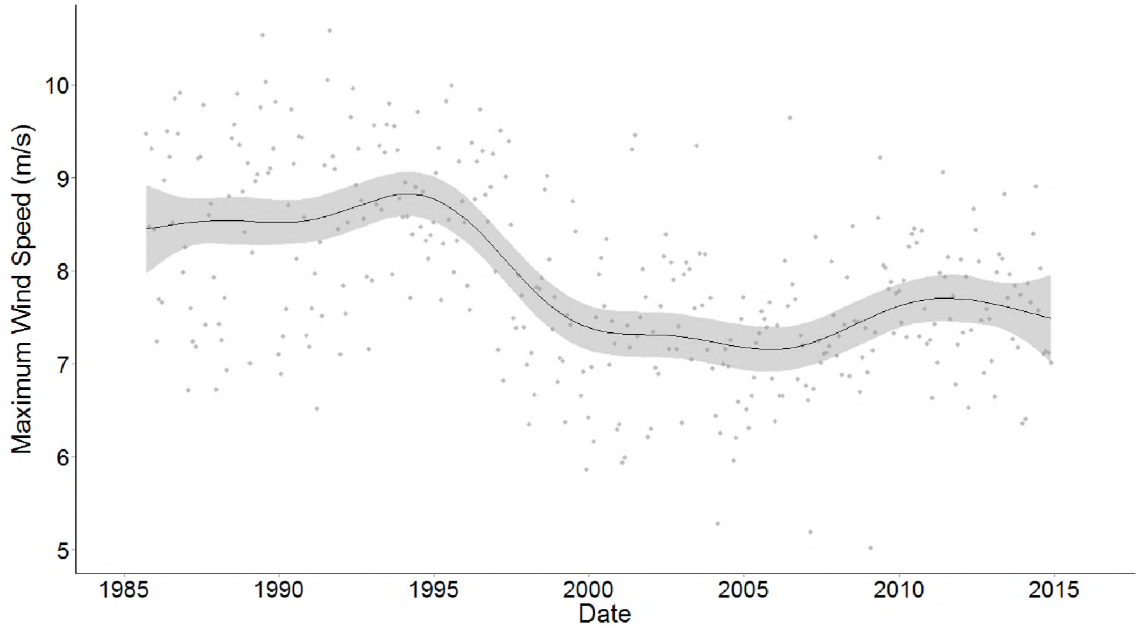

Figure 14: The predicted GAM trend (black line) in annual maximum wind speeds based on observed monthly maximum wind speeds off the coast of South Africa, 1985–2014 (dots), with a 95% confidence interval (shaded area).

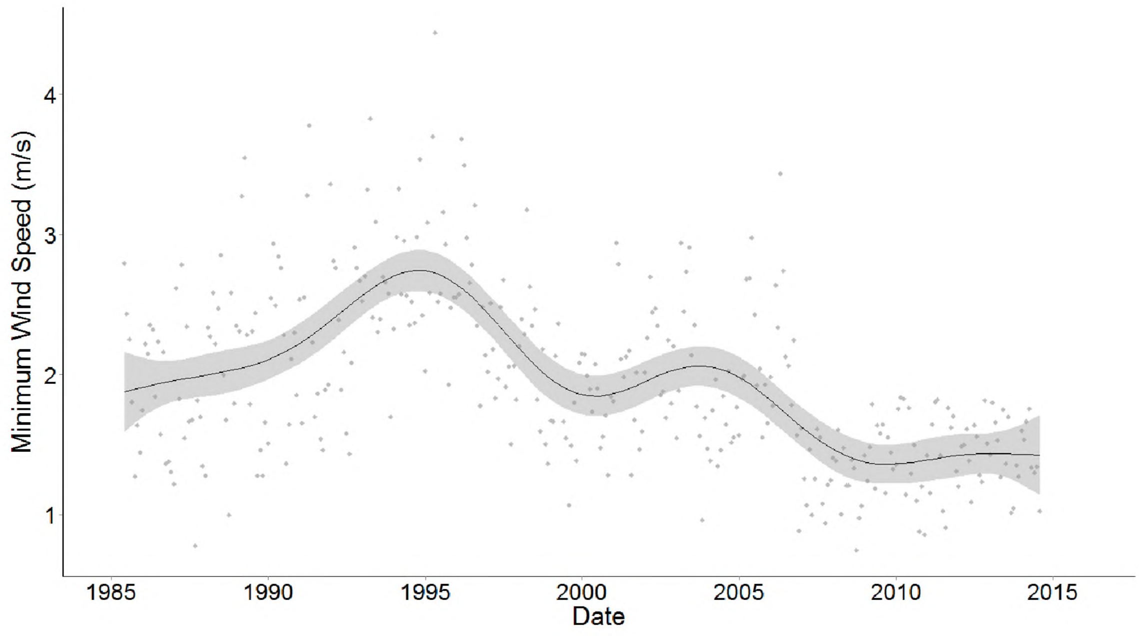

Figure 15: The predicted GAM trend (black line) in annual minimum wind speeds based on observed monthly minimum wind speeds off the coast of South Africa, 1985–2014 (dots) with a 95% confidence interval (shaded area).

4.2.4 Wind direction

The mean wind direction has undergone a major change in the past 30 years (p=0.0191). In 1991 the wind changed from a mean direction of 170° (S) to a mean direction of 200° (SSW) in 1994 (Figure 16). From 1994, the wind direction shifted from a SSW direction to an easterly wind direction (100°) in 2000 (Figure 16). Since 2000, it has remained a mean easterly wind direction (Figure 16). The standard deviation in wind direction has decreased from 110° in 1985 to 72° in 2014 (p=0.0056, Figure 17), indicating increased stability in the wind direction since 2001 (Figure 17). The predominant wind direction prior to 1991 was between 150° and 165° (SSE) (p<0.001, Figure 18). In 1995, the predominant wind shifted to a SSW direction (200°) followed by a shift to an ESE wind (140°) in 2000. The number of hours of easterly winds blowing per day reached a peak of 8.00 hours per day in 1995 and decreased to a minimum of 6.13 hours per day (p<0.001, Figure 19).

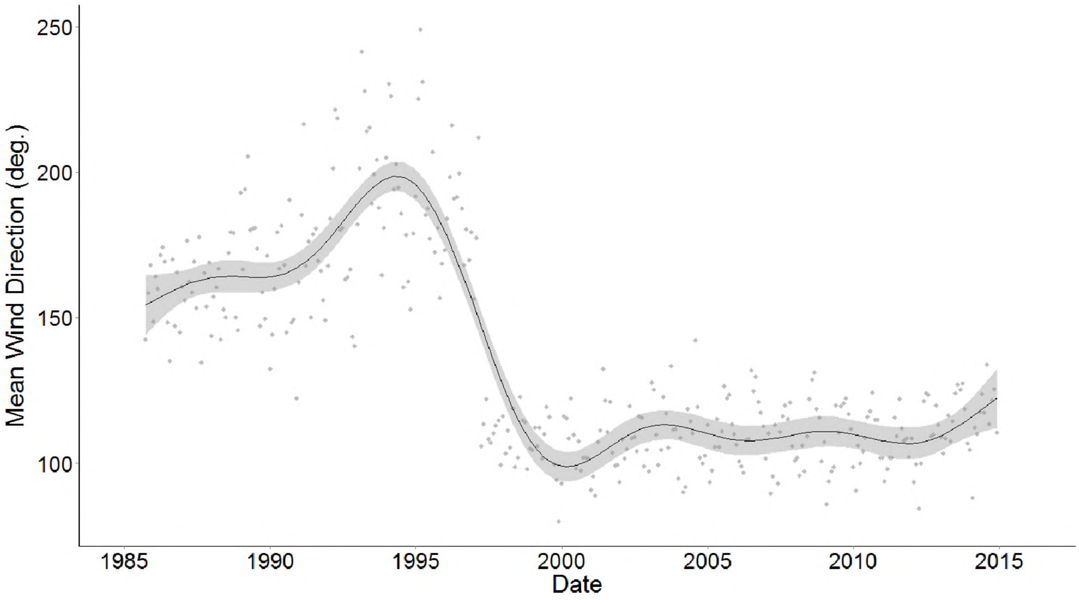

Figure 16: Predicted GAM trend (black line) in annual mean wind direction based on observed monthly mean wind directions off the coast of South Africa, 1985–2014 (dots), with a 95% confidence interval (shaded area).

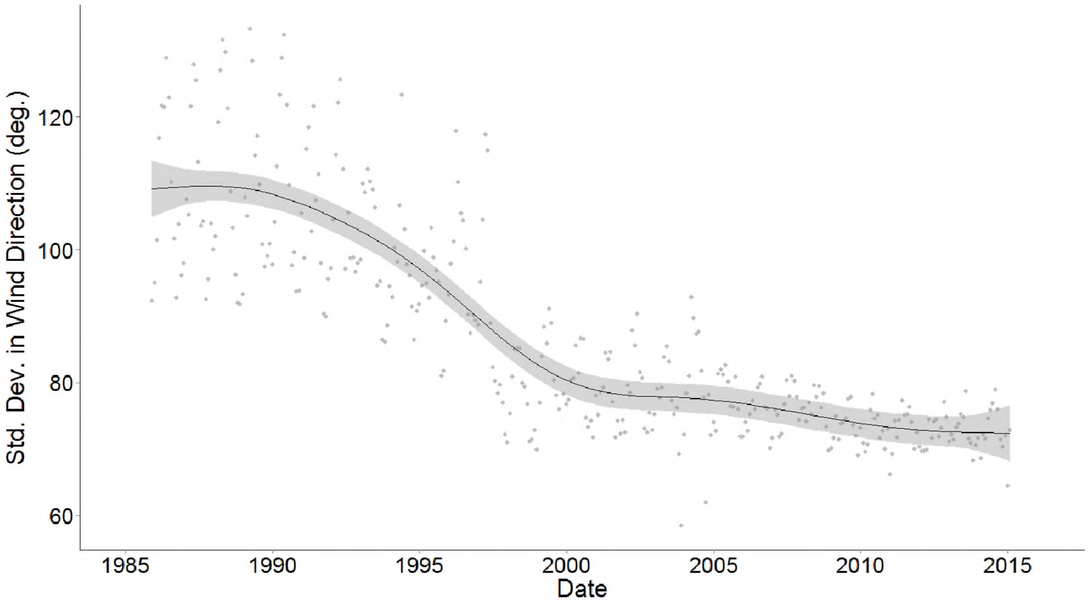

Figure 17: Predicted GAM trend (black line) in annual standard deviations in wind direction based on observed monthly standard deviations in wind direction off the coast of South Africa, 1985–2014 (dots), with a 95% confidence interval (shaded area).

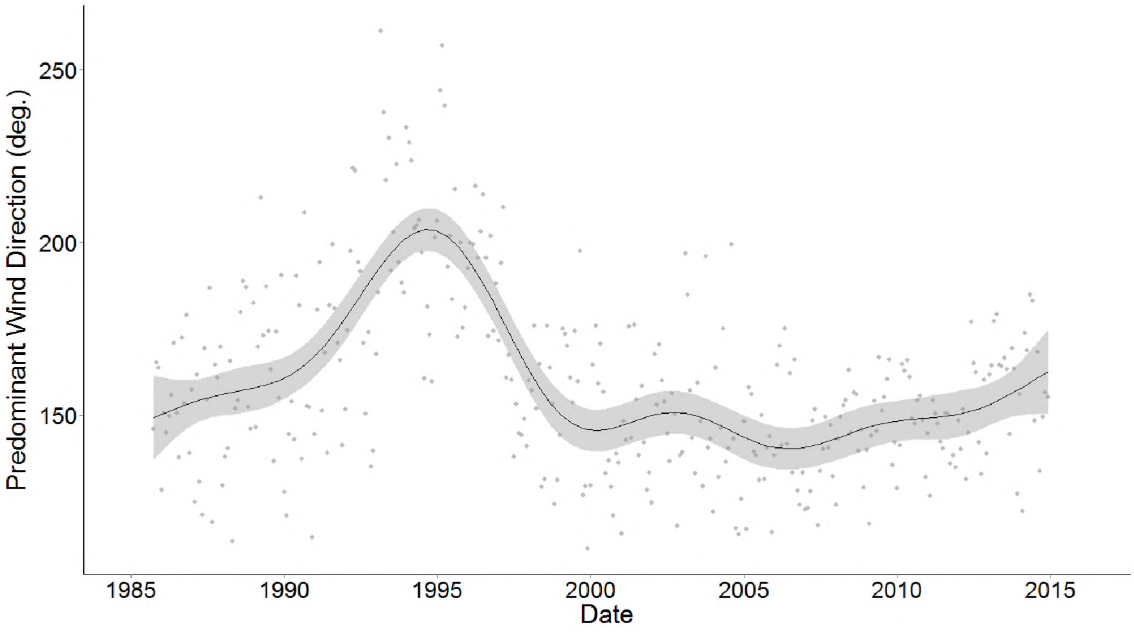

Figure 18: Predicted GAM trend (black line) in annual predominant wind directions based on observed monthly predominant wind directions off the coast of South Africa, 1985–2014 (dots), with a 95% confidence interval (shaded area).

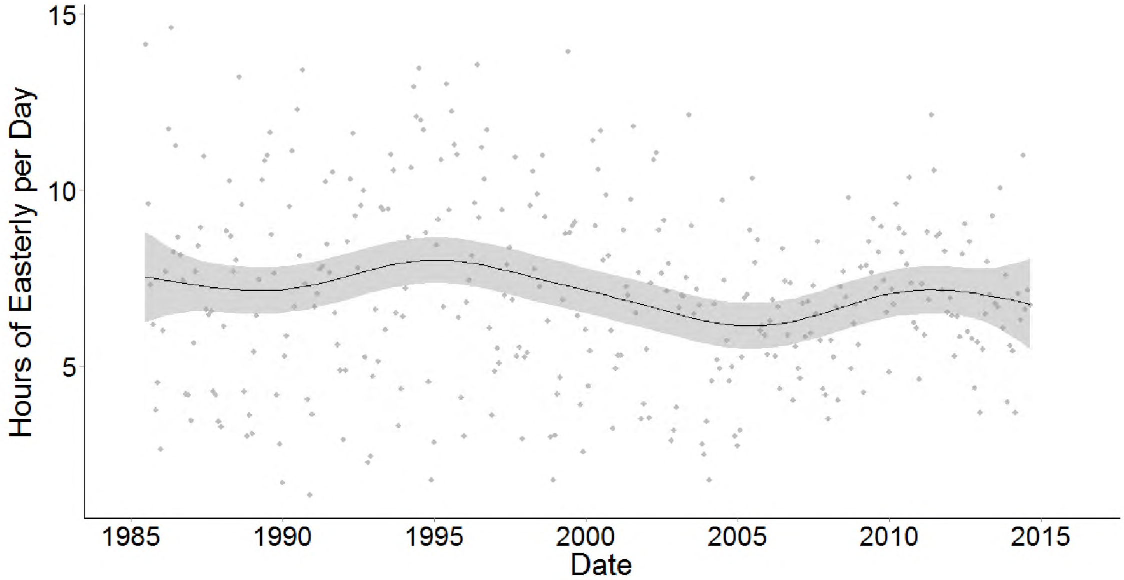

Figure 19: Predicted GAM trend (black line) in annual mean hours of easterly winds per day based on observed monthly mean hours of easterly winds per day off the coast of South Africa, 1985-2014 (dots), with a 95% confidence interval (shaded area).

