Fine-scale drivers of African Penguin prey dynamics in Algoa Bay, South Africa, and their impacts on penguin foraging ecology

by

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Declaration

This thesis reports results of original research I conducted under the auspices of the DST/NRF Centre of Excellence at the Percy FitzPatrick Institute, University of Cape Town. All assistance that I have received has been fully acknowledged. This work has not been submitted for a degree at any other university.

Signed by candidate

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Abstract

African Penguins (*Spheniscus demersus*) have undergone a dramatic decrease in their population since the turn of this century prompting the up-grading of their conservation status to 'endangered'. There is growing evidence that variation in the availability of their principle prey, pelagic shoaling fish, are driving this trend. This prey variability is driven by oceanographic factors as well as commercial purse-seine fishing operations. To isolate the direct impacts of fishing on the foraging performance of African Penguins, the primary oceanographic drivers of fish distribution and abundance were investigated by conducting fine-scale pelagic fish surveys around two of the largest breeding colonies of African Penguins in Algoa Bay, St Croix and Bird islands, between 2011 and 2014. Quantification of fish parameters were facilitated by a novel method using a recreational fish-finder and calibrating this instrument to a conventional scientific device. The specific types of fish assemblages selected for by African Penguins were then evaluated by looking at the correspondence in associations of fish and penguins recorded at sea using both counts and locations of foraging birds tracked simultaneously during a subset of fish surveys. Activity budgets of penguins calculated from these simultaneous deployments were modelled against the abundance of their prey to elucidate hypothesised functional relationships. Finally, the direct influence of purse-seine fishing on both targeted fish assemblages and penguin activity budgets were assessed by modelling interactions between known physical drivers of targeted fish assemblages and different levels of cumulative catches. Physical drivers of the three-dimensional distribution and abundance of fish varied between colonies with primary production playing the most important role around Bird Island but having little influence on fish around St Croix Island where factors associated with surface and sea-profile temperatures had a stronger influence. Results of both penguin count and track data highlight the importance of the vertical distribution of prey to the distribution of foraging African Penguins with the abundance of these assemblages having a significant influence on this species' activity budgets. Evidence for local depletion of pelagic fish was demonstrated for the waters around St Croix Island and the effects of purse-seine fishing on African Penguin foraging effort were significant when controlling for natural drivers of prey distribution. Results of this research should be applied to current conservation measures, most notably alleviating direct competition by purse-seine fishing operations during periods of reduced primary productivity and when the abundance of targeted fish aggregations are significantly diminished three months prior to and during the onset of the African Penguin breeding season.

Acknowledgements

This thesis would never have come into fruition were it not for the support and collaboration of many people who gave of their time and energy to support this worthy endeavor. I would like to acknowledge my supervisors for all the hard work they have contributed toward this thesis. Throughout the duration of this thesis, Peter Ryan has provided valuable insights into the complexities of predator-prey systems and, importantly, how information derived from these studies can be used, objectively, to unravel applied connections with the human influence. This thesis would never have existed were it not for the determination of Lorien Pichegru who was the driving force behind this project. In fact it was Lorien's research that formed the foundations of a lot of the work achieved here. She has developed an immense passion for African Penguins and their environment and continues to develop important research into the factors that limit this species' survival. I have no doubt that the work she has embarked on will help safeguard the ecosystem that African Penguins 'call home' in Algoa Bay. Understanding the complex nature of the interactions between the many facets explored during this thesis required some sophisticated statistical techniques that Miguel Lacerda was so obliging in dispensing during this study. Miguel is a great teacher who has this knack of understanding the limitations that biologists, such as myself, fail to register when diving into perplexing questions that require a level headed approach to objectively assessing dynamic mathematical processes. His patience, creativity and insight into the many analyses conducted during this study have helped immensely.

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A great deal of time during the course of this thesis was spent developing the method to quantify acoustically-derived fish school data from our recreational fish-finder. If my cousin, Murray Christian, had not introduced me to Ben Murrell, I am not sure we would have progressed this far. Ben is a

problem solver of note and took on our peculiar challenge of extracting meaningful data from our recreational fish-finder. Most of the leg work with coding the software used to achieve this was done by Arjun Khoosal for whom I am very grateful. I would like to thanks the staff at the Department of Forestry and Fisheries, Janet Coetzee, Carl van der Lingen, Dagmar Merkle, Johan Rademan and Jan van der Westhuizen for their support of this project both in terms of their logistical support in conducting the calibration survey and for their wealth of knowledge on all matters related to fish.

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Chapter 1

General Introduction

General Introduction

Predators play an integral role in shaping marine food webs through both consumptive, top-down processes which can have far-reaching consequences to marine ecosystem functioning (Estes & Palmisano 1974; Duffy 2002; Myers et al. 2007; Casini et al. 2012), and non-consumptive influences on prey communities (review by Peckarsky et al. 2008), such as their influence on aggregation patterns in schooling fish (Hamilton 1971; Sogard & Olla 1997). Marine top predators are inextricably linked to the availability of their prey, which is mediated by both bottom-up and top-down processes (Hunt et al. 1999). They are therefore indispensable to studies of the state of marine ecosystems and provide important cues for the management of marine resources (Hunsicker et al. 2011). A plethora of information on marine ecological systems has come from research on seabirds largely due to the accessible nature of this predator group (Montevecchi 1993; Piatt et al. 2007). Seabirds are useful indicators of ecosystem state, especially conditions that mediate the availability of their prey (Cairns 1987; Furness & Camphuysen 1997; Furness & Tasker 2000; Einoder 2009). Insights into ecosystem functioning using seabirds can be demonstrated at a variety of spatio-temporal scales. For instance, long-term population trends of certain seabird species reflect important decade-scale bottom-up processes driving large marine ecosystems (e.g. Duffy 1983; Reid et al. 1999). At finer spatio-temporal scales, seabird-prey interactions can reveal underlying mechanisms affecting seabird foraging effort that may have an important bearing on breeding success (Boersma & Rebstock 2009; Bertrand et al. 2014; Boyd et al. 2015). This information is critical for managing marine ecosystems that are intrinsically multi-scaled and where threats to these systems require knowledge of both large-scale drivers of ecosystem processes and finer-scale mechanisms underlying these processes.

Prey data - the missing link in marine predator-prey interaction studies

Research into seabird ecology has been enhanced by recent advances in biotelemetry technologies (Cooke et al. 2004; Hays et al. 2016) which allows detailed seabird movement data to be assessed against proxies for prey availability using oceanographic data (reviews in Wakefield et al. 2009 and Tremblay et al. 2009). This technology has shed light on important drivers of the at-sea distributions of seabirds including potential conflict zones with anthropogenic activities, such as commercial fishing operations (Karpouzi et al. 2007; Grémillet et al. 2015). Numerous studies have looked at the relationship between the distribution and abundance of seabird counts and acoustically determined prey (review by Hunt et al. 1999). Data collected during these studies are often facilitated by large research vessels conducting large-scale ecosystem or fisheries related research (e.g. Erikstad et al. 1990; Axelsen et al. 2001; Certain et al. 2011). Research focused on spatio-temporal patterns relevant to specific seabirds that include long-term but frequent surveys are less common. A serious impediment to these studies is the acquisition of prey data which requires specialised equipment, i.e. expensive calibrated scientific echo-sounders, and expertise in the form of qualified technicians, fishery scientists and acousticians. Research conducted by fishery scientists has mainly been driven by a need to estimate fish biomass to set total allowable catches for the fishing industry (Simmonds & MacLennan 2005) and the scales at which these studies are conducted are not usually conducive to fine-scale assessments. There is therefore a need for more accessible tools to quantify prey data at scales pertinent to marine predator-prey interactions.

Physical processes driving small pelagic fish populations

Small pelagic fish are planktivorous 'forage' fish species (ca < 30 cm) that are typically found at depths < 200 m (Fréon et al. 2005). Some of the largest populations of small pelagic fish are found in Eastern Boundary Upwelling Ecosystems (Chavez & Messié 2009) where a few species of small pelagic fish dominate intermediate trophic levels. Small pelagic fish comprise a significant component of so-called 'wasp-waist' ecosystems (Rice 1995) through bottom-up support for marine predators and top-down influences on lower trophic communities, such as zooplankton (Cury et al. 2000; Ayón et al. 2008). The influence of physical processes on pelagic fish populations is scale dependent (Hofmann & Powel 1998): at the shortest time scales (i.e. hours to days) processes that affect the location of prey, such as ambient light levels or turbidity, are important; over intermediate scales (months) physical upwelling structures play a more significant role, and; over large scales (years to decades) climatic cycles, such as El Niño events, are the primary drivers (Hofmann & Powel 1998; Fréon et al. 2005). Oceanographic processes that are known to affect small pelagic fish populations include: upwelling and associated primary productivity (Cury & Roy 1989; Pauly & Christensen 1995; Bakun & Broad 2003; Bertrand et al. 2004), temperature (Gammelsrød et al. 1998; Richardson et al. 1998; Gutiérrez et al. 2007; Swartzman et al. 2008; Xu et al. 2013; Mhlongo et al. 2015), salinity (Paramo et al. 2003; Fossheim et al. 2005), wind (Lloret et al. 2004; Katara et al. 2011), bathymetry and substratum (Maravelias 1999). These processes are not mutually exclusive and may operate at varying degrees on different life-stages of pelagic fish, i.e. egg, larvae, juvenile and adult stages. Most research involving associations between small pelagic fish and physical processes has been determined at medium- to long-term temporal scales and at coarse spatial resolutions. Knowledge on processes affecting the availability of small pelagic fish at scales relevant to seabirds, especially during the breeding season when their foraging ranges contract to the vicinity of their breeding colonies, are scarce (Bertrand et al. 2008, 2014). These fine-scale relationships are expected to play a significant role in mediating both the abundance and distribution (horizontal and vertical) of fish assemblages targeted by these seabird species.

Influence of fine-scale prey aggregations on the at-sea performance of seabirds

Foraging conditions exhibit a range of responses in seabirds at different temporal lags depending on the life history stage being investigated and are often masked by the ability of certain seabird life-history traits to buffer adverse environmental conditions (Cairns 1987). Population level responses of seabirds to prey abundance have been shown at coarse temporal scales (years to decades) and are usually quantified over coarse seabird distribution ranges (e.g. Duffy 1983; Crawford & Jahncke 1999; Crawford et al. 2006, 2011). Indices related to breeding success, such as chick growth rates and fledgling success, reflect habitat conditions over weeks to months and are generally adversely affected by prey biomass below mean abundance estimates and one-third of maximum biomass recorded (Cury et al. 2011). As with breeding success parameters, the response of fine-scale activity budgets, such as nest attendance rates and foraging effort, to variation in prey abundance are typically non-linear with poor conditions below certain thresholds in prey abundance exhibiting accelerated negative responses (Cairns 1987; Litzow & Piatt 2003; Harding et al. 2007; Cury et al. 2011). Quantification of activity budgets and simultaneous prey data provide opportunities to investigate underlying mechanistic processes influencing predator-prey relationships. These studies are rare (Bertrand et al. 2012; Boyd et al. 2015) but are expected to become more numerous due to technological advances.

Results of studies assessing the spatial dependencies of foraging seabirds, usually birds counted at sea, and their prey are influenced by the scale of local and regional prey distributions (Schneider & Duffy 1985; Erikstad et al. 1990; Piatt 1990; Becker & Beissinger 2003; Benoit-Bird & Au 2003; Vlietstra 2005). Many studies show weak associations between seabird numbers and prey abundance at fine spatial scales (Russell et al. 1992; review by Hunt et al. 1999). This is partly influenced by limitations imposed by specific morphological, behavioural and physiological constraints on different seabird species and how these influence accessibility to certain prey assemblages. For instance, the depth distribution of prey is more influential in determining the distribution of diving seabirds than composite estimates of fish abundance throughout the water column (Zamon et al. 1996; Boyd et al. 2015). These are important considerations when assessing the impacts of external drivers of prey distribution and abundance, such as physical processes and anthropogenic influences, on the performance of seabirds at sea, and, ultimately how this affects breeding success and survival.

Anthropogenic drivers of marine ecosystem change

The global footprint of human activities on the marine environment is ubiquitous (Halpern et al. 2008) with particularly high rates of over-exploitation in coastal areas (Jackson et al. 2001). Rates of ecosystem degradation have accelerated due to human population growth and associated demands for marine resources, the development of more efficient techniques for exploiting these resources, increased pollution, and the disruption of system stability by the combined effects of resource extraction and accelerated climate change (Jackson et al. 2001; Jackson 2008; Doney et al. 2012). The consequences of overfishing may transcend beyond just the target species, disrupting trophic structures (Pauly et al. 1998; Pauly & Palomares 2005) and, in some cases, entire ecosystems, such as the plight of the northern Benguela upwelling region following overfishing of pelagic fish stocks off Namibia in the 1970s (Roux et al. 2013). Top-predators, such as seabirds, are particularly vulnerable to commercial fishing activities both directly through bycatch related mortalities and, indirectly, through competition for the same prey resource (Tasker et al. 2000; Furness 2003). Evidence for negative impacts due to resource-competition are complicated by confounding processes that mask functional relationships between these consumers, such as natural variation in prey availability, trophic interactions, and specific prey assemblages targeted by fisheries and seabirds (Duffy et al. 1987; Furness 2003; Engelhard et al. 2014). Furthermore, demonstrating cause and effect requires evidence of localised prey depletion due to fisheries which has rarely been demonstrated (Rogers et al. 2013).

Penguins (Spheniscidae) are amongst the most threatened seabird taxa (Croxall et al. 2012) with 10 of the 18 species (55 %) currently classified as threatened (IUCN 2015). The genus *Spheniscus* comprises four piscivorous species, three of which are threatened by resource competition due to commercial fishing operations, notably purse-seine fishing (Trathan et al. 2014).