4.2.5 Atmospheric pressure

The annual trend in atmospheric pressure was approximately 1016 hPa from 1985 to mid-2001 ($p<0.001$, Figure 20). In 2001, the atmospheric pressure started decreasing until the value reached 1014 hPa in 2007 (Figure 20). The standard deviation in atmospheric pressure displays a decrease from a high of 5.46 hPa in 1997 to 4.48 hPa in 2014 ($p<0.001$, Figure 21). This shows increased stability and decreased variability in the atmospheric pressure.

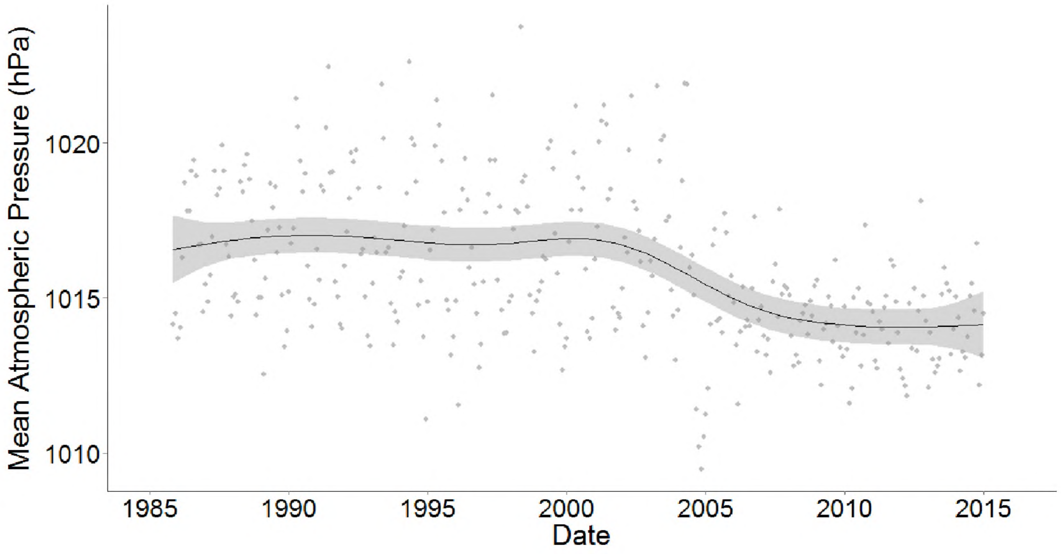

Figure 20: Predicted GAM trend (black line) in annual mean atmospheric pressure based on observed monthly mean atmospheric pressure off the coast of South Africa, 1985–2014 (dots), with a 95% confidence interval (shaded area).

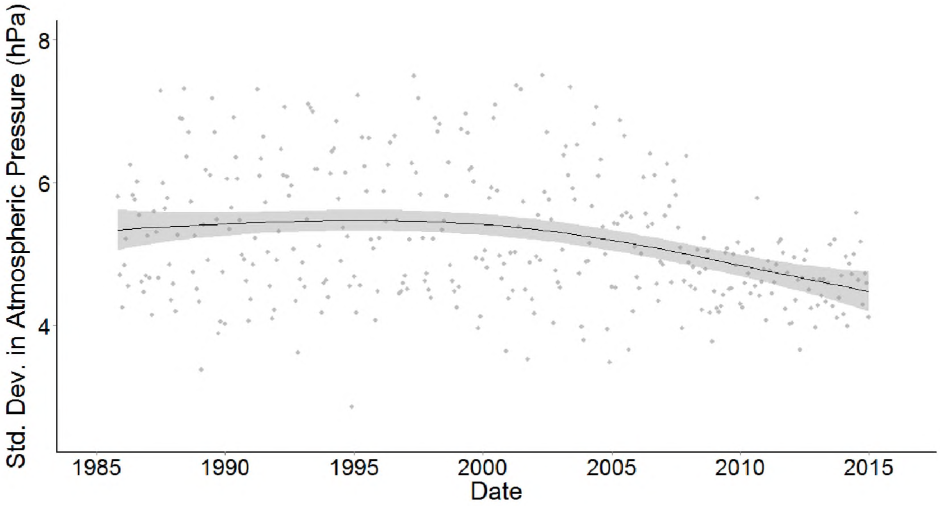

Figure 21: Predicted GAM trend (black line) in annual standard deviation in atmospheric pressure based on observed monthly standard deviations in atmospheric pressure off the coast of South Africa, 1985–2014 (dots), with a 95% confidence interval (shaded area).

4.2.6 Upwelling events and ocean productivity

The trend in the mean number of upwelling events shows a 31% decrease from a mean of one per month in 1991 to a mean of 0.69 per month in 2014 ($p<0.001$, Figure 22). This decrease is mirrored in the productivity of the ocean (measured by the chlorophyll-*a* concentration) which showed a decreasing trend from 9.02 $kg.m^{-3}$ in 2003 to a minimum of 5 $kg.m^{-3}$ in 2007 ($p<0.001$, Figure 23). An increase to 7.59 $kg.m^{-3}$ followed in 2010 with a subsequent drop to 5.4 $kg.m^{-3}$ in 2013 (Figure 23).

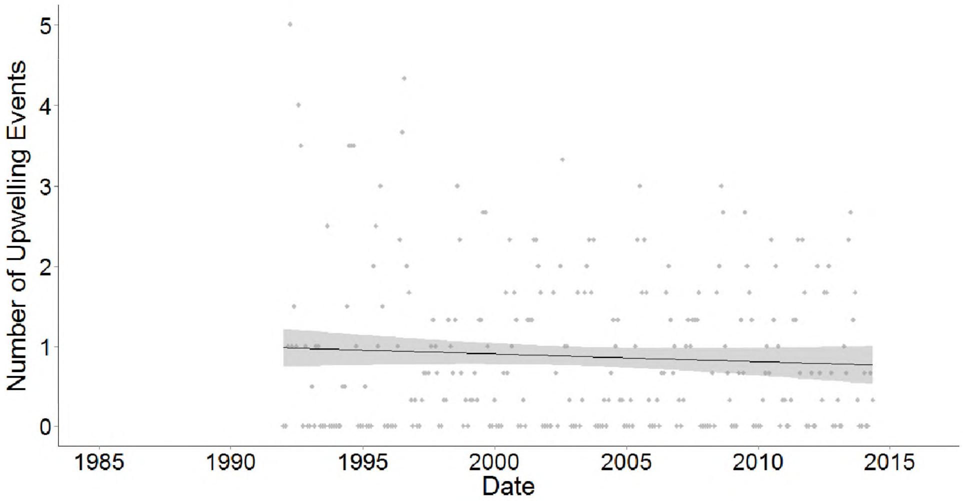

Figure 22: Predicted GAM trend (black line) in annual mean number of upwelling events based on observed monthly numbers of upwelling events off the coast of South Africa, 1985–2014 (dots), with a 95% confidence interval (shaded area).

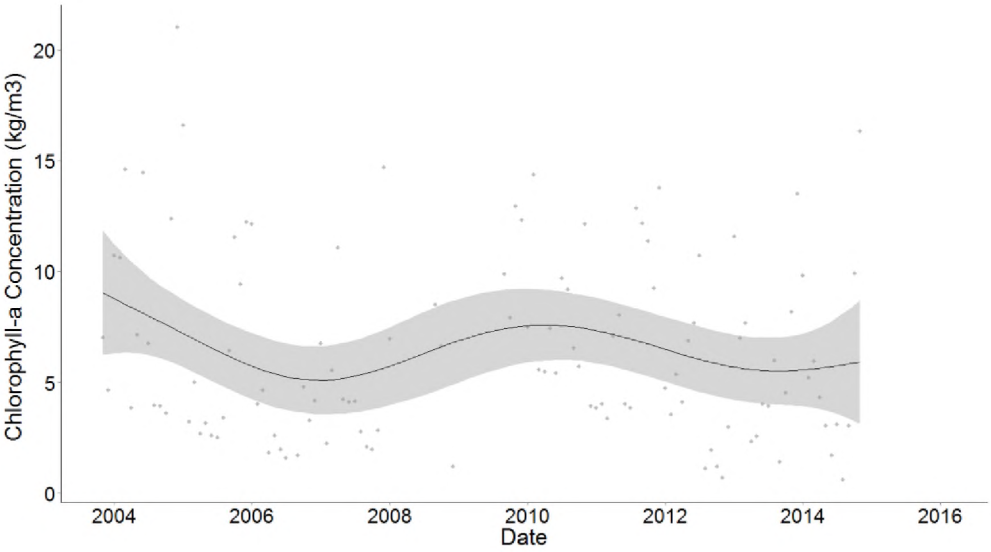

Figure 23: Predicted GAM trend (black line) in annual mean chlorophyll-*a* concentration based on observed monthly means in chlorophyll-*a* concentrations off the coast of South Africa, 1985–2014 (dots), with a 95% confidence interval (shaded area).

4.2.7 Large-scale climatic indices

Large-scale climatic indices allow for a holistic approach when looking for the effect of environmental parameters on the ecosystem. A mean positive ONI value indicates a high likelihood of El Niño events whilst a negative value indicates La Niña events. There were La Niña events in 1999/2000 and again in 2011 ($p<0.001$, Figure 24). The El Niño/ La Niña cycle displays regular changes between states; however, these changes are of varying intensity in different years (Figure 24). The ONI displays the strongest El Niño event (mean=1), which occurred in 2014 without a measured peak (Figure 24). The AAO values have displayed very slight variation since 1985; mean positive values have been recorded from 1985–1988, 1995–2004 and since 2007–2014 ($p<0.001$, Figure 25). The trend line in Figure 25 shows a gradual, well-reported increase in AAO values since 1985.

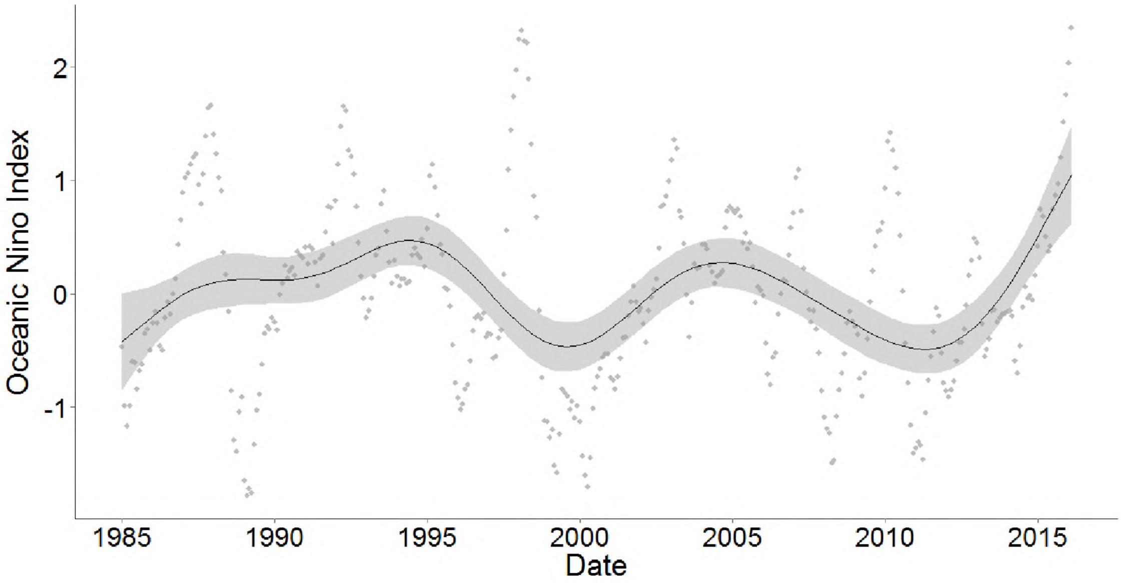

Figure 24: Predicted GAM trend (black line) in annual mean Oceanic Niño Index based on observed monthly Oceanic Niño Index off the coast of South Africa, 1985–2014 (dots), with a 95% confidence interval (shaded area).

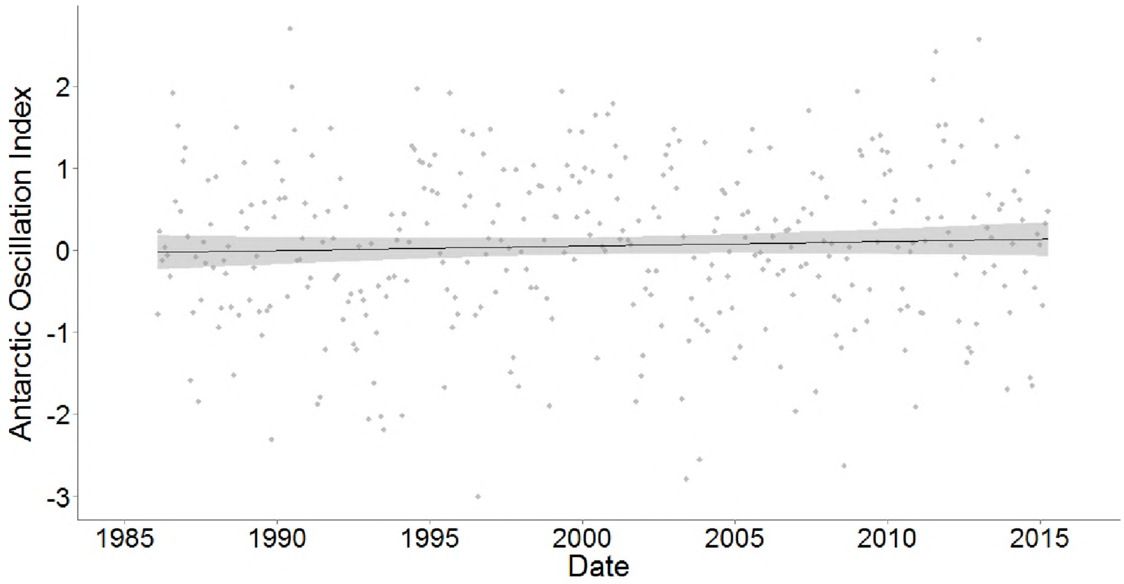

Figure 25: Predicted GAM trend (black line) in annual Antarctic Oscillation Index based on observed monthly Antarctic Oscillation Indices off the coast of South Africa, 1985–2014 (dots), with a 95% confidence interval (shaded area).

4.3 Linear analysis

A NBGLM analysis of each environmental parameter was performed to investigate the strength of its relationship with catch (i.e. independently of the other parameters). A significant relationship ($p>0.05$- Table 1) for each parameter except the maximum wind speed, standard deviation in atmospheric pressure, the ONI and the AAO was exposed, indicating the latter variables do not describe the variation in catch significantly. The relationships between catch and these parameters with insufficient evidence of significant relationships are described in Appendix 3. This result indicates that those environmental parameters that do not have a significant result do not directly correlate to chokka catch and may only need to be investigated when analysing the ecosystem holistically.

To ensure completeness, a NBGLM analysis was also employed to investigate the relationship between catch and the combined environmental drivers to establish which environmental parameters should be focussed on in a holistic model. In this model the lagged environmental variables which indicated a significant relationship with total monthly catch were monthly mean bottom temperature ($p = 0.020$) and standard deviation in SST ($p < 0.001$) (Table 2). Both these parameters have negative relationships with catch, and were lagged by four months. This result confirms that it is important to include all the environmental parameters when establishing a holistic model.

Table 1: Defining statistical outcomes for the individual negative binomial generalised linear model (NBGLM) for each environmental parameter.

	Monthly Lag	Estimate	Std. Error	z value	Pr(>|z|)
AveBT	4	-0.158	0.026	-6.072	<0.001
StdDevBT	10	0.330	0.063	5.242	<0.001
AveSST	10	0.254	0.040	6.340	<0.001
StdDevSST	4	-0.699	0.131	-5.322	<0.001
StdDevWS	0	-0.376	0.091	-4.114	<0.001
AveWD	9	-0.004	0.001	-3.185	0.001
StdDevWD	11	-0.019	0.003	-6.415	<0.001
AveP	10	-0.105	0.019	-5.595	<0.001
StdDevP	10	-0.020	0.015	-1.358	0.175
ONI	3	-0.110	0.062	-1.772	0.076
Chl	8	0.046	0.018	2.490	0.013
MaxWS	9	-0.034	0.048	-0.705	0.481
MinWS	5	-0.352	0.076	-4.618	<0.001
ModeWD	9	-0.005	0.002	-2.601	0.009
Eph	6	-0.078	0.018	-4.303	<0.001
upw	6	-0.282	0.047	-5.994	<0.001
AAO	13	-0.016	0.050	-0.317	0.752

Table 2: Defining statistical outcomes for the negative binomial generalised linear model (NBGLM) incorporating all the environmental parameters.

	Estimate	**Std. Error**	**z value**	**Pr(>|z|)**
(Intercept)	19.063	38.293	0.498	0.619
AveBT	-0.107	0.046	-2.328	**0.020**
StdDevBT	0.122	0.140	0.869	0.385
AveSST	0.052	0.064	0.814	0.416
StdDevSST	-0.561	0.145	-3.880	**<0.001**
StdDevWS	-0.091	0.220	-0.414	0.679
AveWD	-0.015	0.009	-1.710	0.087
StdDevWD	-0.009	0.018	-0.480	0.631
AveP	-0.003	0.039	-0.076	0.940
StdDevP	0.223	0.116	1.928	0.054
ONI	0.078	0.095	0.824	0.410
Chl	0.018	0.015	1.178	0.239
MaxWS	0.187	0.109	1.717	0.086
MinWS	-0.226	0.152	-1.485	0.137
ModeWD	-0.006	0.005	-1.248	0.212
Eph	-0.031	0.043	-0.721	0.471
upw	-0.018	0.114	-0.154	0.877
AAO	-0.057	0.065	-0.880	0.379

4.4 Monthly lag influence on relationship between environmental parameters and catch

A NBGLM analysis revealed the monthly lags of each environmental variable that were best fitted according to Akaike's Information Criterion (AIC). These lags, along with their corresponding AIC values, appear in Appendix 2. Based on Table 3, changes in the consistency in wind speed (standard deviation in wind speed) and ONI influence the chokka catches 0 and 3 months later, respectively. A -month lag of the mean bottom temperature and changes in the consistency (standard deviation) in SST displayed the best fit with the catch data (Table 3). Changes in the minimum wind speed had the best association with the catch five months later (Table 3). Analysis of hours of easterly winds and the number of upwelling events showed that a best-fit model resulted from a six-month lag in the association between the drivers and the chokka catch. The data that were found to best fit the model with a lag between eight and nine months were chlorophyll-*a* concentration (8 months), predominant wind direction (9 months), mean wind direction (9 months) and the maximum wind speed (9 months) (Table 3). The standard deviation (consistency) in bottom temperature (10 months), atmospheric pressure (10 months) and wind direction (11 months), as well as the mean atmospheric pressure (10 months), SST (10 months) and the AAO were found to fit best to the catch data when lagged by 10 to 13 months (Table 3).

Table 3: Number of months by which the environmental parameters were lagged to ensure best fit, based on Aikaike's Information Criteria (AIC).

Parameter	AIC Range	Month lag for Best Fit Model	Best Fit Model AIC value
Standard Deviation	9 646.98- 9 682.99	0	9 646.98
ONI	9 899.91 – 9 916.99	3	9 899.91
Standard Deviation	2 574.81 – 2 607.11	4	2 574.81
Mean BT	9 459.02 – 9 487.095	4	9 459.02
Minimum WS	9 619.82 – 9 655.98	5	9 619.82
Number of upwelling	5 872.86 – 5 889.98	6	5 872.86
Hours of easterly	9 651.71 – 9 683.20	6	9 651.71
Chlorophyll-*a*	3 025.05 – 3 048.97	8	3 025.05
Maximum WS	8 633.95 – 9 192.00	9	8 633.95
Predominant WD	9 651.75 – 9 683.17	9	9 651.75
Mean WD	9 664.08 – 9 682.07	9	9 664.08
Mean SST	3 098.67 – 3 125.40	10	3 098.67
Standard Deviation	9 458.31 – 9 487.09	10	9 458.31
Mean atmP	9 646.64 – 9 683.11	10	9 646.64
Standard Deviation	9 679.67 – 9 683.17	10	9 679.67
Standard Deviation	9 655.37 – 9 709.01	11	9 655.37
AAO	10 375.26- 10 505.31	13	10 375.26

4.5 GAM for environmental factors

4.5.1 GAM for individual environmental parameters

An analysis of the individual environmental drivers uncovered a significant relationship with the catch ($p<0.001$) for each driver, which was consistent with the full model; however, some of these relationships were extremely weak ($R^2<0.1$). The weak relationships were observed between catch and mean bottom temperature, the standard deviation in wind speed, the maximum and minimum wind speed, the predominant wind direction, the hours of easterly winds, the mean and standard deviation in atmospheric pressure, the AAO, the ONI and the chlorophyll-*a* concentration (these relationships are described in Appendix 4).

4.5.1.1 Temperature

4.5.1.1.1 Ocean bottom temperature

In an individual analysis of the influence of the monthly mean standard deviation in ocean bottom temperature lagged by 10 months on the chokka catch, a significant effect ($p>0.001$) was found in relation to catch; however, this relationship was weak ($r^2=0.138$ and deviance explained = 15.9%). The monthly mean standard deviation in bottom temperature reveals a positive relationship to the chokka catch when the mean standard deviation increases above 1.8°C per month, although at mean standard deviations in temperatures lower than this there is a negative effect (Figure 26). The catch response is highest when the consistency in bottom temperature is lowest (standard deviation in bottom temperature is above 3°C). This predicts that the chokka abundance is likely to be highest (four times higher than mean predicted catches) 10 months after the point when the ocean bottom temperature is very unstable. The chokka abundance is predicted to be around the expected mean and below when the bottom temperature is stable.

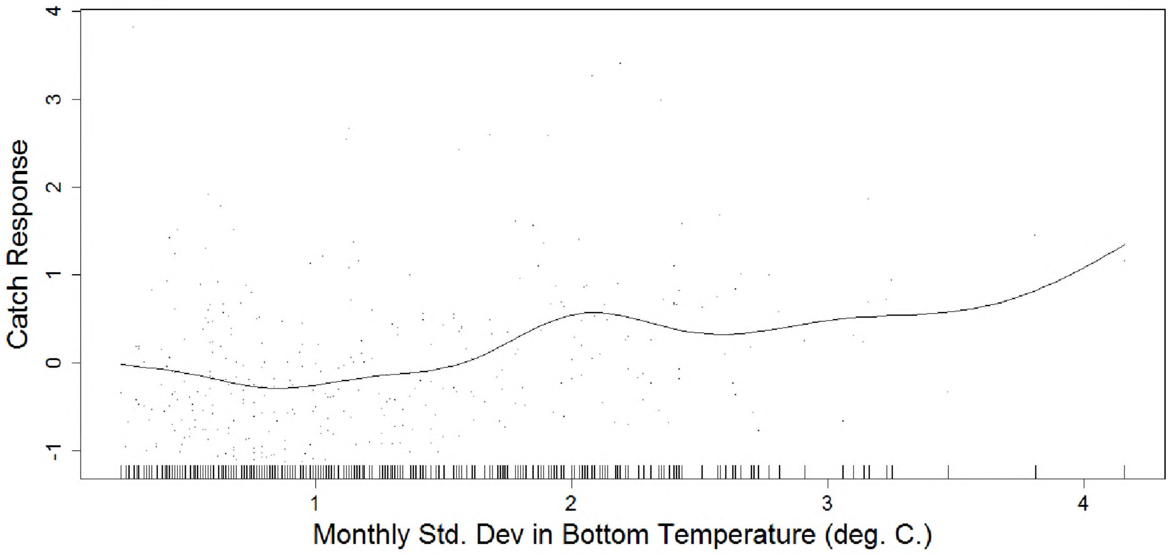

Figure 26: Partial GAM plot predicting (line) the influence of the mean standard deviation in bottom temperature on the response of chokka catch predicted off the south coast of South Africa. A zero catch response depicts the mean predicted chokka catch, whereas a positive catch response predicts an increase in catch, and a negative predicts a decrease in catch. The dots represent the residuals predicted by the GAM.

4.5.1.1.2 Sea surface temperature

An analysis of the individual relationship between a catch response and a 10-month lag in the mean SST exposes a weak positive correlation (R^2=0.38) where only 41.2% of the deviance was explained (Figure 27). A low mean SST (16.5°C and 19°C) predicted a negative catch response, whereas an SST was above 19.5°C (Figure 27) generated a positive catch response. This means that catches are predicted to be higher 10 months after the monthly mean SST is above 19.5°C. The individual relationship between the total monthly catch and a four-month lag in the standard deviation in SST was weak (R^2=0.236) and explains only 34.5% of the deviance. The catch response to the standard deviation in SST is positive at low (between 0.2 and 1.0°C) values, after which the response is negative (Figure 28).

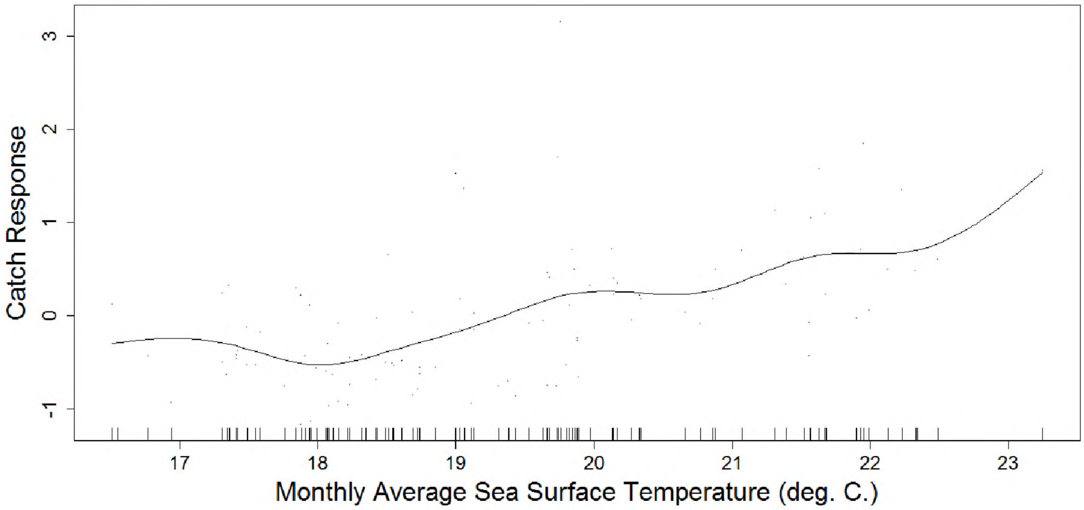

Figure 27: Relationship between the chokka catch and the mean sea surface temperature 10 months earlier; generated using a GAM analysis. The line represents the predicted relationship and the dots represent the GAM-generated residuals used to predict the relationship. The y-axis is the catch response in which a value of 0 represents the mean catch, and positive and negative values represent increases and decreases in catch, respectively.

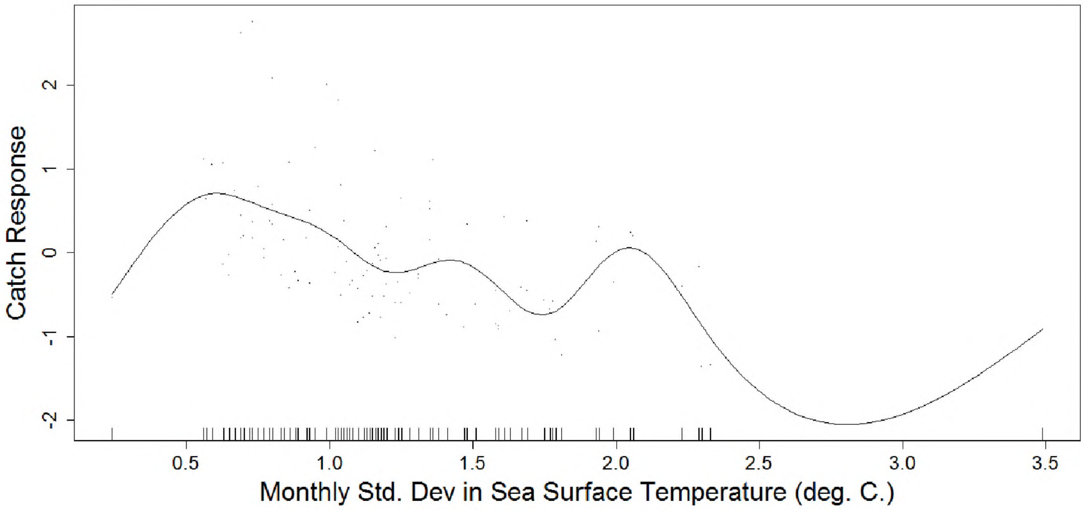

Figure 28: Relationship between the chokka catch and the standard deviation in sea surface temperature 10 months earlier; generated using a GAM analysis. The line represents the predicted relationship and the dots represent the GAM-generated residuals used to predict the relationship. The y-axis is the catch response in which a value of 0 represents the mean catch, and positive and negative values represent increases and decreases in catch, respectively.