Study species - African Penguins *Spheniscus demersus*

Distribution, population trends and threats

African Penguins are endemic to the Benguela Upwelling Region, one of four major eastern boundary upwelling ecosystems globally (Chavez & Messié 2009). The distribution of African Penguins ranges from central Namibia on southern Africa's west coast to Algoa Bay on the south coast of South Africa, currently breeding at 24 islands and 4 coastal localities (Crawford et al. 2011). In the early twentieth century the estimated population was ca 1.5 - 3 million birds (Crawford et al.

2007) which was reduced to ca. 296 000 birds in 1956 (Rand 1963a,b) largely as a result of guano and egg harvesting (Rand 1969; Siegfried & Crawford 1978). Population numbers were estimated at ca 220 000 birds in the 1970s which decreased to ca 180 000 birds in the early 1990s (Crawford et al. 1995) largely attributed to major population decreases in Namibia following overfishing of pelagic fish stocks there in the 1970s (Crawford & Shelton 1978; Boyer 1996; Roux et al. 2013). African Penguins are currently classified as 'endangered' (IUCN 2015) following an estimated 60% decrease in population size between 2001 and 2009 and its population is currently estimated at ca. 34 000 birds, the lowest numbers ever recorded (Crawford et al. 2014). Most of the recent decrease in numbers occurred off South Africa, which supports 80% of the global population. Reasons for this recent collapse include: a shift in the distribution of their predominant food, sardines (*Sardinops sagax)* and anchovies (*Engraulis encrasicolus)* (Roy et al. 2007; Coetzee et al. 2008; Crawford et al. 2011); potential competition with purse-seine fisheries (Crawford et al. 2006; Pichegru et al. 2010, 2012; Weller et al. 2014; Sherley et al. 2015); heightened mortality due to predation (Weller et al. 2016; Pichegru 2012), oiling (Wolfaardt et al. 2009) and disease (Schultz & Whittington 2005); Allee effects on group foraging dynamics (Ryan et al. 2012); and, the impacts of climate change on breeding conditions on land and on marine ecosystem dynamics (Lei et al. 2014; Weller et al. 2016). Since the 1990s, numbers of both breeding and non-breeding African Penguins have been correlated with the abundance of their principle prey species (Crawford et al. 2011). In 2008 the South African Department of Agriculture, Forestry and Fisheries (DAFF) in collaboration with the Department of Environmental Affairs (DEA), scientists and non-governmental organisation representatives formed the Island Closure Task Team (ICTT). The purpose of this initiative was to assess the potential impacts of purse-seine fishing activities on various survival indices of African Penguins by alternating no-take zones to fishing around four of their largest breeding colonies, Robben and Dassen islands off the west coast, and St Croix and Bird islands off the south coast.

Foraging ecology

The African Penguin is an inshore forager (Siegfried et al. 1975) and foraging trips of birds feeding chicks typically last only 1-2 days with birds remaining within 40 km of their colonies (Wilson 1985, Heath & Randall 1989, Petersen et al. 2006, Pichegru et al. 2012). The mechanisms by which African Penguins locate their prey while breeding are likely to be limited by this spatial constraint. African Penguins are visual pursuit divers (Wilson 1985) and are expected to adopt a number of different foraging strategies in response to variations in prey availability. During the chick provisioning stage, penguins should minimise the energy costs incurred during foraging, i.e. swimming costs and those associated with the digestion of food, to maximise the quantity and quality of prey returned to their chicks (Boersma et al. 2009). It is plausible, therefore, to assume that when fishing conditions are favourable, African Penguins provisioning chicks will travel shorter distances, as postulated by central place foraging theory (Orians & Pearson 1979).

Pelagic schooling fish belonging to the family Clupeidae predominate in the diets of *Spheniscus* penguins (Wilson & Wilson 1990). Sardines and anchovies are the most frequently selected prey of African Penguins, although their relative proportions vary between regions, sites and years, with anchovies being more prevalent than sardines in most instances (although this is biased to some extent by most studies having taken place since sardine populations crashed in the 1960s and 1970s, see review by Crawford et al. (2011). The results of diet samples from birds breeding on islands in Algoa Bay between 1992 and 2009 appear to deviate slightly from this trend with sardines playing a more significant role, although sample sizes during these years were often inadequate to distinguish any clear differences (Crawford et al. 2011).

Off southern Africa, the abundances of anchovy and sardine vary greatly at a regional scale and characteristically exhibit decade-scale shifts in relative abundance (Beckley & van der Lingen 1999). These species are trophodynamically distinct, largely due to differences in the morphology of their feeding apparatus, with the smaller anchovy being more selective feeders and targeting larger particulate meso-zooplankton compared to sardines that are typically generalist filter feeders (James 1987; Van der Lingen 2002; Van der Lingen et al. 2006). Size differences between the two species are likely to influence swimming capacity and their ability to cope with stronger currents. In combination, these morphological differences affect habitat selectivity, seasonal movements, diel migratory movements and schooling behaviour (Hampton 1987; van der Lingen et al. 2006). These factors, coupled with reproductive potential (i.e. spawning and recruitment success), constitute the endogenous factors that influence the distribution and abundance of these species. Exogenous factors include oceanographic processes, such as temperature, currents and primary production which have mostly been assessed at coarse spatio-temporal scales (Hampton 1987; Coetzee 1997; Beckley & van der Lingen 1999).

Breeding biology

The breeding biology of African Penguins has been reviewed by Crawford & Whittington (2005). African Penguins are monogamous with high levels of nest-site fidelity having been recorded at breeding sites on the west and south coasts. The onset of breeding has been recorded throughout the year but peak laying dates are typically between January and August. Between one and three eggs (mode = 2) are laid in a variety of nest types including excavated burrows, in vegetation, between rocks, on the surface, and in artificial nests (Pichegru 2012). Eggs are incubated by both parents for 38 - 41 days and the nestling period ranges from 64 - 105 days depending on brood size. Chicks are fed by both adults which alternate guarding duties to ca. 26 days after which they are mostly left unguarded and often form créches.

Study area - Algoa Bay

Algoa Bay is situated at the eastern edge of the Benguela upwelling region and is home to ca. 50 % of the estimated population of breeding African Penguins globally (Crawford et al. 2015). Most penguins breed on St Croix and Bird islands (Figure 1.1), with four smaller satellite colonies on Brenton Rocks, Jahleel, Seal and Stag islands.

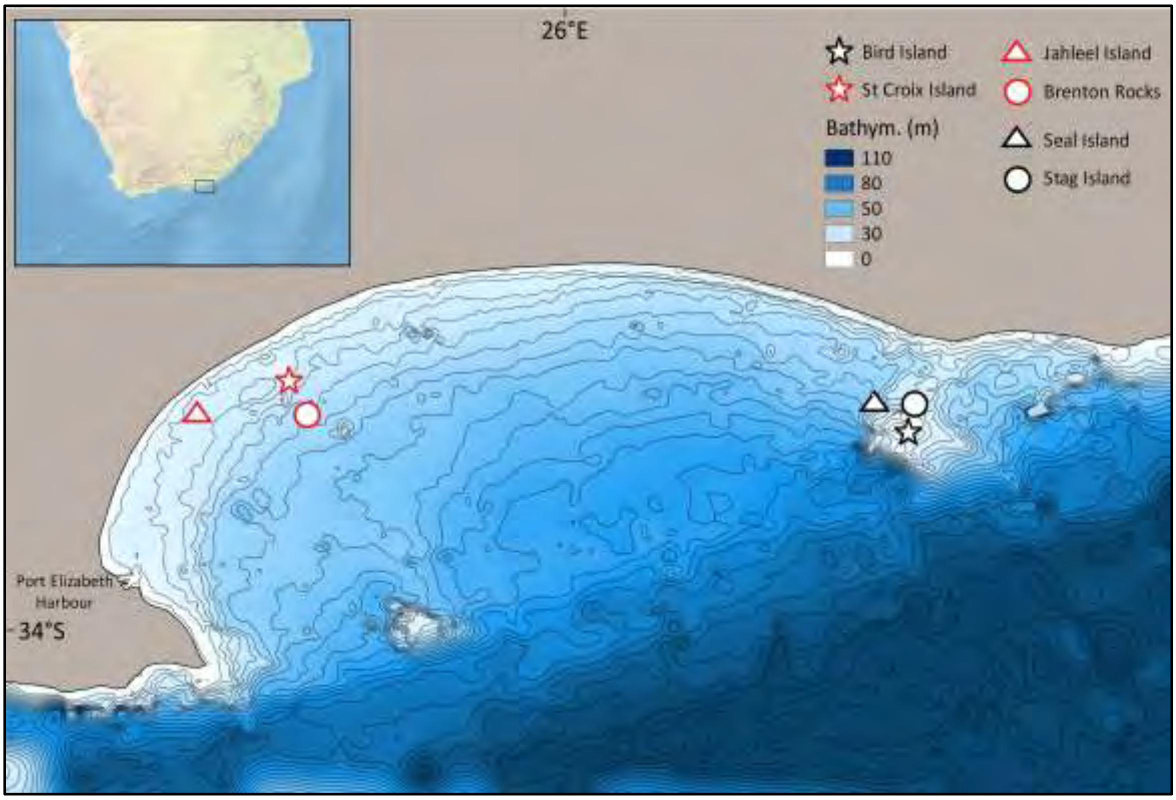

Figure 1.1 Study area, Algoa Bay showing location of the four African Penguin breeding colonies and bathymetry (Bathym.) (5 m resolution).

The physical oceanographic processes of Algoa Bay have been reviewed by Goschen & Schumann (2011). There is great spatial and temporal variation in oceanic conditions within Algoa Bay driven by a relatively steep and extensive bathymetric profile (extending up to 50 km offshore and 150 m deep before the continental shelf edge) (Figure 1.1); strong wind forcing (notably south-westerly and, to a lesser extent, north-easterly winds) and associated currents; larger-scale influences of the Agulhas Current and associated smaller-scale shear-edge eddies, plumes, inshore edge upwelling and larger-scale episodic meanders (the Natal Pulse); horizontal and vertical (thermoclines) sea temperature profiles; upwelling regions on the leeward side of the two prominent capes especially during summer; and sediment processes related to wave and current direction and intensity. St Croix and Bird islands are situated in the western and eastern extremities of the bay, respectively, and, as such, experience disparate oceanic conditions.

Most information on the distribution and abundance of small pelagic fish in this region come from large-scale, regional or national surveys (Armstrong et al. 1991; Barange & Hampton 1997; Beckley & van der Lingen 1999; Coetzee et al. 2010). Three fish species predominate in this system, anchovy, sardine and redeye (*Etrumeus whiteheadii*), with all three found year round and at various life stages. To date there have been no dedicated fine-scale assessments of pelagic fish distribution and abundance in this area.

A purse-seine fishery mostly targeting sardine that operates periodically out of Port Elizabeth harbour. This fishery is comprised of eight vessels and has been subject to alternating island closures since 2009 around St Croix and Bird islands as part of the ICTT initiative. Results of this experiment have shown strong support for island closures around St Croix Island based on reduced foraging effort recorded from birds during fishing closures (Pichegru et al. 2010, 2012), although these have been disputed by Coetzee (2010) due to a lack of control for natural prey variation.

Thesis structure

This thesis addresses hypotheses related to fine-scale responses of foraging African Penguins to their physical and biological environment in an attempt to reveal any limiting factors that may prove crucial to the survival of this species. The thesis focuses on this species' principle prey, small pelagic fish and the processes that mediate the availability of this prey to African Penguins. The research is conducted around two of the largest African Penguin colonies globally, St Croix and Bird islands in Algoa Bay, South Africa. The outline of the major components of this theses are illustrated in Figure 1.2.

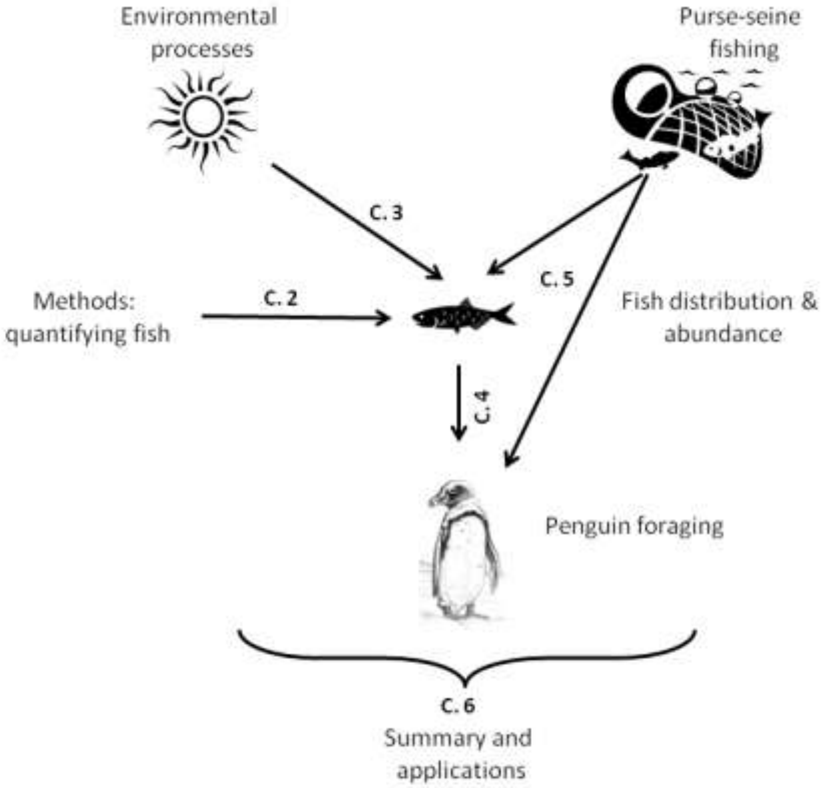

Figure 1.2. Conceptual flow diagram illustrating the relationship between the various themes of this thesis, including references to associated chapters (C.).