4.5.1.2 Wind Direction

A GAM analysis of the relationship between the monthly mean wind direction and the total monthly catch nine months later found the relationship to be strong (R^2=0.604) although only 10.2% of the deviance in the residuals was explained. The model predicted a positive catch response when the wind blows in a direction of 90° to 110° (E) as well as between 180° and 200° (S to SSW) (Figure 29). This indicates that should a monthly mean wind direction be easterly winds and south to south-westerly winds the chokka catch nine months later is predicted to be higher, whilst south-easterly winds will cause a drop in catch, as will westerly and northerly winds.

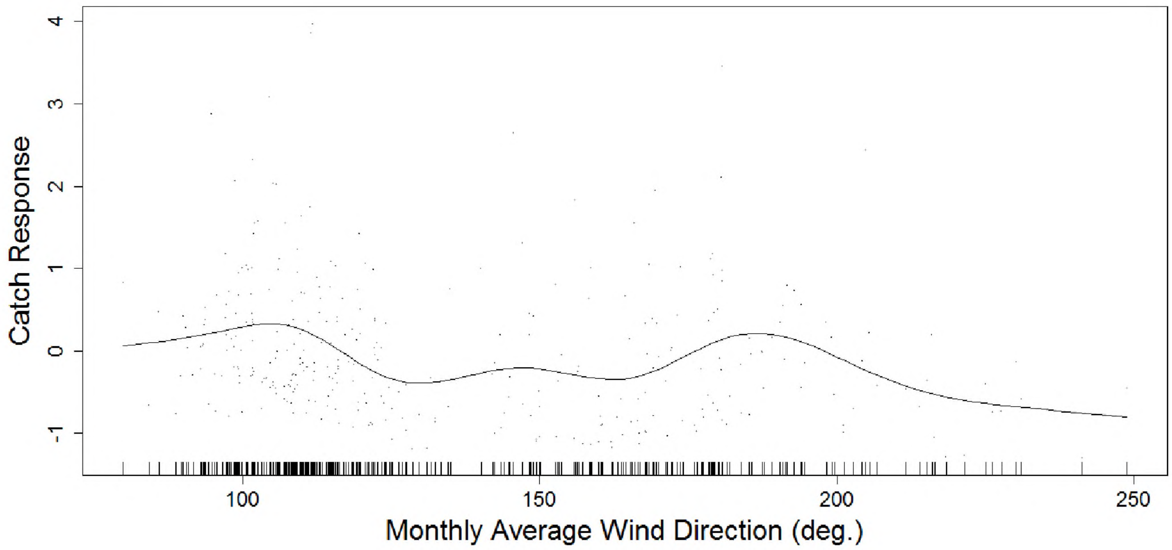

Figure 29: Relationship between the chokka catch and the mean wind direction 9 months earlier; generated using a GAM analysis. The line represents the predicted relationship and the dots represent the GAM-generated residuals used to predict the relationship. The y-axis is the catch response in which a value of 0 represents the mean catch, and positive and negative values represent increases and decreases in catch, respectively.

An individual predictive model for the standard deviation of wind direction predicts a significant relationship with total monthly catch recorded 11 months later; however this model shows a weak relationship (R^2=0.187), and describes only 20.5% of the variability. This model predicts the highest catch responses will occur when there is a low monthly variability in wind direction (up to 75°) (Figure 30), indicating that when the wind direction is stable, the chokka catch will be higher 11 months later.

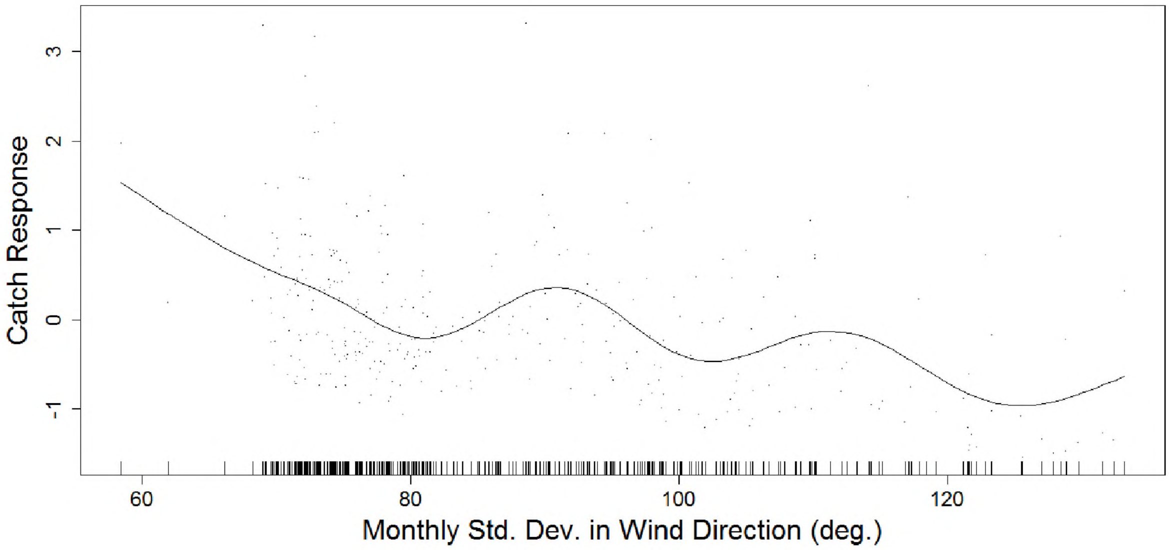

Figure 30: Relationship between the chokka catch and the standard deviation in wind direction 11 months earlier; generated using a GAM analysis. The line represents the predicted relationship and the dots represent the GAM-generated residuals used to predict the relationship. The y-axis is the catch response in which a value of 0 represents the mean catch, and positive and negative values represent increases and decreases in catch, respectively.

4.5.2 GAM for the full model

Although individually several of the environmental variables did not have statistically significant relationships to the chokka catch, it may be necessary to include these parameters in a holistic model. In order to construct a predictive model, the most parsimonious GAM model was necessary. The formulae for the ten most parsimonious models are given in Table 4, Appendix 2. The analysis found that a full (all the environmental factors) GAM with a Poisson distribution presented the best fit, with a strong relationship (r^2=0.707) which explained 81.5% of the deviance.

4.5.2.1 Significant relationships between environmental variables and catch

Analysis of the full model for significant relationships between the total monthly catch and each of the environmental parameters revealed that each of the environmental variables has a significant effect ($p<0.001$) on the catch. It is therefore important to include all the environmental factors when constructing a predictive model.

4.5.2.2 Descriptive analysis of significant relationships and an overview of other relationships

GAM analyses were conducted to reveal the predicted response in the chokka catch (hereafter referred to as catch response) to specific environmental conditions. A GAM of the relationship between catch and monthly mean bottom temperatures from the full model revealed that a high catch at temperatures below 17.5°C and above 21°C, with the lowest catch response at temperatures around 19°C (Figure 31a). This result predicts that the catch will be low four months after temperatures between 17.5°C and 21°C. Whilst the monthly standard deviation in bottom temperatures is predicted to have a significant effect on the catch 10 months later, the relationship indicated that the catch response changes slightly, with a positive catch response at bottom temperature variations between 1.2°C and 2.2°C (Figure 31b). At standard deviation in bottom temperatures higher than 2.2°C, the catch response becomes negative (Figure 31b). This indicates that large changes in temperature (more than 2.2°C) result in a drop in the chokka catch 10 months later.

An analysis of the relationship between the monthly mean SST and the monthly catch 10 months later revealed that the catch response was negative at temperatures between 17.5°C and 20.5°C and positive at temperatures above 20.5°C (Figure 31c). A negative catch response was found when the standard deviation in SST fell between 1.1°C and 3.0°C, with the highest catch response recorded at monthly standard deviations of less than 1.0°C (Figure 31d). This impliesthat high variations in SST lead to low catch four months later, indicating an effect on the chokka paralarvae and juveniles.

Changes in the monthly mean maximum wind speed were found to have a positive catch response at wind speeds above 7.5 $m.s^{-1}$ (Figure 32a). This suggests high catch nine months after strong winds. The monthly mean minimum wind speed was observed to have a negative relationship to the catch response, with catch responses only being positive at wind speeds below 1.6 $m.s^{-1}$ (Figure 32b), which shows that, should the minimum wind speed be higher than 7.2$m.s^{-1}$, the catch will be low. The monthly standard deviation in wind speed indicated a positive catch response at standard deviations between 2.2 $m.s^{-1}$ and 2.8 $m.s^{-1}$ (Figure 32c). At wind speeds above and below this, the catch response is negative.

The monthly mean wind direction leads to a positive catch response when the wind blows on a mean bearing of between 75° and 110° (E) (Figure 32d). At mean wind directions from 110° to 140° (SE) the catch response is negative (Figure 32d). It can thus be predicted that when the wind blows in an easterly direction, the catch is higher nine months later.

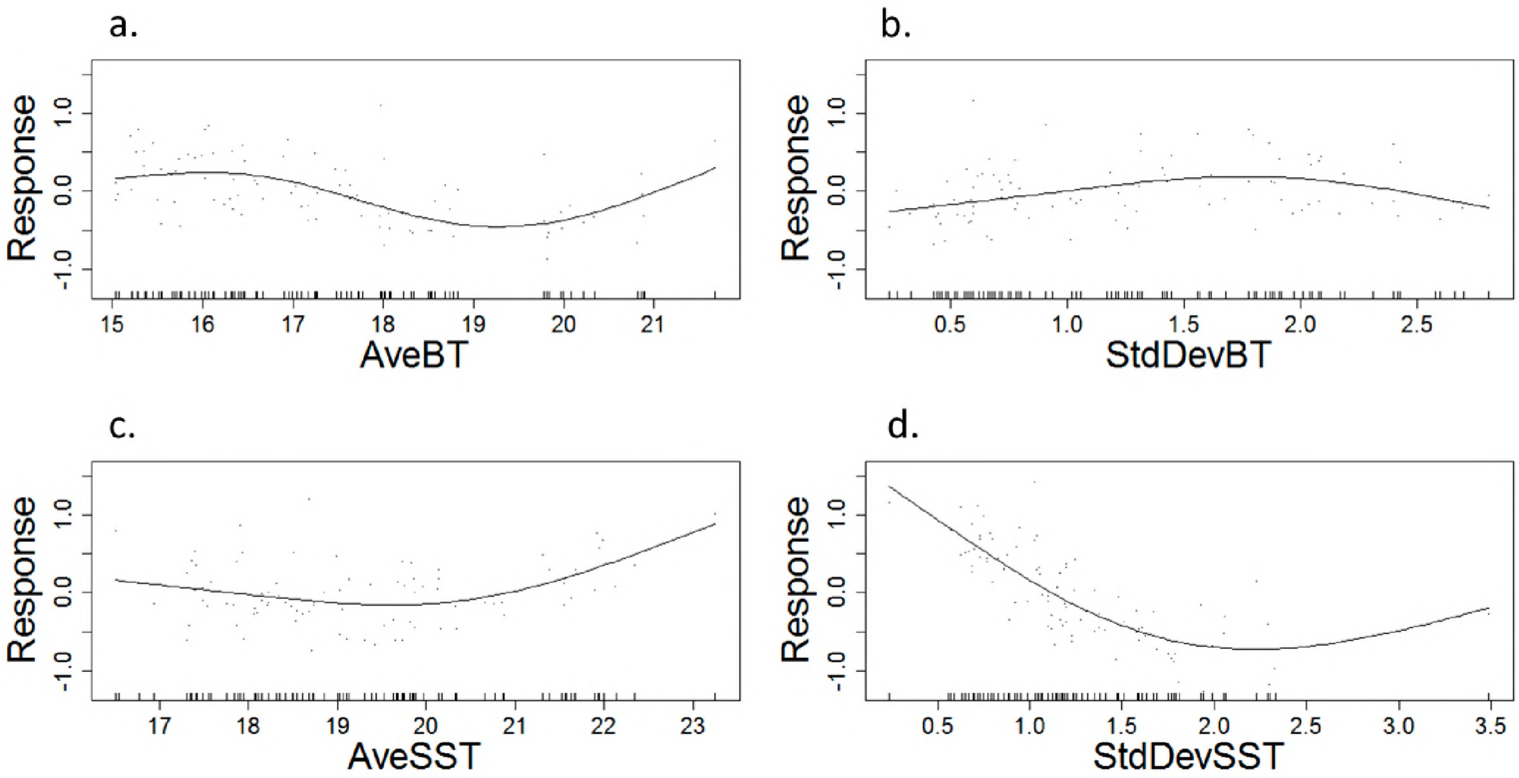

Figure 31: Partial GAM plots for the best binomial and positive models for Loligo reynaudii. The plots show the response shape of the chokka catch of each environmental parameter, independently of the other parameters, in relation to the probability of chokka abundance. The ranges of environmental variables (a. mean bottom temperature; b. standard deviation in bottom temperature; c. mean SST, and d. standard deviation in SST) are represented on the x-axis and the probability of abundance of the species is represented on the y-axis (logit scale). The zero value indicates mean model estimates, while the positive values on the y-axis indicate increases in catches and negative values depict decreased catches. The dots represent the residuals generated by the model.

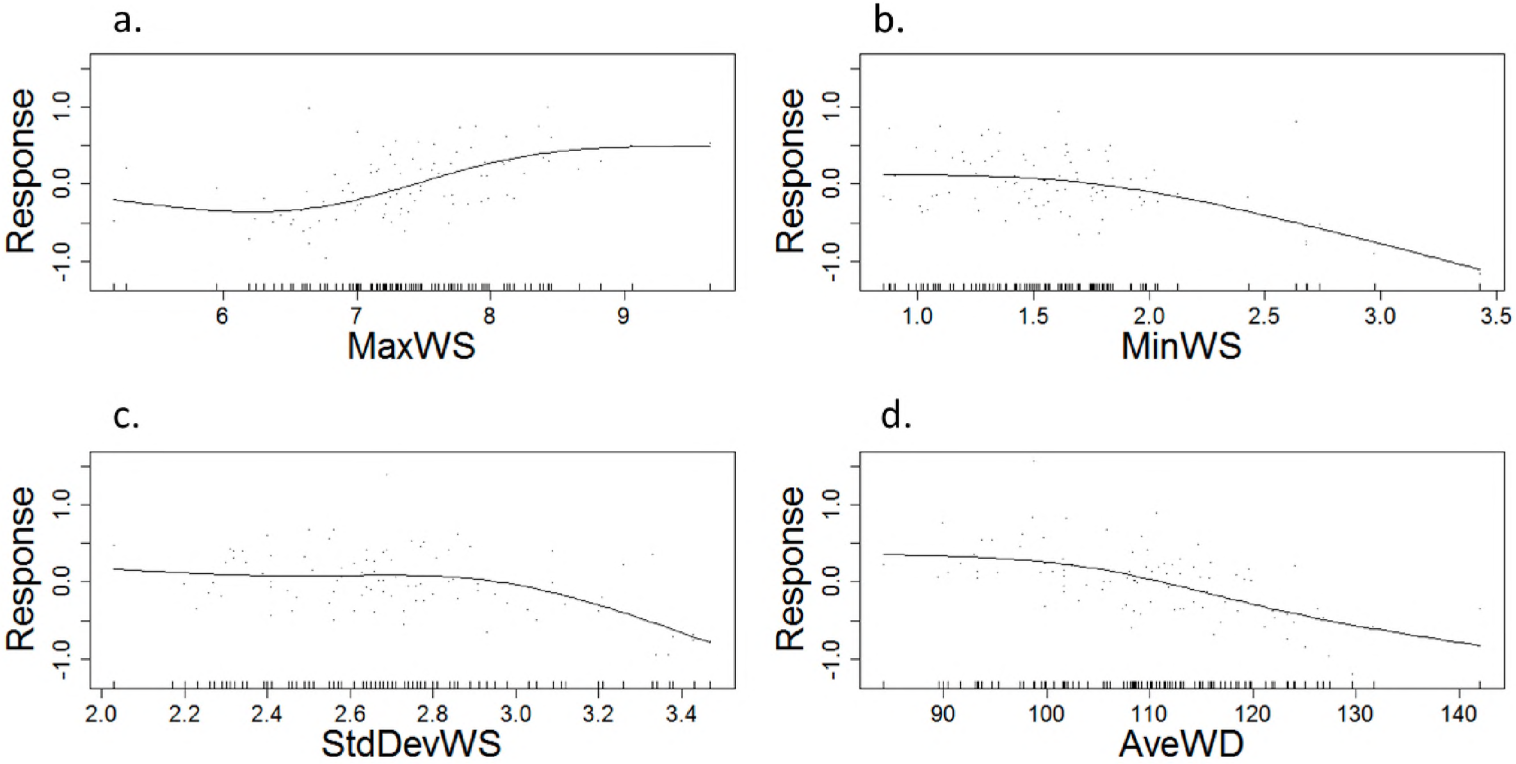

Figure 32: Partial GAM plots for the best binomial and positive models for *Loligo reynaudii*. The plots show the response shape of the chokka catch of each environmental parameter, independently of the other parameters, in relation to the probability of chokka abundance. The ranges of environmental variables (a. maximum and b. minimum wind speed; c. standard deviation in wind speed, and d. mean wind direction) are represented on the x-axis, and the probability of abundance of the species is represented on the y-axis (logit scale). The zero value indicates mean model estimates, while the positive values on the y-axis indicate increased catches and negative values depict decreased catches. The dots represent the residuals generated by the model.

An analysis of the monthly standard deviation in wind direction provides evidence of a positive catch response when the wind direction varies between 50° and 65°, and 75° and 87° (Figure 33a). This denotes that, should the wind direction vary between 65° and 75° or above 87°, the catch will be low 11 months later because the higher variations in wind direction result in unsettled currents, leading to unsuitable mating and spawning conditions. An investigation into the relationship between the monthly predominant wind direction and the catch response indicates a positive catch response when the wind direction blows predominantly in a direction between 110° (ESE) and 150° (SSE) (Figure 33b). At bearings of 150° (SSE) to 200° (SSW), the catch response is negative (Figure 33b). This provides evidence that easterly winds lead to a higher catch and westerly winds to a lower catch nine months later and. This shows the importance of the southeast winds in driving upwelling events and thus increasing the primary productivity of the ocean, and is further supported by the number of hours easterly winds blow. There is a positive catch response when easterly winds blow for more than 10 hours a day (Figure 33c), which indicates a high occurrence of easterly winds predicting a high catch six months later. Analysis of the relationship between the number of upwelling events and the catch showed that few upwelling events (0–1.3 per month) led to a negative catch response, with the response increasing with increased upwelling events (Figure 33d), suggesting that the catch should be higher six months after a higher frequency of upwelling events. A result of increased upwelling is increased chlorophyll-*a* concentration, which, according to Figure 12a, results in an increase in catch response. A low monthly mean chlorophyll concentration (0-5kg.m^{-3}) results in a low catch response (Figure 34a) showing that, at lower chlorophyll-a concentrations, the squid catch response is negative, possibly resulting in a low catch eight months later.

An analysis of the monthly mean atmospheric pressure revealed a positive catch response at pressures above 1019 hPa and between 1012 hPa and 1 015 hPa (Figure 34b), indicating a predicted higher catch 10 months later. When the atmospheric pressures have a standard deviation of below 4.8 hPa and above 6.8 hPa, the catch response is negative, with the optimal catch response being between 5.2 hPa and 6.0 hPa (Figure 34c), suggesting that a high variance in atmospheric pressure could lead to unsuitable conditions for efficient fishing, and a low variance denoting an absence of upwelling.

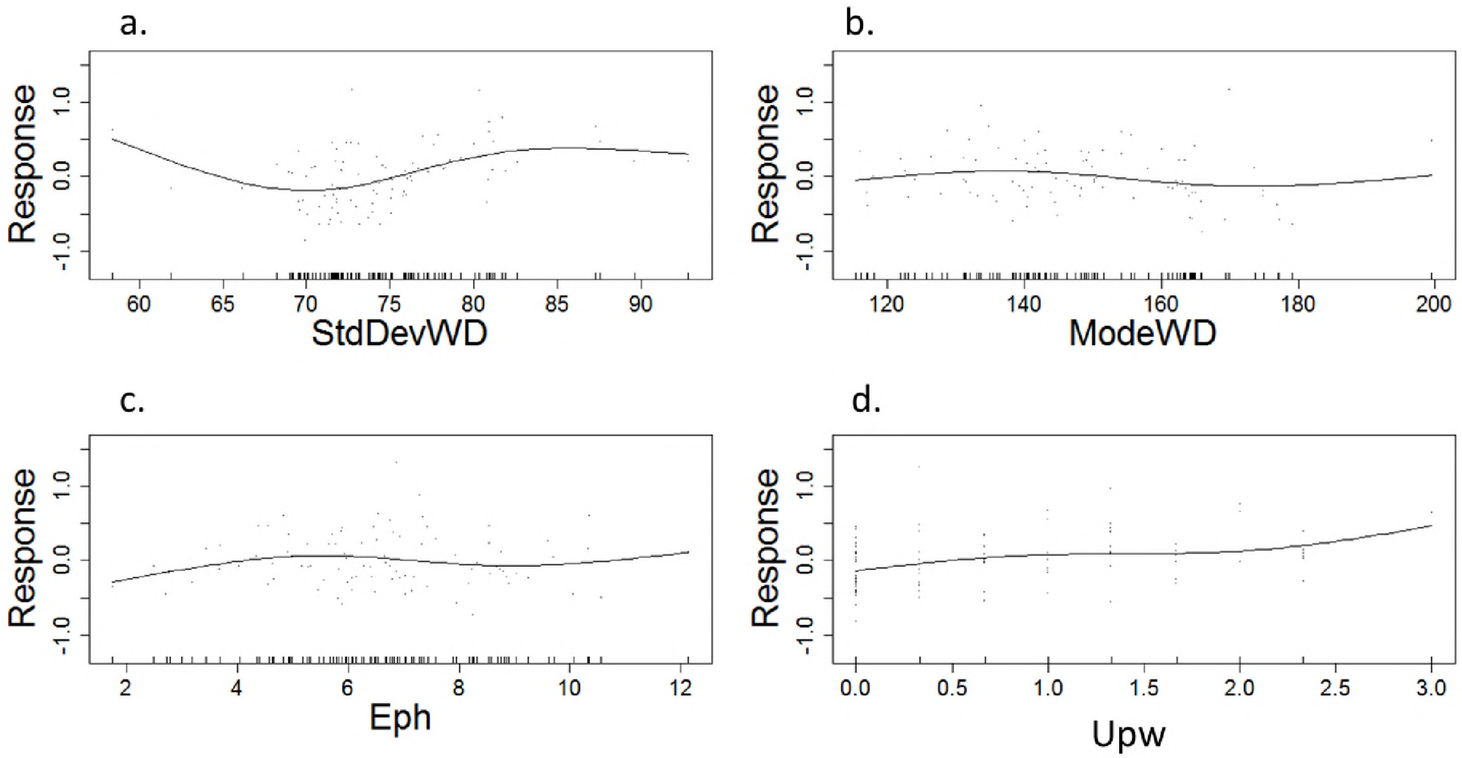

Figure 33: Partial GAM plots for the best binomial and positive models for Loligo reynaudii. The plots display the response shape of the chokka catch of each environmental parameter, independently of the other parameters, in relation to the probability of the chokka abundance. The ranges of environmental variables (a. mean bottom temperature; b. standard deviation in bottom temperature; c. mean SST, and d. standard deviation in SST) are represented on the x-axis and the probability of abundance of the species is represented on the y-axis (logit scale). The zero value indicates mean model estimates, while the positive values on the y-axis indicate increased catches and negative values depict decreased catches. The dots represent the residuals generated by the model.

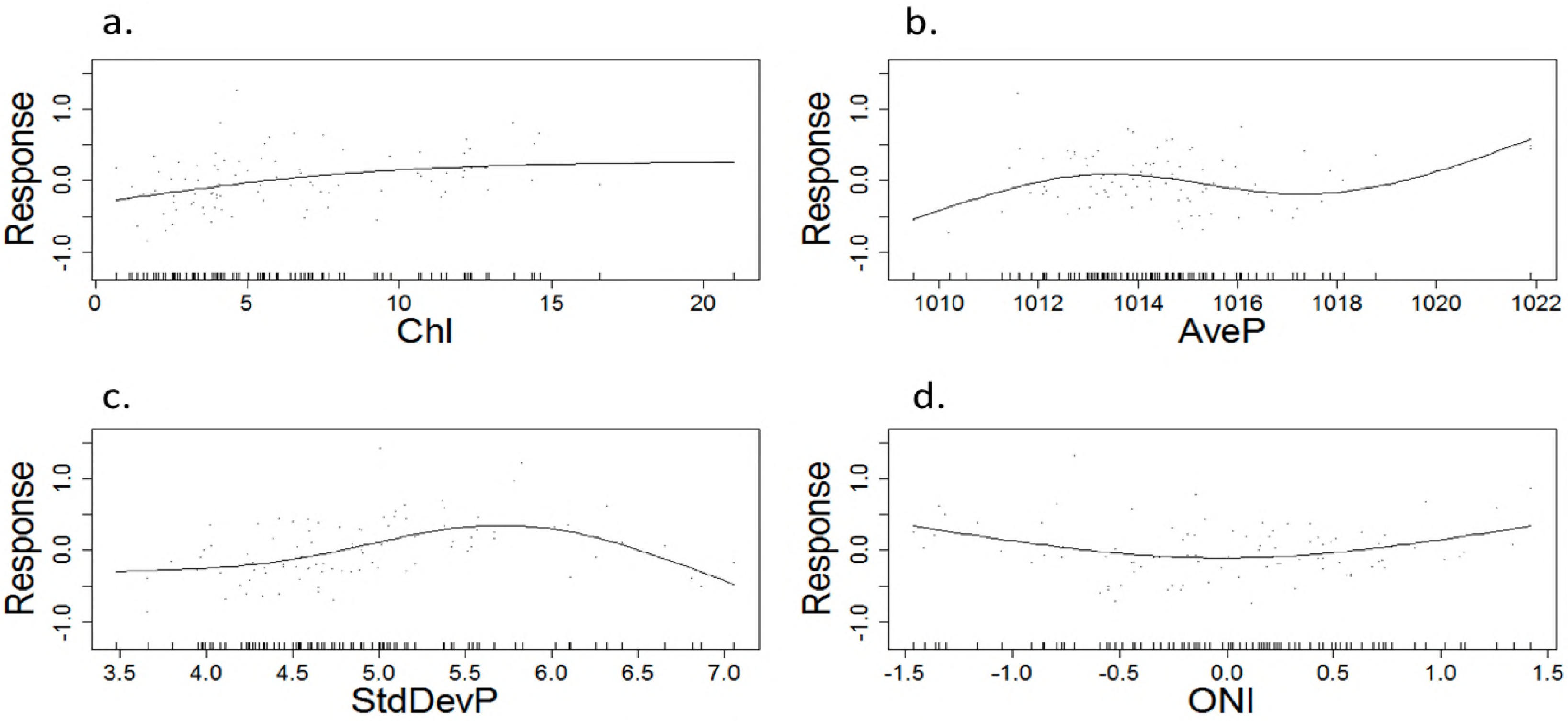

Figure 34: Partial GAM plots for the best binomial and positive models for Loligo reynaudii. The plots display the response shape of the chokka catch of each environmental parameter, independently of the other parameters, in relation to the probability of the chokka abundance. The ranges of environmental variables (a. concentration in chlorophyll-a; b. mean atmospheric pressure; c. standard deviation in atmospheric pressure, and d. the Oceanic Niño Index) are represented on the x-axis and the probability of abundance of the species is represented on the y-axis (logit scale). The zero value indicates mean model estimates, while the positive values on the y-axis indicate increased catches and negative values depict decreased catches. The dots represent the residuals generated by the model.

Large-scale climatic indices were included in the analysis in order to attempt a broader investigation that found that a monthly ONI indicates a negative catch response at values between -0.5 and 0.5 (Figure 34d). At all other values the catch response is positive, indicating a high catch for those years where an El Niño or a La Niña is observed. The AAO index was another large-scale climatic index that was investigated. The plotted model for the relationship between the monthly catch and the corresponding AAO index indicates a positive catch response at negative values (when the pressure cell is found closer to the equator), and negative catch response for positive AAO values (meaning a southward shift of the pressure cell) (Figure 35).