Chapter 2 describes the alternative use of inexpensive recreational fish-finders as a novel method for scientific applications in studying predator-prey interactions. Customised open-source software is used to extract acoustic parameters of schooling fish and outputs are compared to those of a calibrated scientific echosounder, the conventional equipment used by fisheries scientists. The results of this chapter provide opportunities for marine ecologists to explore these relationships cost-effectively and adapt these methods to their specific situations.

Chapter 3 investigates the bottom-up processes driving the distribution and abundance of pelagic fish in Algoa Bay as derived from the recreational fish-finder outputs, at spatio-temporal scales that are relevant to the at-sea distribution of African Penguins during both their breeding non-breeding seasons. Fine-scale acoustic pelagic fish surveys were conducted frequently around St Croix and Bird islands, and the data modelled against ocean physical processes known to influence pelagic fish. Oceanographic variables extracted from in-situ underwater temperature recorders (administered by the South African Environmental Observation Network, SAEON) and ex-situ satellite derived composites, using NASA's Moderate Resolution Imaging Spectroradiometer satellite array (MODIS), of chlorophyll concentration and sea surface temperature were used for this purpose. This chapter compares the associations between oceanographic processes and small pelagic fish between sites and discusses the relevance of these findings to global change phenomena in the context of the foraging ecology of African Penguins.

Chapter 4 uses novel methods to assess the relationship between the foraging distribution of African Penguins and their prey attributes. This chapter uses a unique dataset comprised of concurrent penguin track and acoustic fish data supplemented by penguin dive information that is used to calibrate a machine learning model to classify locality derived behavioural states. These georeferenced behavioural state data are complimented by counts of penguins observed at sea. Both datasets are used to model the relationships between pelagic fish distribution and abundance and penguin locality data. Furthermore, functional predator-prey relationships are explored by modelling the at-sea activity budgets of penguins against fish abundance data.

Chapter 5 assesses the influence of catches from the competing purse-seine fishery on the foraging effort of breeding African Penguins. Evidence for local depletion by the purse-seine fleet is investigated to establish if this fishery has the potential to significantly alter fish biomass in Algoa Bay. The most influential oceanographic correlate with pelagic fish as determined from Chapter 2 is tested as a potential proxy for prey availability. Mixed effects models are used to examine interaction effects of proxies for natural prey variation and different temporal lags of cumulative catches on the at-sea activity budgets of African Penguins. This chapter applies the results of the previous chapters to tackle a crucial question related to the survival of African Penguins, i.e. does fishing limit the availability of prey to African Penguins? Results of this chapter have important resource management implications. Only the indirect impacts of the small pelagic fishery on African Penguins were assessed because as far as is known there are few direct impacts of this fishery on seabirds.

Chapter 6 highlights key findings of the thesis and identifies potential avenues for future research. The implications of the findings for the conservation of African Penguin is discussed and resource management recommendations are proposed to alleviate potential threats to this species.

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Chapter 2

Recreational fish-finders - an inexpensive alternative to scientific echo-sounders for unravelling the links between marine top predators and their prey

Recreational fish-finders - an inexpensive alternative to scientific echo-sounders for unravelling the links between marine top predators and their prey

Abstract

Studies investigating how mobile marine predators respond to their prey are limited due to the challenging nature of the environment. While marine top predators are increasingly easy to study thanks to developments in bio-logging technology, typically there is scant information on the distribution and abundance of their prey, largely due to the specialised nature of acquiring this information. I explore the potential of using single-beam recreational fish-finders (RFF) to quantify relative forage fish abundance and draw inferences of the prey distribution at a fine spatial scale. I compared fish school characteristics as inferred from the RFF with that of a calibrated scientific split-beam echo-sounder (SES) by simultaneously operating both systems from the same vessel in Algoa Bay, South Africa. Customized open-source software was developed to extract fish school information from the echo returns of the RFF. For schools recorded by both systems, there was close correspondence between estimates of mean school depth (R^2 = 0.98) and school area (R^2 = 0.70). Estimates of relative school density (mean volume backscattering strength; S_v) measured by the RFF were negatively biased through saturation of this system given its smaller dynamic range. A correction factor applied to the RFF-derived density estimates improved the comparability between the two systems. Relative abundance estimates using all schools from both systems were congruent at scales from 0.5 km to 18 km with a strong positive linear trend in model fit estimates with increasing scale. Although absolute estimates of fish abundance cannot be derived from these systems, they are effective at describing prey school characteristics and have good potential for mapping forage fish distribution and relative abundance. Using such relatively inexpensive systems could greatly enhance our understanding of predator-prey interactions.

Introduction

Predator-prey interactions are central to ecosystem functioning and shape species evolution (Dawkins & Krebs 1979; Abrams 2000). Recent technological developments have greatly improved our understanding of ecosystem functioning and animal behaviour, especially in the marine environment, where remote sensing and data logging technologies have revolutionized the collection of ecological data (Kerr & Ostrovsky 2003; Turner et al. 2003; Cooke et al. 2004). Numerous studies have used biotelemetry, e.g. data-loggers, attached to marine top predators to gather information on their habitat use and response to ocean physical processes (Wilson et al. 2002; Cooke et al. 2004). Combining these data with diet studies and/or remote sensing of oceanographic covariates provides insights into prey availability and ecosystem functioning (Montevecchi 1993; Piatt et al. 2007; Boersma 2008; Einoder 2009). However, relatively few studies have been able to assess predator responses in terms of fish prey distribution and abundance (see Durant et al. (2009) for a review on seabirds). Such studies generally are over large spatial scales, which often results in a mismatch between prey and predator distributions, e.g. (Grémillet et al. 2008). Far-ranging species occupy a relatively predictable environment with clear associations between prey and oceanic features (Fauchald 2009). However, many marine top predators (especially central place foragers such as breeding seabirds and seals) occupy a relatively small home-range (at least seasonally) within systems that exhibit great variability in prey abundance. Unlike physical processes that, thanks to advances in satellite, mooring and biotelemetry technology, have become increasingly easy to obtain at fine spatio-temporal scales, data on the distribution and abundance of prey remains costly to gather. This is largely due to the specialised nature and application of the surveys, i.e. typically to quantify fish stocks for the setting of quotas, the associated large spatio-temporal scales of study and the costly nature of these operations. Consequently, this lack of prey distribution data beyond the scales of conventional applications remains a serious impediment to marine ecology studies.

The African Penguin feeds almost exclusively on pelagic fish species, predominantly sardine and anchovy, that are also targeted by industrial fisheries (Wilson & Wilson 1990). The population of African Penguins has decreased dramatically since the start of the 21st century, resulting in its conservation status being raised to 'Endangered' (IUCN 2016). Several studies have suggested that decreased localised prey abundance is driving this trend (Crawford et al. 2006, 2011; Weller et al. 2014), prompting an assessment of the impacts of purse-seine fishing on foraging and breeding parameters of these birds by temporarily excluding fishing around selected breeding colonies. Results to date include a significant positive relationship between penguin foraging effort and purse-seine catches in Algoa Bay (Pichegru et al. 2010, 2012) although the earlier results were disputed by (Coetzee 2010) who claimed that the study did not account for natural fluctuations in prey abundance. To address this shortcoming, fine-scale (temporal and spatial) pelagic fish surveys were initiated in Algoa Bay around two of the largest African Penguin breeding colonies in 2011.

Due to the high cost of scientific echo-sounders, I used a recreational fish-finder (RFF) designed to monitor fish in real time mostly to locate favourable fishing grounds. They are not calibrated and hence do not allow for accurate measurements of fish density and biomass as the standard performance characteristics of the system cannot be checked or monitored over time and the reference system sensitivity cannot be established. In contrast to RFFs, scientific echo-sounders (SES) are calibrated frequently/regularly with a standard target sphere with known acoustic scattering properties to determine the transducer directional and response output and receiver sensitivity (Foote 1981). This allows for the determination of fish density if the target strength (TS) of the fish species recorded is known. Other advantages of SES systems include a larger dynamic range and a higher signal to noise ratio.

The use of SESs is invariably associated with hydro-acoustic data-processing software that utilises echo-integration algorithms to compute the mean density of fish and extract quantifiable school descriptors (Weill et al. 2007). A lack of similar software for RFFs is a serious drawback to using these systems for scientific purposes. For this study Hydroacoustic data-processing software for use with a Furuno DFF3 RFF was developed and a pelagic fish survey in Algoa Bay was conducted using both RFF and SES systems on the same vessel to compare school descriptors and density estimates. This chapter focuses on the validation of this approach and demonstrates the suitability of processed RFF data to marine top predator and prey interactions and fishery-related research, using the African Penguin as a case study.

Methods

Fish-finder software (FISH)

To analyse fish data, represented as pixels in a .png format, from the Furuno DFF3 Fish-finder, the Fish-finder Image Segmentation Helper (FISH) programme was developed, written in Java as a plugin to Fiji (Schindelin et al. 2012), an open source image processing platform. Two plugins are used: a processor (FISHproc) and a reviewer (FISHrev). FISHproc requires manual designation of the analysis window (Figure 2.1, step 1-3). Once the window is set, duplicated regions are removed from overlapping contiguous frames. Thereafter, each frame is resized, reconciling the horizontal and vertical scales. In order to extract meaningful signal, several forms of interfering noise are mitigated. First, the spurious signal arising from beneath the seabed must be excluded. To identify the seabed, an edge-detection filter is used to identify the upper edges of all objects, and then find a path that horizontally spans the frame, maximizing the path's occupancy of the detected upper edges while minimizing vertical jumps (with a tunable anti-vertical penalty parameter). This is achieved with a dynamic programming algorithm (analogous to the Viterbi algorithm): $O(N*(2P+1))$, where O is the asymptotic notation, N is the pixel width of the frame, and P is the maximum allowed vertical transition per horizontal change (in this case implementation, $P=2$). This strategy is robust to noise that introduces spurious gaps in the sea bed. Next, speckles of interference are removed by passing each frame through a median filter, and vertical noisy columns are identified as peaks in the echo returns and subsequently removed. The final step of the initial processing phase involves the generation of masks of echo-returns from these previous steps. The second plugin, FISHrev, is used in a post-processing review phase and for subsequent automated feature extraction (Step 4, see Figure 2.1). During the review phase, the user specifies the dimensions of the linking ellipse to define the encompassing area of an aggregated school. This stage enables the user to then scroll through each image with the ability to toggle between the mask or raw image mode to delete unwanted anomalies, e.g. noise, dispersed fish layers or school-like bathymetric features. At the end of the review phase FISHrev extracts school parameters to a .csv output file (Table 2.1).

Inter-calibration procedures

In May 2014, both the RFF and a Simrad EK60 38kHz SES were deployed on a 8.6 m catamaran ski-boat in Algoa Bay, on the South African south coast. The RFF transducer was attached to a 1-m stainless steel pole mounted to the stern of the boat and the SES transducer was mounted to the starboard side of the boat approximately 2 m athwartship from the RFF transducer (Figure 2.2). The distance between the two transducers creates the possibility that different schools could be recorded by the outer edges of the echo beams, or that a school or part thereof will not fall within the beams of both transducers, particularly at shallow depths, so perfect concordance is not expected (Figure 2.2). Specifications for both systems are given in Table 2.2. Beam angles for both transducers are similar but the RFF has a variable ping rate dependent on the depth range. There is also a notable difference in frequencies between the two systems: RFF = 200 kHz versus SES = 38 kHz.

The inter-calibration was performed along a section of a predetermined survey track (Figure 2.3) over a distance of 20 nautical miles in water 15–85 m deep. Weather and ocean conditions were calm with <5 knot winds and swell <2 m. The survey was conducted at a speed of 7 knots and was completed in 3 h.

Data extraction

All echo-returns from both systems were processed through hydoacoustic data processing software, Myriax Echoview© 5 for the SES system, and FISH software for the RFF. Once all data were processed they were filtered to minimise the inclusion of backscattering noise and non-fish-school data with the following exclusion rules: all echo-returns <3 m depth (within the acoustic nearfield) and <0.5 m altitude (i.e. bathymetric anomalies); candidates (i.e. contiguous echo returns) of less than 1 x 1 m (L x H) (non-schooling fish); a minimum backscattering strength threshold (S_v) = –65 dB (following matching between the SES and RFF as explained below). To account for the patchy nature of schools I applied aggregation rules following (Coetzee 2000) and (Lawson et al. 2001) to all candidate targets: a minimum linking ellipse of 10 x 2 m (L x H) was chosen as the aggregator and an aggregated school area of 10 x 5 m (L x H) was chosen as the minimum school size.

Data preparation and statistical approach

Comparing FISH and Echoview outputs

Acoustical terminology follows (MacLennan et al. 2002). Due to the non-concordance in overlapping beams of both transducers and the subsequent inability of both systems to completely insonify the same schools, I identified a subset of candidate schools that were most similar in terms of their location and basic morphometric appearance through visual inspection, hereafter termed ‘matched’ schools.

Least squares linear regressions were used where SES outputs were regressed against RFF outputs for the following school parameters from the matched schools: mean school depth (m) and the log transformed school area (2-dimensional cross-section) (m^2) of the echo-trace.