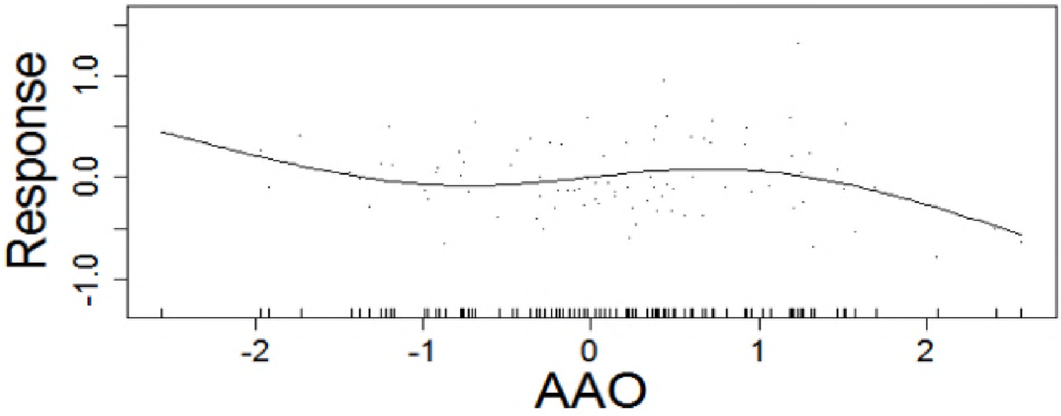

Figure 35: The relationship between chokka squid catch response and the Antarctic Oscillation Index (AAO) off the south coast of South Africa.

4.6 Construction of a predictive model using historical data

To investigate the ability of each of the parameters to predict the catches, individual GAM predictive models were constructed and observed values compared. Each of these individual models predicted that the catch would oscillate regularly over the years. This steady pattern in catches did not emerge in the observations, and thus a single predictor model was not viable as a predictive model. A detailed description of each parameter appears in Appendix 4.

A model was then constructed using the predicted values for a GAM and using all the investigated environmental parameters which showed an increase in catch in 1987/1988 and which were supported by the observed catch in the same years (Figure 36). Peaks in both the predicted and observed catches are evident in 1989, 1994 and 2003/2004 (Figure 36). Drops (or troughs) in both predicted and observed catches are evident in 1986/1987, 1990, 1991, 1992, 1994/1995, 1997, 1999, 2001, 2003, 2005, 2006/2007, 2010, 2012, 2013 (Figure 36). It is apparent that the observed catches (those recorded by the jig fishery) and the predicted catches generated by the GAM analysis of the relationship between the environmental parameters and catches do not come from the same distribution (Figure 37). This is supported by a Kolmogorov-Smirnov test which provides evidence that the data are not drawn from the same distribution ($p=0.004$). Thus, the predictive model failed to predict the catches based on the environmental parameters.

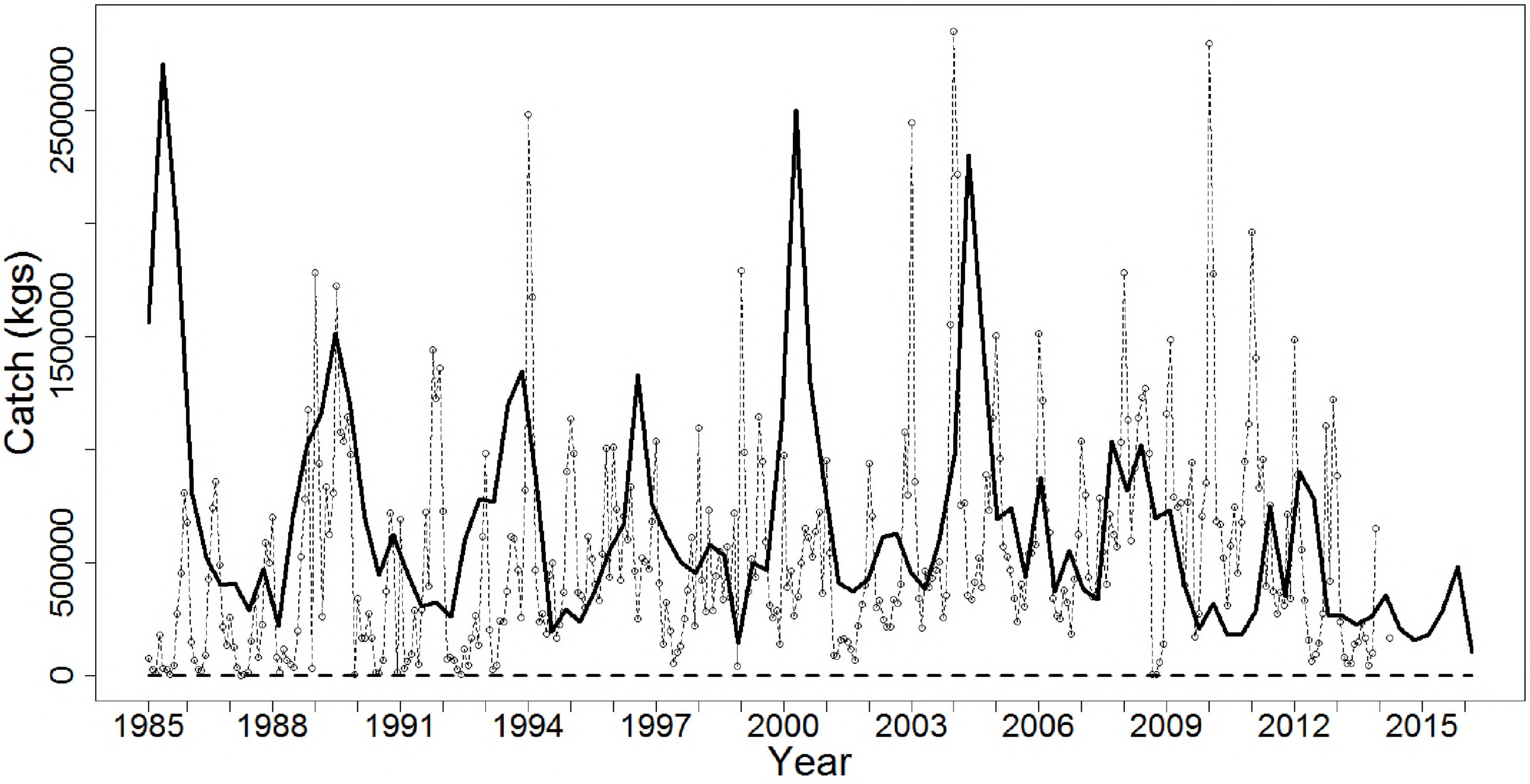

Figure 36: Predicted monthly chokka catch (black line) compared to the observed jig fishery total monthly catch (dotted line) since 1985. Predictions were generated by GAM analysis using environmental parameters.

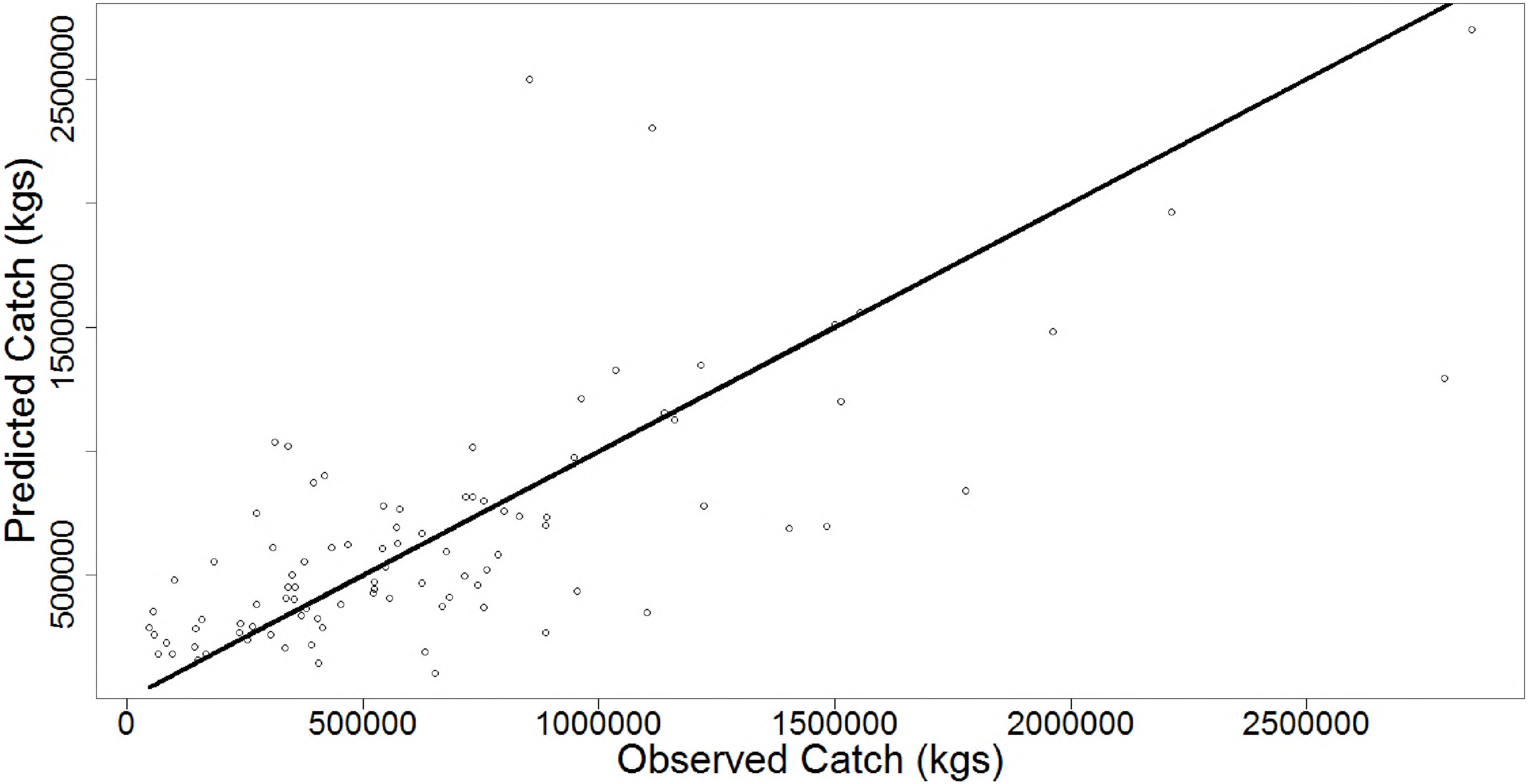

Figure 37: Correlation between predicted and observed catch generated by a GAM for the South African chokka fishery.

CHAPTER 5: DISCUSSION

A dramatic crash in the South African chokka fishery in 2012–2013 led to the initiation of this study. Strong evidence from previous squid studies, both internationally and locally, suggested that, given that fishing effort in this fishery had not increased over the last 30 years, a change in environmental conditions was possibly the underlying cause.

The study aimed to answer the five key questions stated in Chapter 2. The first focused on re-investigating natural cyclical trends in catch variability. The study looked for two types of trends in the catches: a seasonal trend in monthly catches, and an inter-annual trend in catches. In the first case, a strong seasonal trend in monthly catches was observed with a peak in summer catches (Figure 7). Previous studies described two seasonal peaks in chokka catches (Olyott et al., 2006), one in summer, as observed in this study, and a second, smaller peak in winter. These peaks were linked to reproductive seasonality (Olyott et al., 2006). As peaks in catches indicate increased spawning activity in the chokka squid fishery, a change in the seasonal distribution in catches could be due to environmentally driven changes in spawning patterns. It could therefore be hypothesised that the lack of a winter peak, certainly in more recent years, may be caused by shifts in environmental patterns. Similar results were observed by Wedekind and Küng (2010) who found that the *Thymallus thymallus* spawning season shifted by three weeks in response to warming water temperatures. Seasonal trends in catches are important to monitor as they provide information on the spawner biomass. Although seasonal trends in monthly catches are common, inter-annual trends are not. This research did not reveal repetitive patterns in the inter-annual trend in catches, even though a general increase in catches was evident up until 2010. This is a common result for cephalopods which have exhibited high inter-annual variability with low catch predictability due to the high plasticity of the organism (Pierce and Boyle, 2003; Waluda et al., 1999). The inter-annual variability is likely to be a result of variability in the environmental conditions observed in section 3.3 (Shannon et al., 1988). Inter-annual trends in fishery catches are not common in marine ectothermic organisms, except in the King George whiting, which has been found to display a quasi-decadal trend in catches (Jenkins, 2005). The evidence of high inter-annual variability in most fisheries has been attributed to a strong environmental influence on many species (eg. Shannon et al., 1988; Lynam et al., 2004). Both the temporal trend and the inter-annual variability support the evidence of a strong abundance-environment relationship; however, it is unclear which life history stage these environmental parameters are likely to influence.

The potential life history stage of the chokka, with which these environmental parameters were most strongly correlated, was investigated using monthly lags of the environmental data and testing the strength of a NBGLM between the environmental parameter and the catches. Because of the nature of squid development, monthly lags were related to the life history stages as follows: a 0- to 3-month lag was defined as the spawning phase (influences the squid being caught most directly); the 4- to 9-month lag was defined as the juvenile phase (which included all life stages from hatching to sexual maturity), and 10 to 13 months was defined as the hatching phase (the squid being caught would be approximately one year old at sexual maturity). The survival and abundance of a species depends on the recruitment of that species into the ecosystem.

Successful recruitment into the fishery begins with the successful hatching of the eggs. Investigations into the environmental interactions with fishery resources have proved to be important in defining recruitment variability (Cardinale and Arrhenius, 2000). Waluda et al. (2001) found that *Illex argentinus* abundance was linked to hatching success that was influenced by the SST, similar to the findings of this study. The hatching and spawning success of previous generations of chokka is influenced by the mean SST, the variation in BT, the mean atmospheric pressure, the variation in wind direction and the AAO. Hatching time for chokka is influenced by temperature (Oosthuizen and Roberts, 2009), with the optimum temperature range for hatching between 10°C and 13°C (Oosthuizen and Roberts, 2009). Spawning may occur at a time and location when conditions are not favourable and hatching when conditions are favourable, or vice versa (Hancke, 2010). As a result, it is important to consider the environment driving the hatching time, and the strong influence of temperature on spawning and hatching is unsurprising.

The mean atmospheric pressure has been linked to rainfall with increased pressure resulting in decreased rainfall (Nicholls, 2010). As a result, a low mean atmospheric pressure displays high expected rainfall, which would result in high river runoff and high turbidity. In species such as cephalopods, which rely heavily on visual cues during spawning activity (Lauria et al., 2016), high turbidity usually results in decreased spawning success and decreased catches the following year, which the findings of this study support (Figure 34). The AAO is linked to pressure and rainfall and as such could also be expected to influence the spawning success of visually dependent species. Variation in wind direction can result in variability in localised currents and the position offshore of the major currents, such as the Agulhas current (Lutjeharms and de Ruijter, 1996). As currents influence the distribution of paralarvae (Hancke, 2010), the hatching success and recruitment of the juveniles into the fishery is likely to be affected by the currents. These currents also drive nutrient availability and temperature regimes for the hatching eggs. Once the eggs have hatched and enter the paralarval phase, environmental drivers influence the survival and recruitment into the future fishery in different ways.