To allocate energy values to the different pixel colours of the RFF schools I selected three matched schools from the RFF outputs that best represented the full range of pixel variation in our sample by calculating pixel skewness for all matched schools and selecting the three schools with the minimum, closest to zero and maximum skewness values, respectively. For these three scenarios I calculated the mean backscattering strength (S_v) for all combinations of starting values (i.e. the minimum dB values) between -70 dB and -60 dB (0.5 dB increments) and colour step values of between 0.1 and 2 dB (0.1 dB increments). Sensitivity of these adjustments were assessed against the difference in S_v values between the SES outcome for each of these three schools and the corresponding RFF values to isolate combinations in starting values and colour step adjustments with S_v differences closest to zero. To correct for saturation in the RFF system (i.e. smaller dynamic range) I applied a correction factor based on the relationship between the mean backscattering coefficients ($\overline{s_v}$) of both systems for the three above-mentioned scenarios using the optimal starting and colour step values utilising least squares linear regression techniques. The coefficients of these models were used to predict corrected $\overline{s_v}$ estimates for the RFF schools. A $\log_{10}$ transformation was applied to the SES $\overline{s_v}$ values (i.e. the response variable) due to the exponential relationship between both systems' $\overline{s_v}$ values. The corrected $\overline{s_v}$ values for the matched RFF schools were then converted into the logarithmic form S_v and aggregated into 4 dB bins to compare the frequency of S_v values for all three scenarios between both systems before and after application of the correction factor. Wilcoxon signed rank sum tests were applied to the paired S_v values of the matched schools between both systems to test if the shape of the distributions of S_v values between both systems were significantly different with and without application of the correction factor to the RFF schools.

The potential for time-varied gain (TVG) influences on the attenuation of signal strength with increasing depth in the RFF was checked by regressing $\overline{s_v}$ of the matched schools against mean school depth and comparing this relationship with the same schools as derived from the SES. A $\log_{10}$ transformation was applied to the $\overline{s_v}$ values from both systems' schools to scale the responses to comparative estimates of density.

Comparing estimates of relative abundance

To compare estimates of relative abundance from both systems, the nautical area scattering coefficient (s_A) (m^2 nmi^{-2}) of all schools aggregated into 500 m Elementary Distance Sampling Units (EDSU) was calculated, given the formula:

$$s_{A=}4\pi(1852)^2 s_a, \tag{2.1}$$

where $4\pi(1852)^2$ is the nautical mile derived scaling factor and s_a is the integral of $\overline{s_v}$ over a range interval, following [52]. In the context of this study, the range interval is the height of all schools weighted by the length of all schools for schooling fish targets only. I used the corrected $\overline{s_v}$ values as determined from scenario 2 (Figure 2.5), i.e. S_v starting values of -65 dB and colour steps of 1.3 dB.

A logistic regression model was used to determine the relationship between school encounters (fish present = 1, fish absent = 0) in the 500 m EDSUs by both systems. To determine the scale at which s_A estimates were most concordant between both systems I generated rolling sums of s_A values between scales of 0.5 km and 18 km using the R package 'zoo' (Zeileis et al. 2014). This was achieved by summing all s_A values over the rolling window and dividing this value by the scale length. Least squares linear regression models were used to compare the coefficients of determination (R^2) of the relationships between s_A values of both systems at 18 different scales within this range. Log transformations were applied to both variables after adding 0.1 to account for EDSUs with no schools recorded. After transformations both variables were approximately bell-shaped.

All statistical analyses as well as graph outputs were completed in the statistical package R (R Core Team 2015).

Results

Comparing FISH and Echoview outputs

After applying the filtering procedures, 93 schools were recorded by both the RFF and the SES, of which 36 schools (38%) were classified as matched and were used for comparing the two systems. Estimates of mean school depth between matched schools from both systems were highly significant (R^2=0.98, Figure 2.4), as were estimates of school area (R^2=0.70, Figure 2.4). Estimates of mean school depth ranged from 5.1 to 53.7 m (mean±SD = 26.5 ± 12.6 m) and 4.5 to 57.7 m (27.6 ± 13.6 m) for the SES and RFF, respectively. Estimates of school area ranged from 25.8 to 831.9 m^2 (195.7 ± 217.9 m^2) and 18 to 1076 m^2 (225.4 ± 260.3 m^2) for the SES and RFF, respectively.

Density estimates and applying the correction transformation

The three matched schools selected to determine optimal starting and colour step dB increments for the RFF pixel values had skewness values of -0.4, -0.001 and 3.5 representing the matched schools with the lowest pixel colour values (i.e. left skewed), the most moderately skewed pixel values (i.e. closest to 0), and the most saturated pixel values (i.e. right skewed), respectively. The differences in S_v values between SES and RFF for all starting and colour step combinations for these three scenarios are illustrated in Figure 2.5a. For all three scenarios there was a negative linear relationship between Sv differences with starting values and optimal colour step values (i.e. as shown by the dark blue points in Figure 2.5a) with the centrally located starting values showing a good spread in the distribution of optimal starting values. Based on these results a S_v of -65 dB was selected as the baseline starting value to compare different corresponding optimal colour step values in the three different scenarios; this was deemed appropriate to facilitate comparisons with the SES starting values, i.e. also -65 dB. The optimal colour step values at this baseline starting point were 1.4, 1.3 and 0.9 dB for the three school scenarios 1-3, respectively, and these values were mapped to the 36 matched schools in each case.

Results of the least squares linear regressions between the $\overline{s_v}$ values of both systems with the new mapped pixel values for the RFF schools are shown in Figure 2.5b. All three scenarios have almost identical positive linear trends with very similar intercepts but varying slope coefficients. Applying these model predictions as a correction to the RFF S_v values and comparing binned S_v values between systems before and after correction showed improvements in dynamic range for all three cases, especially scenarios 1 and 2 (Figure 2.5c). This was evident in the medians and variances in the corrected school S_v values as well as the improvements in Wilxon signed ranked sum test probabilities (Table 2.3). Despite this improvement, the concordance in dynamic range after correction was still limited in the RFF system outputs especially for schools with higher densities (Figure 2.5c, Table 2.3).

Comparisons of the influence of depth on $\overline{s_v}$ estimates, i.e. the potential influence of TVG, for the RFF and SES systems are shown in Figure 2.6. Both systems showed similar negative trends with $\overline{s_v}$ values decreasing with increased depth but these relationships were weak explaining 29% and 22% of the variation in the RFF and SES comparisons, respectively.

Comparing estimates of relative abundance

Table 2.4 shows the detection frequency of schools recorded by both systems within 500 m EDSUs. In the majority (67%) of the 76 EDSUs, both systems recorded either the presence (37%) or absence (30%) of schools, concurrently. The RFF detected schools in ten of the EDSUs where the SES failed to detect any schools and the SES detected fish schools in 15 instances where the RFF failed to detect any schools. Results of the logistic regression showed a significant relationship between the concurrent detectability of both systems ($P < 0.01$). Using s_A as a measure of relative abundance, comparisons of these values aggregated for each 500 m EDSU showed no significant differences in these estimates between systems: RFF (median, interquartile range = 17.3, 532.9 m^2 nmi^{-2}); SES (16.1, 279.3 m^2 nmi^{-2}), Wilcoxon rank sum test ($P=0.9$). Comparisons of relative abundance estimates at different scales are illustrated in Figure 2.6. There is a clear positive linear trend in the relationship between model fit estimates (R^2) and scale reaching an asymptote at approximately 12.5 km at which point this particular scale explains 91% of the variation between systems.

Discussion

The small proportion (39%) of matched schools compared to the total number of schools recorded by both systems during the calibration survey can be attributed to the athwartship displacement of the transducers (2 m) (Figure 2.2) and the inability to synchronise the pings between both transducers. These differences are known to influence the comparability of school parameters recorded by different echo-sounders used on the same vessel, although it is often impractical to avoid these sources of error (Korneliussen et al. 2008). A combination of these factors is likely to have some bearing on the unexplained variation in the associations between $\overline{s_v}$ values between the matched schools (Figure 2.5b). However, the limited dynamic range of RFF systems is likely to have had a larger influence on this variation, especially for higher density schools. The correction factors applied to the RFF schools improved the dynamic range for all three pixel substitute scenarios although these were still limited for schools with higher densities and I caution against using these devices for accurate measures of abundance such as is possible with more sophisticated SES technology. Notwithstanding these limitations, relative abundance estimates using all schools from both systems showed strong congruence especially at scales > 10 km and the RFF matched the SES system in terms of school detectability, a potential proxy for relative abundance estimates (Brierley & Cox 2015). Comparisons of potential influences of TVG (i.e. depth dependencies on energy values) showed little evidence for this effect in the RFF outputs. This is because both systems showed similar weak, negative associations between depth and $\overline{s_v}$ estimates despite the SES system having been calibrated to ameliorate this source of error. These trends are more likely to have been influenced by factors other than TVG, such as sound attenuation that is known to occur in high density schools (Coetzee et al. 2008) and the diverging depth dependencies of different fish species, notably redeyewhich occupy deeper depths than other forage fish species during the day in this region (Roel & Armstrong 1991; Lawson et al. 2001).

Despite large differences in the fabrication of the two echo-sounder systems, their use, specifications and costs, results of the inter-calibration survey, as quantified by the FISH programme, demonstrate the ability of a Furuno RFF to produce comparable outputs to the SES used in this assessment. This is strongly encouraging for marine ecology studies that require estimates of prey distribution and relative abundance but lack the budget or expertise to use SES systems.

This study has demonstrated the ability of the FISH programme to extract accurate estimates of school depth and size (i.e. school area). These parameters can provide valuable inputs into marine ecology studies. For instance, the vertical location of prey is significant in terms of its accessibility in relation to a predators maximum and optimal dive depths (Mori 1998; Wilson et al. 2010) and school depth relative to the seabed (i.e. school altitude) is likely to affect predators that pursue their prey from below, e.g. baleen whales (Pivorunas 1979), seals (Davis et al. 1999) and penguins (Wilson & Duffy 1986; Ropert-Coudert et al. 2000). School depth and altitude data have proven to be effective acoustic determinants of pelagic fish species identification in South Africa, especially when coupled with ancillary data (i.e. location, sea surface temperature and time of day) although the use of this information needs to be calibrated for the region of interest and the period during which the surveys take place (Lawson et al. 2001). The frequency and distribution of schools of different sizes can be used to test hypothesis related to school encounter and detectability rates and hunting success. For example, (Wilson 1985) inferred the tendency of African Penguins to target small schools of anchovy and postulated the benefits in terms of increased encounter rates when compared to larger more patchy schools.

The efficacy of using seabirds as indicators of ecosystem function and in informing marine conservation management depends on the predictive power of the various ecological parameters that can be harnessed from these species (Einoder 2009). Activity budgets and breeding parameters (e.g. colony attendance and chick growth rates) provide a convenient yardstick to infer variation in the marine prey base. However, informative thresholds of prey yield are confounded by these species' ability to adapt to variability in food supply (e.g. (Ricklefs et al. 1985; Piatt 1990)). Functional relationships between seabird behaviour parameters and prey quantity, as originally hypothesised by (Cairns 1987), are typically curvilinear, the position of the informative 'tipping points' being dependent on the influence of the inherent behavioural plasticity on the parameter used (e.g. Cury et al. 2011). Simultaneous data on prey availability is essential if these thresholds are to be determined and it is only recently that empirical studies of this nature have been conducted.

(Harding et al. 2007) determined these relationships by simultaneously measuring prey abundance while recording breeding parameters of Common Murres (*Uria aalge*). Their findings reflected (Cairns 1987) non-linear response predictions providing quantifiably more meaningful determinants of ecosystem change. These relationships need to be determined for each potential indicator species and the missing element in realising these is often concurrent prey data.

An important focus of this research into the impacts of purse-seine fishing on African Penguins is teasing out the natural fluctuation in prey abundance from the effects of fishing. Prior to regularly surveying fish distribution and abundance in the foraging area of breeding penguins in 2012 (Figure 2.3) using the techniques described in this chapter, most data on pelagic fish abundance was collected from annual stock assessment surveys conducted over large spatial scales by DAFF. These were typically undertaken in November of each year, after African Penguins had ceased breeding. In 2009, the first of the six-year island closure experiments was implemented around St Croix Island, the world's largest African Penguin breeding colony (Pichegru et al. 2010). Comparative results of penguin foraging effort parameters, using bio-logger technology, before and after the closures, showed significant differences in the amount of effort these birds put into their at-sea activities (Pichegru et al. 2012). As alluded to previously, the efficacy of these results were undermined by a lack of data on the natural variability in the prey base. Information gathered from RFFs can be used to offset this shortfall.

Conclusions

The results of this study apply specifically to the Furuno RFF system used and the context within which this system was operated, i.e. in-shore forage fish species in the Benguela Upwelling Region. Prospective users of these systems need to weigh the merits of adopting such an approach against the circumstances of their particular study. Some key considerations include: the programming capacity to modify the FISH software to different RFF models; the species targeted for and the ability of the RFF to quantify meaningful parameters of these targets; the depth range of the RFF, and; access to a SES and technical expertise for calibration purposes. I have attempted here to give context to the colour scale display of the RFF and the outputs derived are broadly comparable with those obtained from the SES at scales relevant for marine predator-prey interaction studies. This should allow for meaningful comparisons of relative fish density and biomass and school descriptors within surveys conducted using RFFs. However, estimates of fish abundance derived from such systems should be used with caution given the inability to calibrate RFFs and monitor their performance over time. Provided there is no large drift in the performance of the RFF over time, comparisons of fish school parameters between surveys should be possible. The development of hydroacoustic data processing software for RFF echo returns (FISH) greatly facilitates data capture, and can be modified for use with echo returns from other RFF models. The programme and its source code are available from http://www.cbio.uct.ac.za/~arjun/. The methods outlined in this study can be adapted to a broad range of marine top predator studies that utilise boat-based survey or observation techniques.

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Table 2.1. School parameters and their descriptions for Fishfinder Image Segmentation Helper (FISH) outputs.

Parameter	Description
File	Source file name
Time	HH:MM:SS
Date	YY/MM/DD
PicRef	File name of picture
Lat_dd	Latitude in decimal degrees
Long_dd	Longitude in decimal degrees
LeftLat	Latitude of left extent of school
LeftLon	Longitude of left extent of school
RightLat	Latitude of right extent of school
RightLon	Longitude of right extent of school
BotAltitude (m)	Altitude at bottom of school
TopDepth (m)	Depth at top of school
MeanAltitude (m)	Mean altitude of school
MeanDepth (m)	Mean depth of school
BotDepth (m)	Depth of sea floor
SchoolHeight (m)	Vertical extent of school
SchoolWidth (m)	Horizontal extent of school
Area (m2)	Area of school
AreaLV (m2)	Area of school less vacuoles
Perimeter (m)	Perimeter of school
MaxCalDiam (m)	Length of maximum diameter
MinCalDiam (m)	Length of widest point perpendicular to maximum diameter
MaxCalAngle (°)	Angle of maximum calibrated diameter
Pixel value count	Number of pixels for each pixel type*

*Recreational fishfinders (RFF) typically classify pixels on a sequential numeric scale with no reference to actual dB values. These need to be calibrated to a scientific echosounder (SES).

Table 2.2 Specifications of the scientific echosounder (SES) and the recreational fish-finder (RFF).

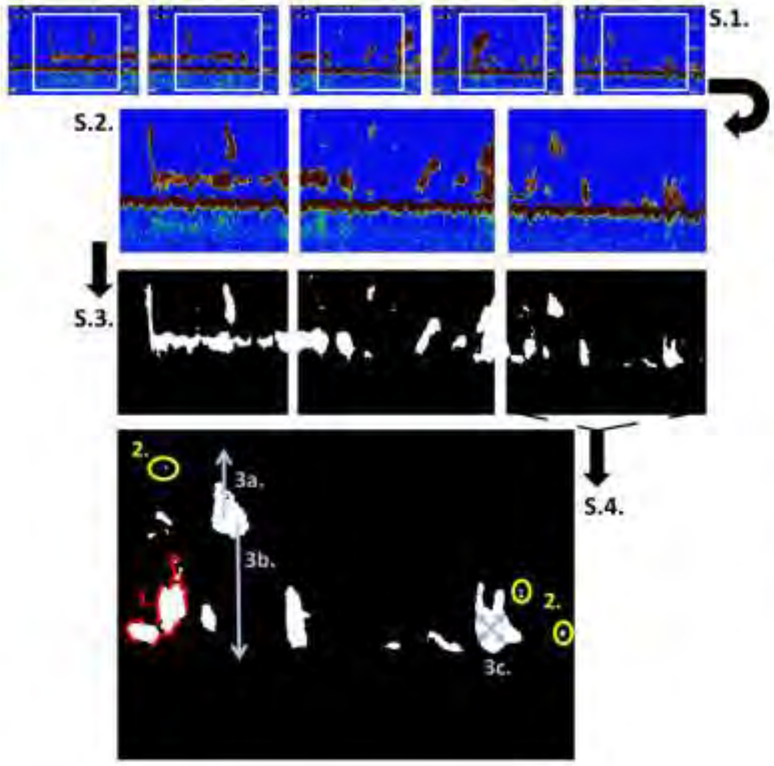
Boat and sounder details	**SES**	**RFF**
Transducer mount	side	transom
Transducer depth	0.5 m	0.5 m
Transducer	Simrad ES38-12	Furuno 525TID-PWD
Settings		
Frequency	38 kHz	200 kHz
Gain	21.22 dB	default
Time varied gain (TVG)		2
Sa correction	-0.67 dB	none
3dB beam angle	12°	11°
Power	1000 w	600 w
Receiver band width	2.41 kHz	not specified
Max ping range	250 m	206 m
Ping rate	2 - 5 p/s	4 - 10 p/s (100 m - 30 m range)

Table 2.3 Summary statistics of mean volume backscattering strength (S_v) estimates for 36 matched schools as insonified by the scientific echosounder (SES) and the recreational fish-finder (RFF) using outputs for three scenarios representing different pixel derived outputs for the RFF system: IQR - interquartile range, p - Wilcoxon signed rank statistic probability estimates between the pairs of schools derived from different system outputs, i.e. between all RFF scenarios and the SES outputs (shaded row).

	Scenario	**dBi**	**min**	**max**	**median**	**IQR**	**p**
SES Sv		1	-53.7	-31.5	-45.3	8.6	
RFF Sv	1	1.4	-56.7	-46.2	-48.1	2.6	0.0002
RFF corrected Sv	1	1.4	-53.9	-37.9	-44.2	6.5	0.94
RFF Sv	2	1.3	-57.4	-47.6	-49.4	2.5	2.05E-006
RFF corrected Sv	2	1.3	-54.1	-38	-44.2	6.5	0.94
RFF Sv	3	0.9	-60	-53.1	-54.5	2	2.91E-011
RFF corrected Sv	3	0.9	-54.4	-38.4	-44	6.2	0.94

Table 2.4. Frequency of fish school encounter scenarios of the recreation fishfinder (RFF) and the scientific echosounder (SES) quantified by 500 m Elementary Distance Sampling Units (EDSU).

RFF	**SES**	**No. EDSUs**
fish	fish	28
fish	no fish	10
no fish	fish	15
no fish	no fish	23



Step 1. Setting the mask (manual) and detecting the seabed (automated).

Step 2. Cropping to exclude recurring schools & non-school data (automated).

Step 3. Generating masks (automated).

Step 4. Review phase:

1. Setting the linking ellipse (manual)
2. Deleting non-fish targets (manual)
3. Extracting school parameters (automated):
   a) Depth
   b) Altitude
   c) Morphometrics & density

Figure 2.1 Flow diagram illustrating the workflow of FISH software showing the different steps in the processing phase (steps 1 – 3) and the review phase (step 4).

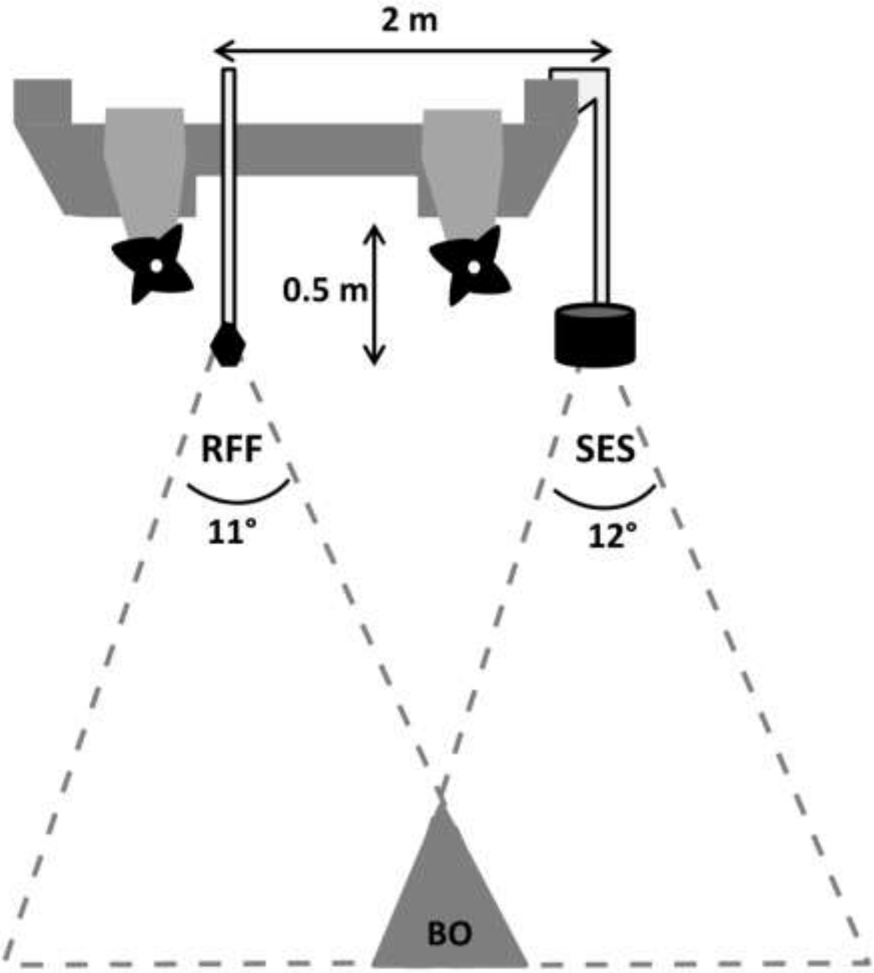


Figure 2.2 Transducer placements on catamaran ski-boat (profile view of stern) for the recreation fish-finder (RFF) and the scientific echo-sounder (SES) showing athwartship displacement (2 m), transducer depths (0.5 m), beam angles and area of beam overlap (BO), not to scale.

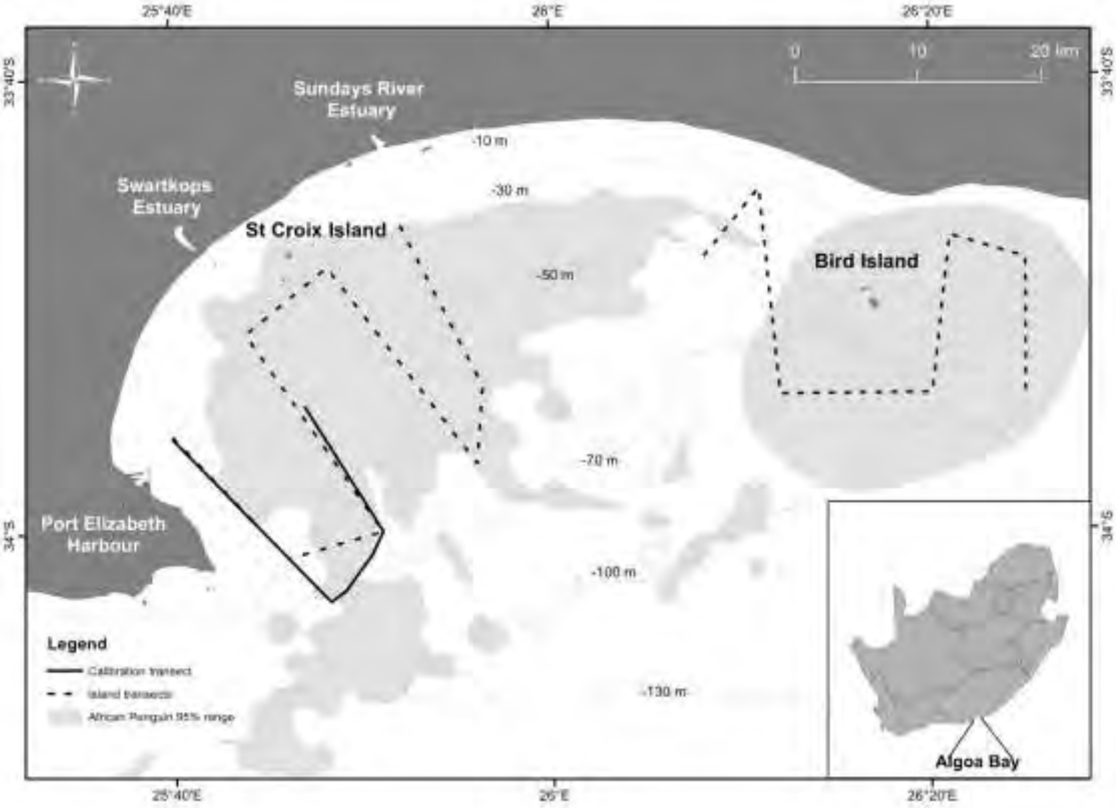


Figure 2.3. Map of study area showing regular pelagic survey transect routes (dashed lines) around the African Penguin colonies on Bird and St Croix islands and calibration survey route (solid line). Shaded areas denote the 95% kernel density foraging range of African Penguins provisioning small chicks on St Croix and Bird islands between 2008 and 2011 (extracted from Pichegru et. al 2012).

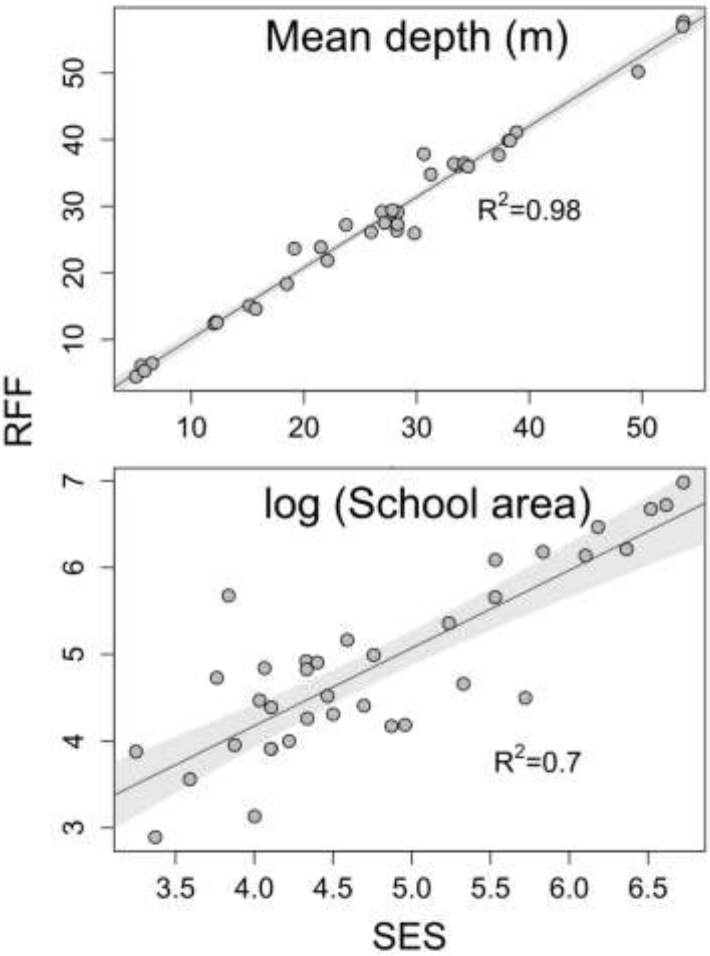


Figure 2.4. Linear regressions showing the relationships between school desciptors, mean depth (top graph) and log transformed school area (bottom graph), for 36 matched schools from the recreational fish-finder (RFF) and the scientifc echo-sounder (SES). Shaded areas denote 95% confidence intervals.