The juvenile and paralarval phase is vulnerable to environmental drivers that affect the growth rate. The survival of this phase is the key driver in the recruitment into marine demersal fisheries (Myers and Cadigan, 1993). Growth and mortality of marine organisms have been related to temperature, which by inference, was related to latitude (Houde, 1989). This relationship exposed a positive linear relationship ($r^2=0.57$) and a relationship between temperature and the larval stage duration was also found (Houde, 1989). Temperature (SST and BT) is therefore likely to be correlated to the developmental time of organisms, with optimal growth rates and high fecundity rates found in temperature ranges specific to certain species (Pörtner et al., 2001). The temperature-growth relationship is due to temperature-specific oxygen binding by blood cells and is found in both teleosts (Pörtner et al., 2001) and cephalopods (Zielinski et al., 2001). The growth and survival of marine organisms have also been related to water depth and turbidity (Hudson, 1981), and food availability and quality (St. John et al., 2001).

In this study, the growth phase was correlated to variation in the SST, mean bottom temperature, the minimum and maximum wind speed, the number of upwelling events, the number of hours of easterly winds blowing, the chlorophyll-*a* concentration, the predominant wind direction and the mean wind direction. Primary productivity was related to upwelling events, but this relationship is not directly proportional and can be heavily dependent on the cessation of heavy winds (Botsford et al., 2006). The minimum and maximum wind speed, number of upwelling events, the hours of easterly winds blowing, the predominant and mean wind direction and the chlorophyll-*a* concentration are all related to the intensity and frequency of upwelling events (Botsford et al., 2003). As upwelling leads to increased productivity (increased chlorophyll-*a* concentrations) of the ocean, an increase in the growth and survival of the juvenile phase is to be expected (Botsford et al., 2006, 2003). Previous studies have shown that upwelling is related to the abundance of cephalopods and influences the distribution of organisms (González et al., 2005). The same has also been found in finfish fisheries (Daskalov et al., 2003; Santos et al., 2012), and off the coast of West Africa, *Sardinops sagax* was shown to experience faster growth rates and better retention of juveniles in the area as a result of upwelling events (Daskalov et al., 2003). This provides strong evidence of the importance of upwelling events during the growth phase of juvenile marine organisms, which in turn results in strong recruitment into the spawning stock of the fishery.

The spawning phase was determined as 0 to 3 months because the fishery targets the spawning aggregations and a minimal lag would directly influence these spawning organisms. The variability in the wind speed and ONI were found to best fit the chokka catches when they were lagged by 0 and 3 months, respectively. It is thus hypothesised that the influence of the wind speed and the ONI is strongest when the chokka are spawning. As this stage is also directly related to the catching success of the fishers, these direct relationships could also reflect optimum fishing conditions. This has also been found for wind speed (Drinkwater et al., 2006) which is one of the drivers of wave activity and therefore a strong determinant of seagoing conditions. Variability in wind speed has previously been found to expose a significant linear relationship to the survival of *Engraulis mordax* larvae during the spawning season (Peterman and Bradford, 1987) because the concentration of larval food during hatching was maintained (Peterman and Bradford, 1987). Similarly, in this study, high wind variability during the spawning season led to a negative catch response (Figure 32). Thus, the relationship between the chokka catch and the wind speed variability is complicated and needs further investigation.

The spawning aggregations were also influenced by the ONI, which indicated a positive influence on chokka catches in both El Niño and La Niña events (Figure 34). This was unexpected as previous studies have found that El Niño events cause a drop in cephalopod catch (Arntz et al., 2006; Jackson and Domeier, 2003). However, a local study by Roberts (1999) indicates that El Niño events can result in no change in the chokka catches because of interactions with other environmental parameters, such as SST anomalies. These conflicting results emphasise that further studies need to be conducted into the direct effects of the ENSO on South African chokka.

In summary, this study highlighted important relationships between different life history stages of the chokka and specific environmental variability based on the lagged data. With these relationships exposed, it was important to quantify the relationship further.

Globally, quantified relationships between fishery resource abundance and environmental parameters have been highly sought after for many years (eg. Shannon et al., 1988; Houde, 1989; Bellido et al., 2001; Daskalov et al., 2003). The results of several studies have varied across species (Hedger et al., 2004; Klyashtorin, 2001; Lynam et al., 2004), gender (Pecl et al., 2004) and locality (Challier et al., 2005), as well as over time (Daskalov et al., 2003). The relationships revealed have proved to be complicated and rely on the selection of parameters as well as statistical and modelling technique (Stergiou and Christou, 1996). A GAM analysis in this study provided evidence of a strong relationship (r^2=0.707), defining 81.5% of the deviance. The 17 environmental parameters used in this study all proved to have a significant relationship to the catch when incorporated into the model. Other studies have found the relationship between abundance and environmental parameters to be strengthened by selecting a few parameters rather than incorporating the entire suite of parameters (Bigelow et al., 1999). The strong relationship exposed in this study supports a long-standing hypothesis of environmental influence on the survival and abundance of marine organisms and, like many others, was intended to be used to construct a predictive model.

Predictive models have been constructed using GAM analyses with varying success. For example, Murase et al. (2009) found that GAM analyses on the distribution and biomass of krill, Japanese anchovy and sand lance provided a good prediction of the pattern of distribution, but the GAMs underestimated the biomass in the cells (Murase et al., 2009). GAMs are useful tools in quantitative ecological modelling; however, their predictive implementation is limited. This finding is supported by Denis et al. (2002) who also found that the trends in Loliginid distribution and abundance were explained by GAMs, but that the predictions in biomass were incorrect (Denis et al., 2002). Further studies found that GAM analyses were not appropriate for predicting abundances and should rather be used to improve knowledge of environment-abundance relationships (Daskalov et al., 2003). Similarly, although this research found a strong GAM relationship, the predictive ability of the analysis was weak. The GAM predicted the general trend in peaks and troughs of catches from 1985 to 2005, but failed thereafter. Although a similar trend was observed in the predictive model, there was a high level of under- and over-estimating abundances, suggesting a cautious approach when using the model to establish management strategies.

The failure in prediction observed in this study could be due to the selection of incorrect or insufficient environmental parameters, or to the use of an inappropriate model, or the presence of other influences that cause noise about the model. The selection of correct environmental parameters in developing a predictive environment-abundance model is crucial to the success of that model. Although this study initially considered many environmental parameters, some could not be used because the data were inaccessible. Schon (2000) found that key environmental parameters used to model environment-chokka catches were turbidity, lunar cycles and wave height. Many other studies also found turbidity to be important in influencing the distribution and behaviour of organisms (eg. Daskalov et al., 2003; Puerta et al., 2014). However, historical data for turbidity are unavailable.

Current has also been found to be an influential environmental driver. Hancke (2010) found that current strength and direction were key components in the distribution of chokka paralarvae. Similarly, Arkhipkin et al. (2006) found that the distribution, and therefore survival, of *Loligo gahi* paralarvae in the Patagonian Sea largely depended on the position and strength of the Falkland Current. *In situ* historical current data were also unavailable.

Environmental parameters such as bathymetry, wave activity and spatial data (latitude and longitude) have also been found to be important environmental parameters used in environment-fishery modelling (Bigelow et al., 1999; Hsieh et al., 2009; Murase et al., 2009). Further parameters which have been hypothesised as influencing the successful spawning of chokka squid include wave surge and darkness-light during fishing (Roberts, 1998). This study made use of environmental data across the entire chokka spawning area, which eliminated spatial environmental and bathymetrical variability. The incorporation of spatial data has been found to alter the results of relationships considerably (Keitt et al., 2002), and as such, could be used in future attempts to model the environment-abundance relationship for chokka. This study could be improved by investigating the spatial distributions and abundances of chokka in relation to the localised changes in environment. This higher resolution in data could also lead to the construction of more accurate abundance-relationship models. The inclusion of further ecological (such as predator abundances) and biological indicators (such as egg biomass) could decrease the noise around the predictive model and result in a more accurate prediction of catches.

An alternate reason for the failure of the predictive model could be weaknesses in the modelling approach. GAMs have the advantage of seeking strong correlations between multiple environmental indices and fishery abundances. However, these are based on the goodness-of-fit of the data (Santos et al., 2012) and thus the predictive uses of the models are limited. However, GAM analyses remain one of the strongest modelling approaches that can include multiple datasets. For example, in comparing the ability of data-driven models to predict the relationship between mortality after hospitalisation and acute myocardial infarction, Austin (2007) found that GAM analyses were amongst the strongest predictive models which use previously collected data. At the time of writing this thesis, the use of GAM analyses in modelling ecosystem interactions was considered the best modelling technique because of the flexibility of underlying regression functions (Lauria et al., 2016), and hence its choice for this study. The predictive model, however, did not provide evidence of a cause for the crash in the chokka fishery in 2012–2013.

Local fishers reported that the drop in chokka catches during the 2012–2013 decline was not isolated in spatial or seasonal distribution (Sauer, pers. comm.). Changes in the abundance were probably due to substantial changes in the environment or changes in fishing pressure. Because of the strong relationship this study found between the environment and the chokka abundance, it is possible that an environmentally driven crash in the fishery would probably coincide with a drastic change in environment. This was not observed. Although some drastic changes were observed over time (e.g. wind direction shift between 1991 and 1994) (Figure 16), the timing of these changes was too early to have influenced the catches. A drop in the mean SST in 2011 was the only environmental indicator that could have influenced the recruitment success of the 2012 cohort. The annual mean SST should thus be monitored further for its influence on chokka catch.

Although changes in fishing pressure should not be an influence due to a constant TAE since 1987, there has been evidence of increased fishing efficiency that could lead to uncontrolled increases in TAE. Furthermore, some of the chokka boats have begun to use two anchors from the bow which are manipulated to hold the boat over the spawning aggregation for longer periods of time (Zeidberg et al., 2004). Further work on the potential damage of additional anchors on the chokka egg beds is currently underway.

Other possible reasons for the decline in chokka catches include predator-prey relationships which were not explored in this study and could cause noise around the environmental-abundance relationships (Cherel et al., 2004; Christensen, 1996; Roberts, 1998). The incorporation of predator and prey abundance into ecological studies such as these could provide a stronger relationship with higher predictive accuracy. For example, a high abundance of predators has been linked to a decrease in prey species on coral reefs (Hixon and Beets, 1993), and a similar relationship can be found for cephalopods (Caddy and Rodhouse, 1998).

Future work should investigate the relationship between chokka and the environment on a finer spatial and temporal scale to obtain a finer resolution of the relationship. The direct effects of environmental parameters on different ontogenetic stages of the chokka should also be investigated to provide a better understanding of the behavioural, genetic and physiological responses of chokka to the environment. Importantly, to advance this area of research and to define the relationship between environmental parameters such as turbidity and current, time series data of these parameters are necessary and methods to obtain such long-term data need to be developed.

In conclusion, this study intended to define and quantify the relationship between the environment and chokka squid catches. This relationship was compelling and implied a heavy influence of the environment on the survival and recruitment of cephalopods. However, when this relationship was tested and a predictive model constructed, the relationship decayed. It is thus evident that the environment-abundance relationship of these cephalopods is, like many others, highly complex and yet to be accurately defined.

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APENDICES

Appendix 1

The data appears to be Poisson distributed rather than Gaussian distributed (Figure 28). This was incorporated into all the analyses in order to account for this assumption. The GLM model was inspected for overdispersion of residuals and was found to have an overdispersion value of 109011 and thus a negative binomial GLM was performed as the overdispersion value of this model was 1.30.

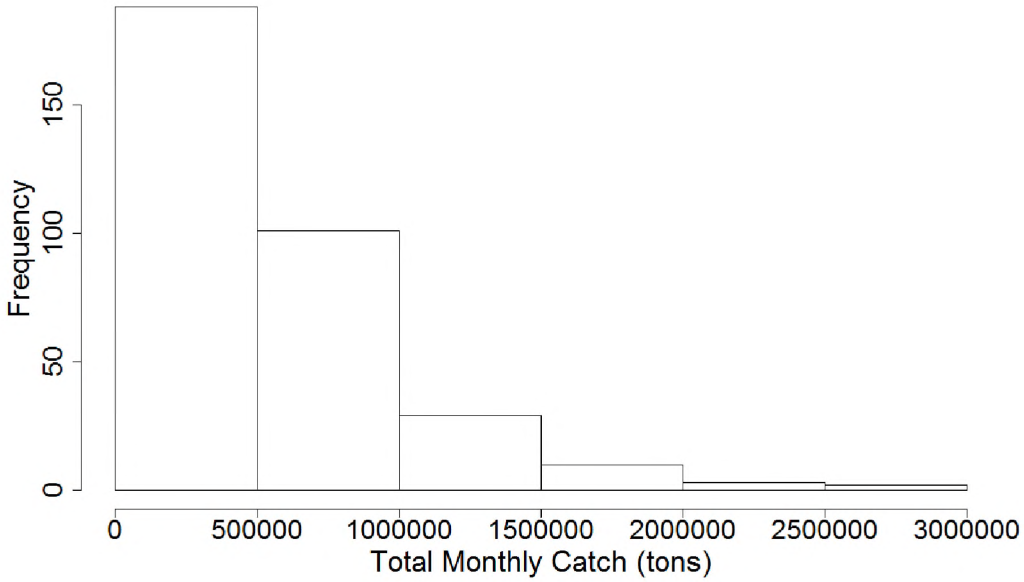

Figure 38: The frequency histogram of the data distribution of catch over the years.

The first panel of Figure 29 provides a test for heteroscedasticity of the residuals, which when accompanied by a residual vs fitted linear test can be found to describe the residuals as heteroscedastic (p=0.9388). The QQ-plot in the second panel of Figure 29 provides evidence for non-normal distributed (p=0.55) residuals and the fourth panel indicates that, although there are some observations which do have higher leverage than others (observation 253, 301 and 321); all the observations fall within Cook's distance and thus do not affect the outcome significantly.