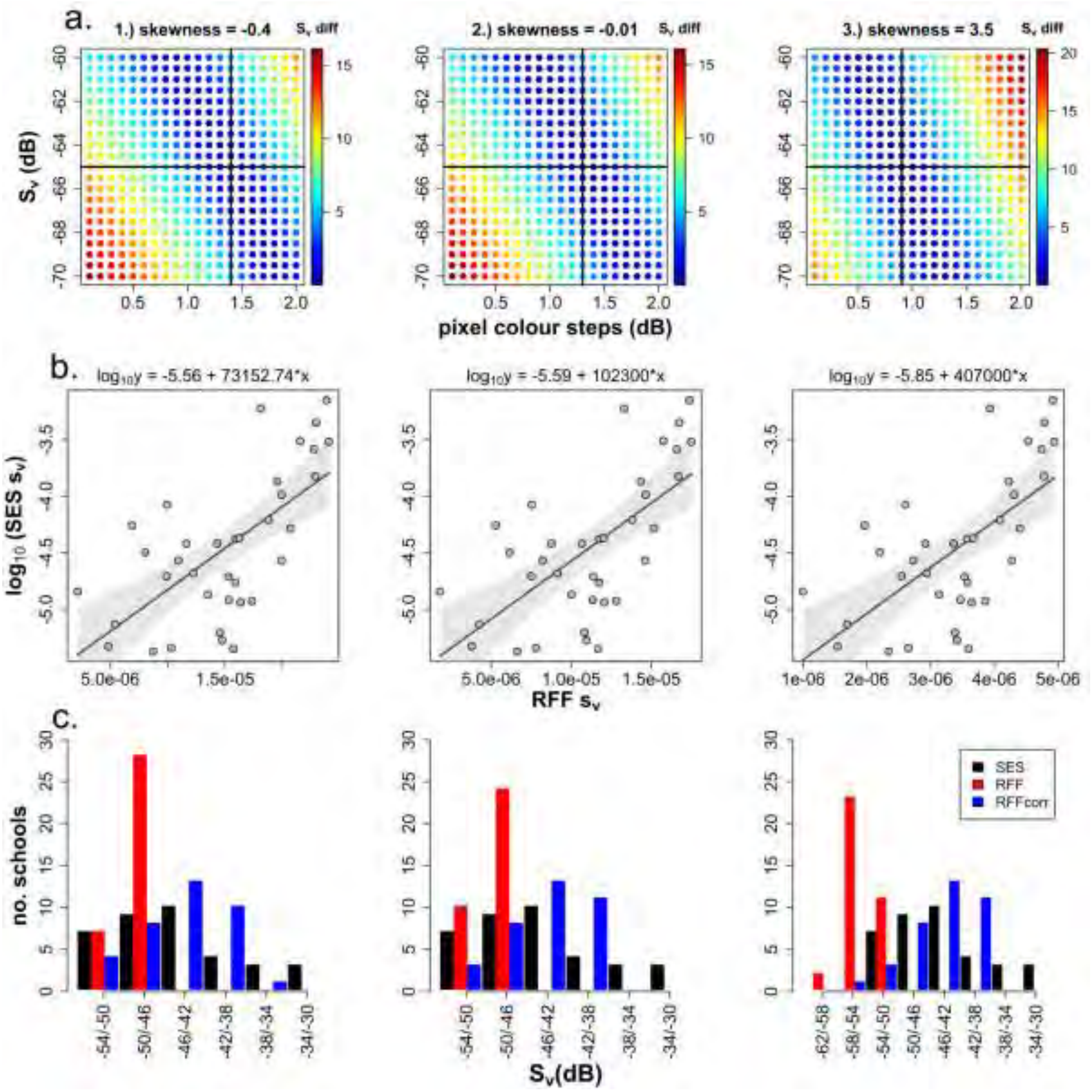


Figure 2.5 Plots for three scenarios, 1-3, representing three schools selected from the recreational fish-finder (RFF) outputs with different pixel skewness values: a) 2D scatter plots showing the influence of different combinations of mean volume backscattering strength (S_v) starting values and colour step values on the difference in S_v values (S_v diff) between the RFF and the scientific echosounder (SES) outputs (colour scale bar - low values indicate optimal estimates), cross-hatch denotes optimal colour step values at starting values of -65 dB; b) least-squares regressions between volume backscattering coefficients ($\overline{s_v}$) of the SES (transformed) and RFF outputs of the 36 matched schools using starting and colour step values for the RFF outputs as determined by the 2D scatter plot analyses , coefficients are given at the top of each plot and shaded areas denote the 95% confidence intervals; c) histograms showing the frequency of schools in 4 dB S_v bins for the SES-derived schools, the RFF-derived schools before application of a correction factor as predicted by the

linear regression models (b), and the RFF-derived schools with this correction factor applied (RFF corr).

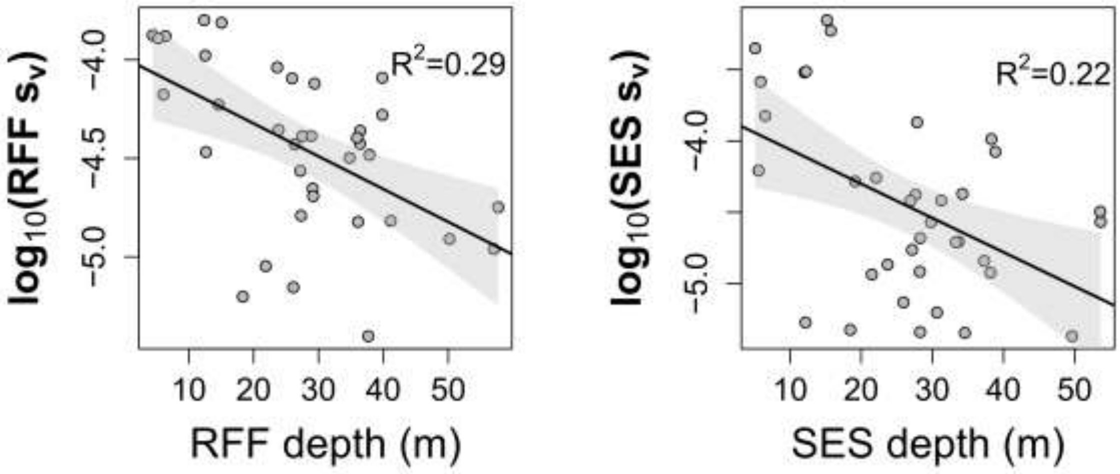


Figure 2.6 Least squares linear regressions showing the relationship between volume backscattering coefficients ($\bar{s_v}$) and mean school depth for the 36 matched schools insonified by the recreational fish-finder (RFF) and the scientific echosounder (SES). Shaded areas denote 95% confidence intervals.

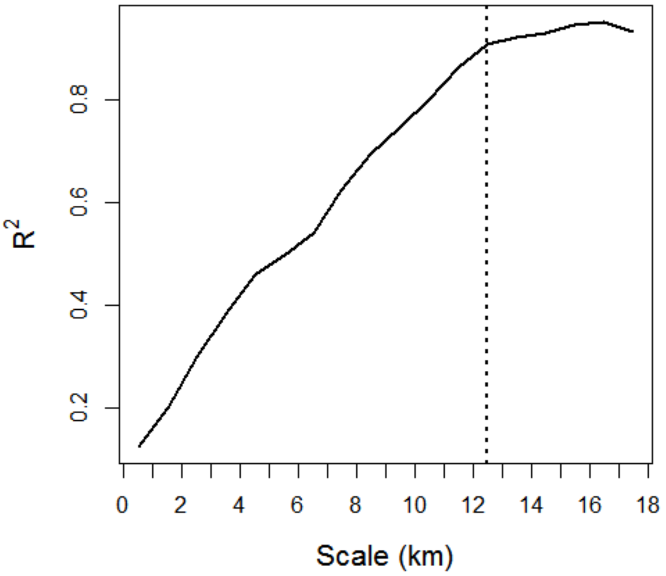


Figure 2.7 Coefficient of determination (R^2) values of least squares regressions for 18 models comparing relative abundance estimates using the nautical area scattering coefficients (s_A) (m^2 nmi^{-2}) between schools from the scientific echo-sounder (SES) and the recreational fish-finder (RFF) at different scales: 0.5 km – 18 km, hatched vertical line denotes asymptote (12.5 km).

Chapter 3

Oceanographic influences on pelagic fish assemblages at spatio-temporal scales relevant to top predators: the case of forage fish availability to the endangered African Penguin in Algoa Bay, South Africa

Oceanographic influences on pelagic fish assemblages at spatio-temporal scales relevant to top predators: the case of forage fish availability to the endangered African Penguin in Algoa Bay, South Africa

Abstract

Pelagic fish in upwelling ecosystems play a significant role in regulating the foraging activities of marine top predators yet there is little information on oceanographic drivers of fish assemblages at temporal and spatial scales relevant to their predators. The perpetuity of endangered African Penguins is closely linked to the availability of its pelagic fish prey and this resource is only accessible to breeding birds within ~40 km of their colonies. This study assesses the influence of oceanography on the spatio-temporal dynamics of pelagic fish in Algoa Bay, South Africa, home to two of the largest African Penguin colonies globally, St Croix and Bird islands. Results using a combination of bivariate and multivariate model types highlight the complex and variable nature of this system with fish around both islands responding differently to physical processes. Chlorophyll concentrations were good predictors of fish abundance within one ($R^2 = 0.44$) and two ($R^2 = 0.37$) month lags around Bird Island but had little influence on fish around St Croix Island, possibly due to the masking effect of purse-seine fishing operations which were mostly only permitted in the waters around this island during the study period. Increased sea-surface temperatures (SST) coincided with larger fish schools around St Croix, potentially related to an increase in sardine schools during summer. The horizontal distribution of fish schools around Bird Island was more clustered under cooler SST (upwelling) conditions. Although there was no apparent oceanographic influence on the horizontal distribution of fish around St Croix Island, the vertical distribution of fish was strongly influenced by the combined effects of increasing SST and stratification, suggesting that fish occur higher up in the water column during strong thermocline conditions. Fish were significantly deeper in the water column during summer around Bird Island, possibly due to an influx of redeye, which reside closer to the seabed. Primary production was suppressed during the summer of 2011/2012 by increased southwesterly winds and briefly enhanced during April and May 2012 due to a large episodic meander that advected offshore bottom waters into the bay. The bio-physical associations identified

by these findings should prove valuable in controlling for natural prey variability when assessing the impacts of purse-seine fishing activities on survival indices of African Penguins.

Introduction

Small pelagic fish, or forage fish, play a crucial role in influencing both upper and lower trophic levels in marine upwelling ecosystems (Cury et al. 2000; Bakun 2006; Shannon et al. 2008). They comprise a major food source for many top predators, such as seabird and mammal species whose populations are often mediated by the availability of these prey (Crawford et al. 2000, 2008; Cury et al. 2011). Research linking the influences of physical drivers to pelagic fish distribution and abundance have invariably quantified these relationships at broad geographic scales (Agenbag et al. 2003; Palomera et al. 2007; Katara et al. 2011) and often over decadal temporal scales (Chavez et al. 2003; Bertrand et al. 2004; Shannon et al. 2004; Blamey et al. 2015). This is not surprising given the economic significance of these species, contributing to 19% of the biomass of global marine and freshwater fishery catches in 2012 (FAO 2014), and the need to investigate causes of population level variability. Studies of these interactions at finer spatio-temporal scales are less common (but see e.g. Bertrand et al. 2008, 2014) despite being relevant to top predator species that are often confined to smaller geographic regions and are therefore significantly influenced by the local variability in this prey source. Top predators include seabird species endemic to these upwelling areas that have endured significant decreases in their populations over the last few decades and have therefore become the focus of more directed research into the causes of their population declines (Crawford & Jahncke 1999; Jahncke et al. 2004; Crawford et al. 2014; Paleczny et al. 2015).

The Benguela Upwelling Region (BUR) is one of four major eastern-boundary upwelling ecosystems (Chavez & Messié 2009). Three threatened seabird species endemic to the Benguela region are largely reliant on small pelagic fish species for their survival: Cape Gannet (*Morus capensis*), Cape Cormorant (*Phalocrocorax capensis*) and the African Penguin (Crawford & Jahncke 1999). These bird species differ in terms of their foraging ranges with the African Penguin, the only non-flighted species, having the most limited range, especially during the breeding season (Heath & Randall 1989; Wilson et al. 1989; Petersen et al. 2006; Pichegru et al. 2012). The conservation status of this species has recently been uplisted to 'Endangered' following a >60 % decrease in its population during the first decade of the 21st century, which is believed to be associated with the availability of their principle prey, anchovy and sardine (Crawford et al. 2011; Sherley et al. 2013; Weller et al. 2014). African Penguins compete with purse-seine fisheries for the same food source and there is currently a research drive to quantify the direct impacts of this activity on the penguin's population (Pichegru et al. 2010, 2012; Sherley et al. 2015). This study has included the implementation of an island closure feasibility study around four of the penguin's largest breeding colonies including Bird and St Croix islands in Algoa Bay. Interpretation of the results of this experiment have been controversial, with the absence of suitable controls for natural variation in the prey base being a key limiting factor (Cherry 2014). Understanding this natural variability is limited by a lack of research on the interactions between physical processes and small pelagic fish distribution and abundance at scales relevant to African Penguins, i.e. within their foraging range during the breeding season, ca 40 km (Heath & Randall 1989), and at a temporal frequency that can potentially signal variation in processes aligned to the penguin's phenology, notably periods leading up to and including the breeding season. These relationships are crucial for building reliable ecosystem models that allow projections of the species' population trends to be assessed under different scenarios of climate change and fishing pressure.

Two of the largest breeding colonies of African Penguins globally are situated in Algoa Bay, St Croix and Bird islands, the combined population of which currently contributes to >50% of their global population (Crawford et al. 2014). These islands are situated at opposite ends of Algoa Bay in a region that is characteristically diverse in terms of various physical processes that are known to influence productivity (reviewed by Goschen & Schumann 2011). Physical drivers of primary production in the Algoa Bay region include: frequent but short-term wind induced upwelling (approximately 3 - 7 days) associated with north-easterly winds during summer (Schumann et al. 1982, 2005; Goschen et al. 2012); shear-edge upwelling in the vicinity of Port Alfred with cooler waters propagating into the eastern region of Algoa Bay (Lutjeharms et al. 2000); and, infrequent (typically one or two events a year) but more persistent (between approximately 10 and 40 days) and widespread upwelling events in the form of offshore, cool bottom waters propagated from large episodic meanders (LEM) originating from Natal Pulses in the Agulhas Current (Goschen & Schumann 1988; Lutjeharms & Roberts 1988; Goschen et al. 2015). The vertical thermal structure of Algoa Bay varies seasonally with stratification predominantly a summer phenomenon and mixed temperature profiles being typical of winter (Goschen & Schumann 2011).

This chapter determines the extent to which oceanographic factors can influence forage fish assemblages at a response scale that is likely to influence African Penguin foraging activity and hence, potentially, survival. To achieve this, both *in situ* temperature and wind data, and satellite derived surface temperature and chlorophyll data were compared to acoustic-derived pelagic fish survey data in the core foraging ranges of penguins from the two breeding islands. I examine fish parameters that are known to influence predator response: estimated biomass (Cairns 1987; Piatt 1990; Cury et al. 2011), dispersal (Wilson 1985; Fauchald & Tveraa 2006; Fauchald 2009) and vertical distribution (Zamon et al. 1996; Boyd et al. 2015). Oceanographic data include indicators of primary production, sea-surface temperature, profiled temperature data and thermal stratification, all factors known to influence the distribution and abundance of pelagic fish (Agenbag et al. 2003; Palomera et al. 2007; Bertrand et al. 2008; Katara et al. 2011). Finally, the influences of mechanistic forces on proxies for primary production are assessed using influences of wind and mesoscale offshore processes (i.e. LEMs), to better understand the underlying drivers of productivity within the context of pelagic fish habitat in this region.

Methods

Oceanographic data

I used four primary datasets: two *in situ* datasets, wind and underwater temperature profile data, and two *ex situ*, satellite-derived datasets, sea-surface temperature (SST) and chlorophyll-a concentration (chla).

Wind direction and velocity data were provided at 14h00 daily for two South African Weather Service recording stations, Bird Island and Port Elizabeth Harbour. Wind direction was classified into two bearing ranges based on the predominant directions responsible for upwelling and mixing in the bay, respectively: north-easterly (bearing range: 11 - 79°) and south-westerly (bearing range: 191 - 259°). For the purposes of comparative time-series plots a 14-day rolling mean was calculated on wind velocities for both directional bins.

Underwater temperature data were extracted from semi-permanently moored Onset Hobo Pro V2 underwater temperature recorders (UTRs) moored at 5 - 10 m depth intervals throughout the water column and with a recording accuracy of ± 0.2 °C. We used data from two UTR moorings maintained by the South African Environmental Observation Network (SAEON): Algoa Bay Central (ABC, max. depth = 55 m) and Bird Island Offshore (BIO, max. depth = 70 m) (Figure 3.1), selected based on their proximity to the fish survey routes and the temporal representivity of the datasets. Two metrics were calculated from the UTR data: mean temperature (the average temperature through all depths at 12h00) and thermal stratification (calculated as the standard deviation of temperature in the upper 30 m following Boyd et al. (1992) also at 12h00). The use of standard deviation has been shown to be an effective index of thermocline strength (Fiedler 2010). Mean temperature was included to account for thermal tolerance levels of forage fish species (Mhlongo et al. 2015) while stratification was used as a proxy for thermocline strength and the influence this has on the vertical distribution and concentration of chlorophyll and associated primary and secondary production in the water column (Shannon et al. 1984). Only data-series with complete coverage for all depths on a given day were used in these analyses.

SST and chla data were obtained from the NASA ocean colour group's Moderate Resolution Imaging Spectroradiometer (MODIS) satellite array, quantified into 1 km grid cells. These data were aggregated over a 20 km radius around each penguin breeding island (excluding land areas) to encompass the full extent of the fish survey routes (Figure 3.1). Due to spatially incomplete datasets on days with cloud-cover, a period of 30 days was used as the minimum composite span to ensure adequate coverage of the study area. SST was used as an indication of upwelling intensity and chla as a proxy for primary production.

A visual assessment of the distribution of potential upwelling areas during the study period was created by calculating SST skewness. Skewness is a measure of the asymmetry in a probability distribution and is zero for a normal distribution (White 1980). Skewness was calculated over the greater regional expanse of Algoa Bay for three years commencing in 2011 by, firstly, calculating a two-week rolling mean for each 1 km-grid cell, and, secondly, calculating skewness over these averages. In the context of this region, negative skewness values are indicative of areas prone to a higher propensity and/or intensity of cool upwelling events.

Fish acoustic data

Pelagic fish surveys were conducted around the two African Penguin breeding colonies, Bird and St Croix islands, between October 2011 and July 2013. A Furuno DFF3 recreational fish-finder with a 200 kHz transducer was transom mounted to a 7.6 m catamaran ski-boat (see Chapter 2 for more details). Surveys were conducted at 7 knots along transects traversing the known foraging ranges of African Penguins (Pichegru et al. 2010, 2012, L. Pichegru & A. M. McInnes unpublished data) (Figure 3.1), at depths ranging from 20 to 98 m in conditions suitable for operating a small boat and conducting observations, i.e. winds < 15 knots and swell < 2.5 m. All surveys were carried out during daylight hours between 09h00 and 16h00 for Bird Island and between 7h00 and 16h00 for St Croix Island.

The echo-returns from the display unit of the fish-finder were recorded using two methods. For surveys conducted between October 2011 and November 2012 we used a mounted GoPro video camera to record echograms from the monitor display. All subsequent surveys used digital images recorded directly onto an SD memory card which required the manual activation of a function key to record each image, hereafter referred to as digital outputs. A small gear-motor with a button pushing device was mounted to the console to facilitate a constant stream of image grabs every 30 s. Echo-returns were processed using Fishfinder Image Segmentation Helper (FISH) software (Chapter 2) which has two versions for processing both GoPro and Digital formats.

Echo-return data were filtered to eliminate non-school data and a correction factor was applied to the density estimates of each school, the mean backscattering coefficients ($\bar{s_v}$), following the methods described in Chapter 2 using the scenario 2 regression equation:

$$y = 10^{-5.59+102300x}, \tag{3.1}$$

where y and x are the corrected and uncorrected mean backscattering coefficients ($\bar{s_v}$), respectively.

Relative pelagic fish abundance was determined using two metrics. Firstly, for aggregated (survey level) estimates, the nautical area scattering coefficient (s_A) (m^2 nmi^{-2}) of all schools aggregated over the survey length was used, given the formula:

$$\boldsymbol{s_{A}= 4\pi(1852)^2 s_a}, \tag{3.2}$$

where $4\pi(1852)^2$ is the nautical mile derived scaling factor and s_a is the integral of the mean backscattering coefficients ($\bar{s_v}$) over a range interval. In the context of this study, the range interval is the height of all schools weighted by the length of all schools for schooling fish targets only. Secondly, for assessing the influence of individual school biomass, total volumetric abundance (TVA) (kg) was calculated as:

$$TVA = 10^{\frac{S_v - TS_a}{10}} \times V, \tag{3.3}$$

where S_v is the mean volume backscattering strength, TS_a is the target strength (dB kg^{-1}) for anchovy at a caudal length of 13 cm using the formula of Barange et al. (1996), and V is the school volume (m^3) assuming a cylindrical shape for the school using the formula $V = \pi r^2 h$, where *r* is half the school length (m) and *h* is the school height (m). Anchovy was selected to calculate TS because it is the most common prey species of African Penguins in Algoa Bay (Crawford et al. 2011; Pichegru et al. 2012), and the 13 cm caudal length is the most common size class collected by the South African Department of Agriculture, Forestry and Fisheries (DAFF) while conducting spawner biomass surveys in Algoa Bay between 2011 and 2012, as well as in African Penguin diet samples collected in 2012 and 2013 (A.M. McInnes & L. Pichegru unpublished data). To assess the accuracy of s_A in determining relative fish abundance at the survey scale, we compared this estimate to the total number of fish schools recorded for each survey. School number and abundance estimates are positively correlated in a range of schooling species (Brierley & Cox 2015).

Aggregation patterns of forage fish schools were determined by a fish dispersal index (FDI), calculated as the variance to mean ratio of the number of fish schools recorded in 1 km segments along the fish survey routes; higher values indicate more clustered spatial aggregations while lower values indicate more scattered patterns. A school altitude index (AI) was calculated as the average height above the seabed of schools relative to the seabed depth with values of one approaching sea-level and values close to zero indicating fish near the seabed. For survey level models this metric was aggregated over all schools using the mean altitude index (MAI). A portion of the acoustic surveys, mostly around Bird Island at various locations along the survey route, had broken or absent seabed in the echo-returns and these data were removed from analyses that used AI as response variables.

In order to distinguish potential morphometric and/or ancillary fish school characteristics that could help interpret potential species assemblages from our non-classified echo-returns, we plotted species-specific school parameters, MAI, and mean volume backscattering strength (S_v) as a measure of school density, and school cross-sectional area coming from DAFF spawner biomass surveys conducted during November of each year between 2010 and 2014 (DAFF unpublished data). These surveys used intermittent mid-water trawls to sample small pelagic fish species for morphometric and identification purposes and quantified catches in terms of the proportional species composition of three small pelagic fish species found in this region, sardine, anchovy and redeye. All data were filtered to include only samples from Algoa Bay within a similar depth range covered by our surveys, i.e.< 120 m, and only for fish sampled between 08h00 and 16h00.

Device effects

To assess differences between GoPro and Digital echogram outputs we conducted a survey on 10 April 2014 along the St Croix survey route using both systems simultaneously and compared school cross-sectional area and school depth for both systems using least squares regressions. The automated calculation of school density for the GoPro outputs was not possible and hence we adopted a modelling approach to predict these values based on the relationship between $\overline{s_v}$ (a measure of school density) and three variables, two continuous covariates, school area and school depth, and site as a fixed effect, using pelagic fish schools from all surveys that generated Digital outputs. Site was included to account for potential regional differences in school densities. Generalised additive models (GAMs) were used where the response variable is modelled as smoothing functions of the explanatory variables (Wood 2006). Computations were carried out in R (R Core Team 2015) using the package 'mgcv' (Wood 2006) where the smoothing functions are penalised regression splines. The degree of smoothness of the splines was determined by Generalised Cross Validation criteria. I used the Gamma error family with an identity link function to accommodate the non-normal error distribution. To ascertain the robustness of the relative abundance estimates, including the effects of both devices, I computed the relationship between the number of schools and s_A for each survey using least squares regression with both variables log-transformed.

Aggregated (survey level) bio-physical models

The influence of oceanographic variables, i.e. mean temperature, stratification, SST (30-day lag) and chla (30- and 60-day lags), were modelled against three dependent fish variables: relative fish abundance (s_A), fish dispersion index (FDI) and mean altitude index (MAI) for surveys from each penguin breeding island modelled separately. Justification for splitting the models between sites was based on the assumption that bio-physical interactions would differ between islands given the high levels of oceanographic variability across the bay (see Introduction for more details).The response variables for these models comprised one aggregated metric per survey with lagged explanatory variables being aggregated in the lag period before each survey date. Multiple regression techniques were avoided due to the limited sample size in fish surveys for each island and the associated inadequate degrees of freedom. I initially used GAMS to gauge potential non-linear trends in the explanatory variables. If a linear relationship was evident (i.e. estimated degrees of freedom ≈ 1), the model was re-fitted either as a generalised linear model (GLM) for non-normal data or a least-squares regression for normal or transformed data. Depending on the nature of the response variable and the model diagnostic outputs, one of two error distributions were used, a Gamma distribution with a log link function for continuous non-normal data, or a Gaussian distribution for normally distributed data (original or log-transformed). For models including satellite-derived data (SST and chla) where the explanatory variable was a composite of 30 days or more, I weighted these regressions with the frequency of data points for each satellite-derived sample so that periods with better coverage (i.e. less cloud cover) would have a stronger bearing on the relationship between these variables and the response. All computations were carried out in R and goodness-of-fit (R^2) statistics for GLM models were calculated using maximum likelihood pseudo R^2 values using R package 'pscl' (Jackman 2015). To explore potential density-dependent influences on fish dispersal I applied the same modelling protocol to assess the relationship between relative fish abundance (s_A) and FDI for data from each island.

Disaggregated (school level) bio-physical models

Mixed effects models were used to assess the relative significance of oceanographic and temporal variables on two responses using pelagic fish school data, i.e. TVA as an indication of school biomass, and school altitude index (AI). The following oceanographic covariates were used: chla (30-day lag), SST (30-day lag), stratification and mean temperature. Temporal covariates included year and season (summer: October - April; winter: May - September) to control for possible annual and seasonal variation. To account for variability between survey days, survey date was set as a random effect. All models were run for each island separately. As with the modelling protocol adopted for the aggregated models, I initially explored the potential for non-linear relationships using generalised additive mixed effects models (GAMM) and, if linear relationships were evident, resorted to linear mixed effects models (LMM) using log-transformed response variables where necessary. Akaike's Information Criteria (AIC, Akaike 1973) was used to assess the best fitting model following a step-wise procedure by initially including all explanatory variables and dropping non-significant terms sequentially until the lowest AIC value was achieved. All computations were carried out in R using packages 'mgcv' for the GAMMs and package 'lme4' (Bates et al. 2015) for the LMMs.