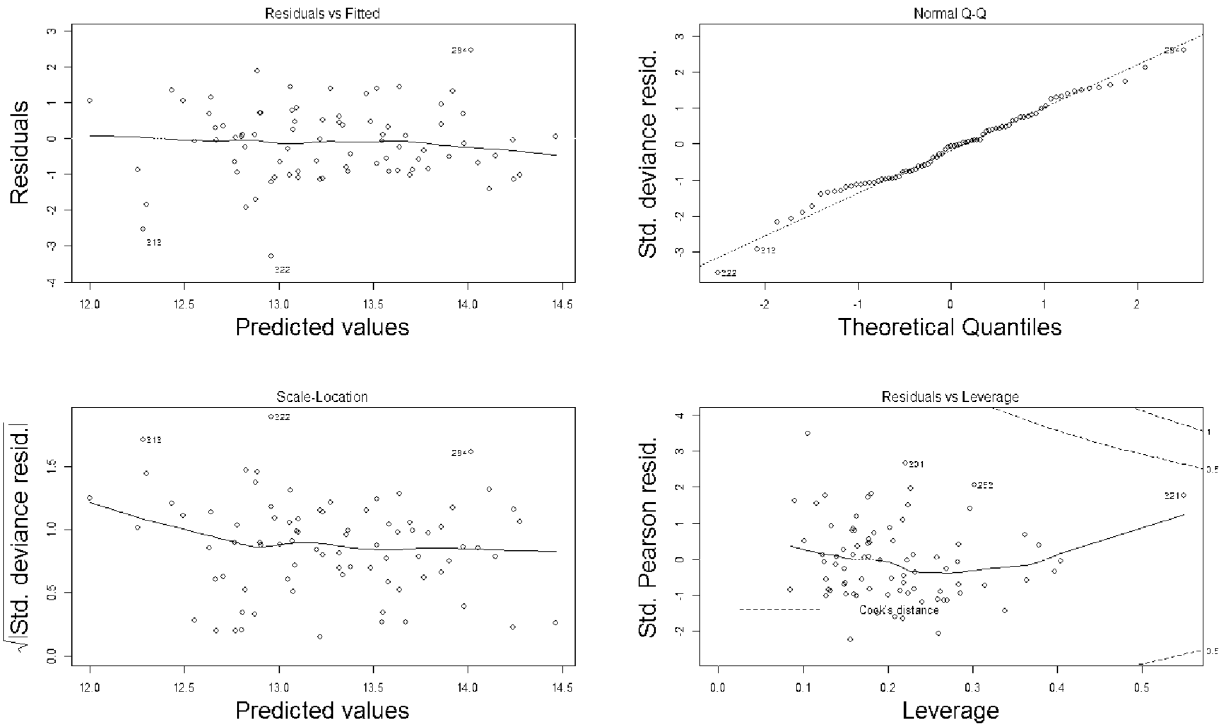

Figure 39: The diagnostic plots for the negative binomial generalised linear model, which included all the environmental variables investigated.

In the GAM the residuals are not normally distributed (p=7.459e-07 and Figure 31); however, this is not an assumption made by a GAM and thus is not necessary to be met. The distribution of the residuals appears to be of the Poisson distribution (Figure 30). The residuals are randomly distributed (Figure 32).

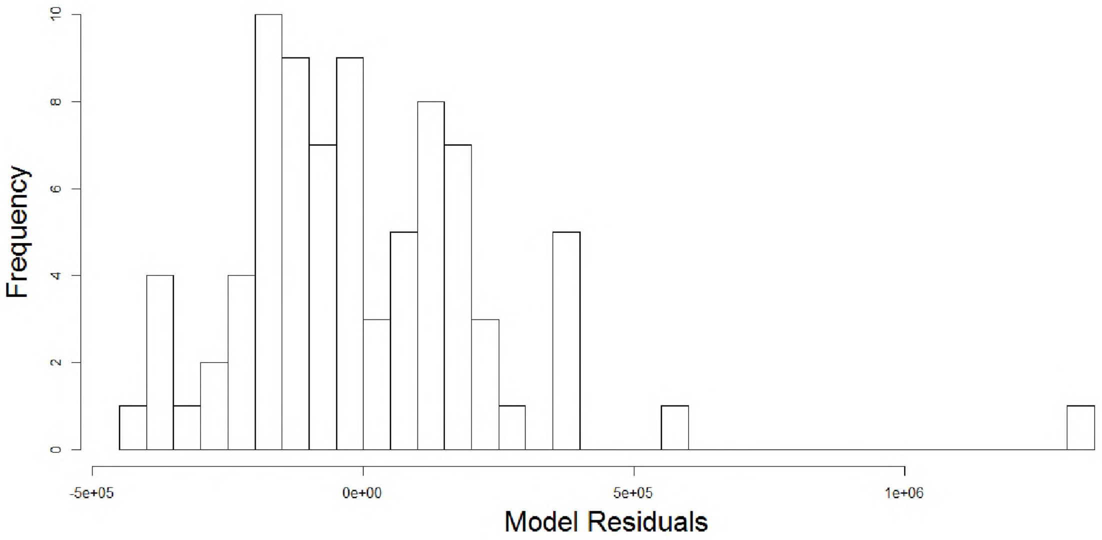

Figure 40: A frequency histogram indicating the distribution of the residuals in the generalised additive model.

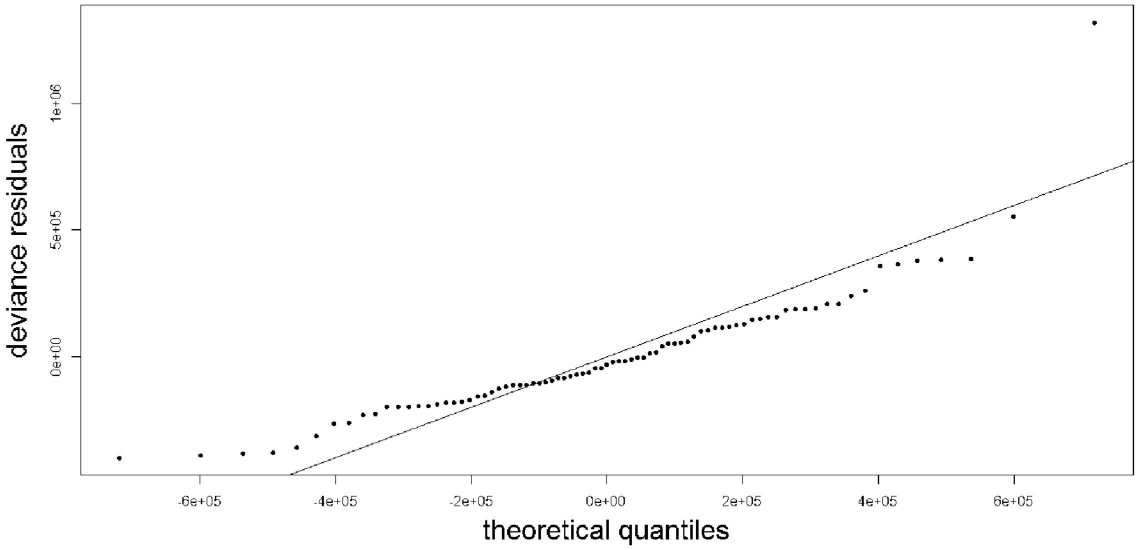

Figure 41: The quantile-quantile plot of the generalised additive model residuals with a cubic smoother to test for normality.

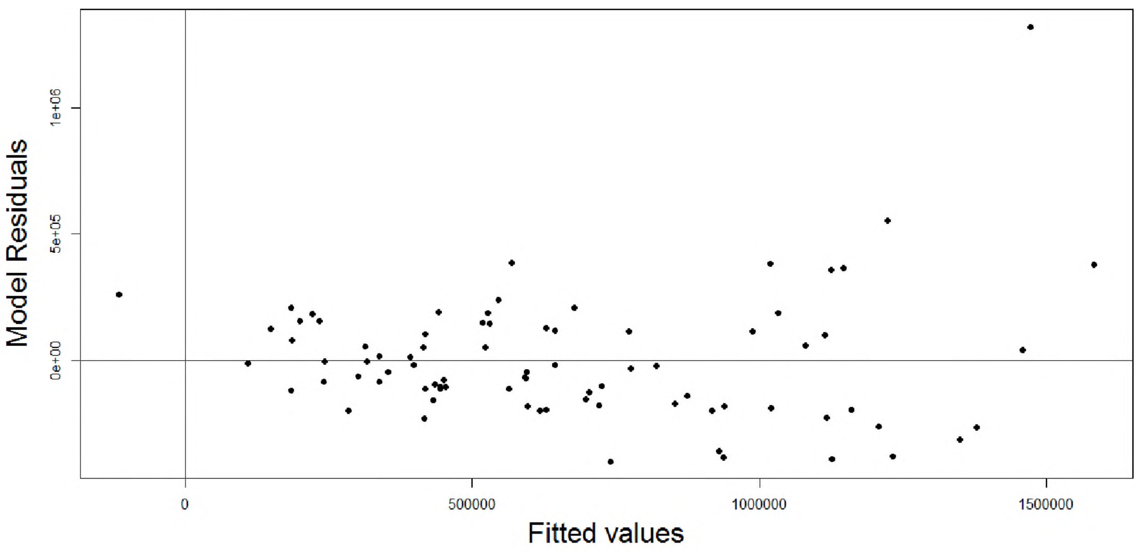

Figure 42: The distribution of the residuals against the fitted values to test for homoscedasticity of the residuals.

Appendix 2

Table 4: The relative Aikiake's Information Criteria for the monthly lag for each of the environmental variables.

Parameter	Month lag	AIC value
Standard Deviation in WS	0	9646.98
ONI	3	9899.91
Standard Deviation in SST	4	2574.812
Mean BT	4	9459.02
Minimum WS	5	9619.8
Number of upwelling events	6	5872.857
Hours of Easterly	6	9651.705
Chlorophyll Concentration	8	3025.049
Maximum WS	9	8633.95
Predominant WD	9	9651.75
Mean WD	9	9664.08
Mean SST	10	3103.664
Standard Deviation in BT	10	9458.31

Mean atmP	10	9646.64
Standard Deviation in atmP	10	9679.67
Standard Deviation in WD	11	9655.37
AAO	13	10375.26

Appendix 3

Table 5: The calculated AIC values indicating the ten models that are most parsimonious.

Formula	AIC value
Catch~ AveBT + StdDevBT+ AveSST+ StdDevSST+ StdDevWS+ AveWD+ StdDevWD+ AveP+ StdDevP+ ONI+ Chl+ MaxWS+ MinWS+ Eph+ upw+ AAO	5921724
Catch~ AveBT + StdDevBT+ AveSST+ StdDevSST+ StdDevWS+ AveWD+ StdDevWD+ AveP+ StdDevP+ ONI+ Chl+ MaxWS+ MinWS+ ModeWD+ Eph+ upw+ AAO	5874290
Catch~ AveBT + StdDevBT+ AveSST+ StdDevSST+ StdDevWS+ AveWD+ StdDevWD+ AveP+ StdDevP+ ONI+ Chl+ MaxWS+ MinWS+ ModeWD+ upw+ AAO	6005782
Catch~AveBT + StdDevBT+ AveSST+ StdDevSST+ StdDevWS+ AveWD+ StdDevWD+ AveP+ StdDevP+ ONI+ Chl+ MaxWS+ MinWS+ ModeWD+ Eph+ upw,	6005795
Catch~AveBT + StdDevBT+ AveSST+ StdDevSST+ StdDevWS+ AveWD+ StdDevWD+ AveP+ StdDevP+ ONI+ Chl+ MaxWS+ MinWS+ ModeWD+ Eph+ AAO	6042239
Catch~AveBT + StdDevBT+ AveSST+ StdDevSST+ StdDevWS+ AveWD+ StdDevWD+ StdDevP+ ONI+ Chl+ MaxWS+ MinWS+ ModeWD+ Eph+ upw+ AAO	6172088
Catch~AveBT + StdDevBT+ AveSST+ StdDevSST+ StdDevWS+ AveWD+ StdDevWD+ AveP+ StdDevP+ Chl+ MaxWS+ MinWS+ ModeWD+ Eph+ upw+ AAO	6175200
Catch~AveBT + StdDevBT+ AveSST+ StdDevSST+ StdDevWS+ StdDevWD+ AveP+ StdDevP+ ONI+ Chl+ MaxWS+ MinWS+ ModeWD+ Eph+ upw+ AAO	6441505

Catch~AveBT + StdDevBT+ AveSST+ StdDevSST+ StdDevWS+ AveWD+ StdDevWD+ AveP+ ONI+ Chl+ MaxWS+ MinWS+ ModeWD+ Eph+ upw+ AAO	6548630
Catch~AveBT + StdDevBT+ AveSST+ StdDevSST+ StdDevWS+ AveWD+ StdDevWD+ AveP+ StdDevP+ ONI+ Chl+ MinWS+ ModeWD+ Eph+ upw+ AAO	6558751

Appendix 4

According to the mean bottom temperature predictive model the catch were predicted to constantly fluctuate since 1985 between 200000kg and 800000kg (Figure 20a). As seen in section 3.1, this trend was not observed and thus the mean bottom temperature cannot be used as a single predictor of the chokka catch. The standard deviation in bottom temperature predicted a peak in catch in 1998 (Figure 20b); however this peak was not observed in the catch in 1998 and thus this model cannot reliably predict trends in catch or observed catch. The SST predictions present fluctuations in catch ranging between 500000kg and 1100000kg with no significant drops and large peaks (Figure 20c and d). The observed catch fell across a broader range of values and thus provide evidence for the rejection of the SST values as single predictors of chokka catch.

The maximum wind speed predictions indicate peaks in catch of 1250000kg and 1300000kg in 1987/1988 and 1990, respectively (Figure 21a). All other years show catch fluctuating around 500000kg (Figure 21a). These peaks were not observed in the collected data and thus the predictions in catch based on the maximum wind speed The predictions made by the minimum wind speed shows fluctuations from 300000kg to 600000kg with a constant catch of around 600000kg since 2007 (Figure 21b). The standard deviation in wind speed predicts that the catch in 1991 the catch dropped from 500000kg to 100000kg (Figure 21c). The catch exhibited increased fluctuations ranging between 400000kg and 750000kg since 2003 with no distinct drops in catch (Figure 21c).

The mean wind direction predicted that the catch would fluctuate between 250000kg and 600000kg (Figure 21d). The standard deviation in wind direction predicted fluctuations between 250000kg and 750000kg, with peaks of 2250000kg and 2200000kg in 2003/2004 and 2004/2009 respectively (Figure 22a). The predominant wind direction has predicted that the catch would fluctuate between 400000kg and 700000kg with a drop to 200000kg in 1991/1992 (Figure 22b). The number of hours of easterlies blown per day indicates a fluctuation in catch between 400000kg and 900000kg, with the fluctuations decreasing in consistency from 2005 to between 400000kg and 600000kg (Figure 22c).

The number of upwelling events per months predicted a constant fluctuation between 300000kg and 800000kg, throughout the entire period (Figure 22d). The chlorophyll concentration provides evidence of an irregular fluctuation in catch, with a minor drop from 1000000kg in 2007 to 500000kg in 2013 (Figure 23a).

The mean atmospheric pressure provides a prediction of a constant fluctuation of between 450000kg and 700000kg every year between 1985 and 2004 (Figure 23b). In 2004 there was a predicted catch of 1100000kg, after which there is a fluctuation in catch around 550000kg with drops in catch to 400000kg in 2005, 2007, 2008, 2010, 2011, 2012 and 2013 (Figure 23b). The standard deviation in atmospheric pressure predicts a constant annual catch trend with catch increasing to around 500000kg in 2008 (Figure 23c). There is one peak in catch in 1993 (Figure 23c).

The ONI predicts jagged fluctuations in catch with no predictions of drops in catch around2013 and 2014 (Figure 23d). The AAO predicted fluctuations in catch with drops in catch predicted in 1988, 2012 and 2014 (Figure 24).