Mechanistic drivers of primary production

Generalised least squares (GLS) regressions were used to gauge the influence of monthly averages of north-easterly and south-westerly wind speeds on monthly composites of chla around Bird and St Croix islands. To account for potential non-independence of these time series an autocorrelations structure of order 1 was included in the model (i.e. corAR1 using the package 'nlme' in R, Pinheiro et. al 2015). To approximate the assumptions of a normal error distribution the response variable was log-transformed.

Potential upwelling events associated with large episodic meanders (LEMs) were identified using the classification of Goschen et al. (2015), i.e. a decrease in average bottom temperatures over seven days or more. The UTR data from Algoa Bay Central at the 50 and 55 m depth gauges were used to quantify the initial stages of these events. Visual inspection of (MODIS) SST satellite images over these flagged periods was used to confirm or invalidate these events.

Model validation

Model validation procedures following Zuur et al. (2009, 2010) were carried out on all model outputs. These included visual inspection of homogeneity by plotting the residuals versus the fitted values, and of normality by plotting the model residuals versus the theoretical quantiles. For models with multiple explanatory variables, collinearity between variables was assessed using variance inflation factors following (Zuur et al. 2009), setting the minimum allowed threshold to five.

Results

Device effects

Comparisons of fish school characteristics for the GoPro and Digital outputs using least-square linear regression models were completed on 18 schools insonified along the St Croix survey route. Results of these comparisons show highly significant positive relationships for both school area ($R^2 = 0.96$, $p<0.001$) and mean school depth ($R^2 = 0.98$, $p<0.001$) between both output types.

GAM results of the relationship between school area and school density estimates ($\overline{s_v}$) for all Digital outputs were highly significant ($p<0.001$) with greater precision in estimates of school area for schools smaller than 200 m^2 (Figure 3.2a). The relationship between school density and school depth was also highly significant ($p<0.001$) with a sharp exponential decline in $\overline{s_v}$ as school depth increased (Figure 3.2b). There was a small but significant effect of site on this model outcome (β (se) = $7.6x10^{-7}$ ($3.72x10^{-7}$), p = 0.04) with higher density fish schools recorded off St Croix Island. These variables explained 30.9 % of the residual deviance in the model. When using this model to predict GoPro $\overline{s_v}$ values, a large proportion (>90%) of the schools' metric values (Figures 3.2c & d) fell within the most confined confidence intervals of the GAM outputs (vertical dotted lines in Figures 3.2a & b).

Robustness tests of our relative abundance estimates using linear regression revealed strong positive associations between the number of schools recorded for each survey and s_A values for all three device scenarios tested: outputs from both devices combined (β (se) = 1.14 (0.1), p <0.001,R^2 = 0.73), for Digital outputs only (β (se) = 0.86 (0.17), p <0.001,R^2 = 0.47) and for GoPro outputs only (β (se) = 1.26 (0.12), p <0.001,R^2 = 0.88) (Figure 3.3).

Fish surveys

A total of 36 acoustic fish surveys were conducted in Algoa Bay between 21 October 2011 and 31 July 2013: 18 surveys around Bird Island (mean ± SD survey length: 64.4 ± 6.6 km) and 18 surveys around St Croix Island (mean ± SD survey length: 85.5 ± 15.2 km) (Table 3.1). The number of fish schools (corrected for survey length) recorded for each island ranged from 22 to 513 schools for Bird Island (mean ± SD: 187 ± 133) and from 11 to 342 schools for St Croix Island (mean ± SD: 127 ± 96). Relative fish abundance (s_A) was greater around Bird Island (median ± inter-quartile range (IQR), Bird Island: 1001.9 ± 1528.6 $m^2 nmi^{-2}$, St Croix Island: 328.7 ± 651 $m^2 nmi^{-2}$; Mann-Whitney test, w = 232, p = 0.03) and fish schools occurred significantly higher above the seabed around St Croix than Bird Island (mean altitude index ± SD, Bird island: 0.2 ± 0.06, St Croix Island: 0.3 ± 0.06; T-test, t = -2.5, p=0.02). There was no difference in fish dispersal index values between sites (median ± IQR, Bird Island: 4.9 ± 3.2, St Croix Island: 3.6 ± 2.1; Mann-Whitney test, w = 207, p = 0.16).

Comparisons between the frequency and composition of pelagic fish schools caught during DAFF surveys are shown in Figure 3.4. Most (68 %) fish aggregations comprised more than one species. Of the single species aggregations caught, anchovy schools were recorded significantly higher in the water column than other species (median ± IQR AI, anchovy: 0.9 ± 0.04, round herring: 0.38 ± 0.7, sardine 0.36 ± 0.23; Kruskal-Wallis test, χ^2= 38.7, p<0.001); sardine schools were significantly denser (median ± IQR S_v, anchovy: -44.6 ± 10.87 dB, round herring: -54.44 ± 5.44 dB, sardine -30.16 ± 2.7 dB; Kruskal-Wallis test, χ^2= 111, p<0.001); and sardine schools were significantly larger (median ± IQR cross-sectional area, anchovy: 54.13 ± 97.19 m^2, round herring: 22.79 ± 45.24 m^2, sardine 100.95 ± 117.42 m^2; Kruskal-Wallis test, χ^2= 52, p<0.001).

Aggregated (survey level) bio-physical models

Pelagic fish school data aggregated from 18 surveys conducted in the vicinity of each island between 21 October 2011 and 31 July 2013 were used in this analysis. Model outputs are given in Table 3.2 with significant outputs (p<0.05) illustrated in Figure 3.5. The most influential variable on relative fish abundance estimates (s_A) around Bird Island was chla, which had a strong positive effect over a 60-day lag period (Figure 3.5a) and a positive non-linear effect over a 30-day lag period (Figure 3.5b), explaining 37 and 44 % of the variation in the responses of these two models, respectively. Neither chla variables (lagged 30 or 60 days) had a strong influence on s_A around St Croix Island. SST, stratification and mean temperature had little effect on s_A around either island (Table 3.2).

Models using fish dispersal index (FDI) as the response variable showed no significant influences of oceanographic covariates around St Croix Island. There was a strong negative association between SST estimates over a 30-day lag on FDI values around Bird Island, with this variable explaining 46% of variation in this response (Figure 3.5c). Around St Croix Island, SST explained 11% of variation in FDI but was not significant at the 0.05 level. Fish dispersal around both islands was positively correlated with relative fish abundance (S_A) up to ca 1000 m^2 nmi^{-2} (Figures 2.6a & b). Results of the linear regression were highly significant for St Croix Island ($R^2 = 0.53$, t = 4.47, $p<0.001$) but for Bird Island there was no apparent trend at s_A values > 1000 m^2 nmi^{-2} (Figure 3.6b). These disparities between sites are likely due to the relatively low s_A values recorded around St Croix Island with the highest fish abundance estimated at 1142 m^2 nmi^{-2} during April 2013 at this site compared to Bird Island which had a maximum of 6803 m^2 nmi^{-2} recorded during May 2012 (Table 3.1).

There was very little influence of oceanographic variables on mean school altitude (MAI) around Bird Island. However, for surveys conducted around St Croix Island, this was the only response that was significantly associated with covariates. Both SST (30-day lag) and stratification had positive influences on MAI (Figures 2.5d & e) explaining 53 and 38% of variation, respectively. SST and stratification were positively correlated (Spearman's rank correlation, r = 0.67,s = 3178, p = 0.003), with fish schools recorded higher up in the water column as SST and stratification increased.

Disaggregated (school level) bio-physical models

Two data sets for each island were used for these analyses: one comprising all school data for fish school biomass (TVA) as a response and a data set with erroneous altitude data omitted for school elevation above the seabed (AI) as a response (see Methods). For Bird Island, the final filtered data sets comprised 2807 schools (mean ± SD: 156 ± 98 schools per survey) and 1597 schools (mean ± SD: 89 ± 61 schools per survey) for the TVA and AI models, respectively, whereas the comparative samples sizes for St Croix Island were 2591 schools (mean ± SD: 144 ± 112 schools per survey) and 2447 schools (mean ± SD: 136 ± 105 schools per survey). Checks for collinearity between covariates in the LMMs showed that all variables had variance inflation factor scores <5 so all were included in the initial models.

Results of the step-wise model selection process are shown in Table 3.3. The best fitting model for TVA around Bird Island only included chla (30-day lag), which positively influenced fish school biomass (Table 3.4, Figure 3.7a). For St Croix only SST (30-day lag) was included in the best fitting model, with lagged surface temperature having a positive influence on fish school biomass(Table 3.4, Figure 3.7b). The best fitting model for AI at Bird Island included season as a significant fixed effect with schools being higher in the water column during winter (Tables 2.3 & 2.4, Figure 3.8a). For St Croix Island both chla (30-day lag) and especially SST (30-day lag) had positive influences on normalised AI data (Figure 3.9, Table 3.4).

Mechanistic drivers of primary production

As expected, north-easterly winds had a positive association and south-westerly winds had a negative one with chla around both islands (Table 3.5). These relationships were stronger around St Croix, especially for the influence of north-easterly winds, although none of these results was significant (Table 3.5). To ascertain the potential influence of wind on the differences in chla levels between the summers of 2011/2012 and 2012/2013 (Figure 3.10d) I compared average wind speeds for north-easterly and south-westerly winds between these two periods. North-easterly winds were generally stronger around Bird Island during 2012/2013 (median ± IQR 7.6 ± 4.7 m s^{-1}) than 2011/2012 (6.5 ± 4.4 m s^{-1}), although these differences were not significant (Mann-Whitney test, w = 246, p = 0.31). South-westerly winds were significantly stronger around Bird Island during 2011/2012 (6.1 ± 4.2 m s^{-1}) than 2012/2013 (5.2 ± 3.2 m s^{-1}; Mann-Whitney test, w = 3278, p = 0.03). Average north-easterly winds were stronger during the summer of 2011/2012 at PE Harbour, close to St Croix (7.5 ± 4.8 m s^{-1}) than 2012/2013 (5.9 ± 3.3 m s^{-1}) but again these differences were not significant (Mann-Whitney test, w = 615, p = 0.16). As with Bird Island, south-westerly winds were stronger around St Croix Island in 2011/2012 (9.8 ± 5.1 m s^{-1}) than 2012/2013 (8.8 ± 4.9 m s^{-1}) but these differences were not significant (Mann-Whitney test, w = 4760, p = 0.14).

Five potential LEM events were identified during the study period, of which two events were confirmed through visual inspection of SST images: one from 11 April 2012 and one from 19 May 2013, with both events lasting ca 2 weeks (Figure 3.11). The 2012 event coincided with the highest levels of monthly chla around both islands for 2012 (Figure 3.10d).

Discussion

Device effects

Using recreational fishfinders to quantify fish distribution and abundance has been shown to give comparable estimates to those from scientific echo-sounders, the conventional tool used in quantitative acoustic surveys (Chapter 2). The results of this chapter lend further weight to these findings by demonstrating the strong positive linear correlation between the number of schools recorded for each survey and relative fish abundance (s_A) (Figure 3.3). Positive associations have been demonstrated for other pelagic species: Antarctic krill (*Euphausia superba*) through the use of multi-beam sonar (Brierley & Cox 2015) and Atlantic herring (*Clupea harengus*) using a split-beam echo-sounder (Jech & Stroman 2012). This relation held for both of our methods used in recording echo-returns; in fact the relationship was stronger for the GoPro outputs, adding support for the GAM parameters used to predict density values from the GoPro-derived surveys (Figure 3.2). Furthermore, the positive non-linear association between school area and s_A for the digital-derived schools are very similar to the findings of Misund et al. (2003) for sardine schools in False Bay, South Africa. However, it is not known if this relationship holds for other small pelagic fish species in this region.

Effects of oceanography on fish abundance

The three dominant species of forage fish in Algoa Bay obtain most of their energy from zooplankton, although to some extent they are trophically distinct, with anchovy and redeye consuming larger zooplankton than filter-feeding sardine (James 1987, 1988; van der Lingen 2002). For the purposes of this chapter, therefore, I assume that pelagic fish collectively occupy a similar trophic position in terms of their likely response time to bottom-up processes. This approach is supported by the objectives of this study, i.e. to quantify the response of pelagic fish species that comprise prey for top predators, notably African Penguins which feed on all three of the common pelagic fish species (Randall & Randall 1986; Crawford et al. 2011).

Model results show strong positive influences of chla on fish abundance around Bird island which is evident for both aggregated data at two lag periods, 30 and 60 days in mean chla, and for the biomass of individual schools at 30-day lags. Results of models using multiple covariates highlight the relative importance of this factor in mediating fish abundance in this area as it was the only oceanographic variable remaining in the best fitting model for this analysis (Table 3.3). Consistent results at both the 30- and 60-day lags seem to indicate that pelagic fish in this region may be more or less sedentary for at least two months within a relatively restricted area during favourable conditions, but becoming more mobile/ephemeral in less productive periods. In contrast to these findings around Bird Island, chla had little influence on fish abundance around St Croix Island (Table 3.2). Levels of chla were consistently more elevated around Bird Island compared to St Croix Island, which corresponds to either a greater propensity of upwelling events or stronger retention of chla around Bird Island over the study period (Figure 3.1). Despite the differences in productivity between sites, variation in mean monthly chla varied consistently around both islands, which fails to explain the lack of a response by fish to chla around St Croix Island (Figure 3.10d). This discrepancy can be better explained by the differences in fish abundance between sites, due to greater and more variable fish abundance around Bird Island (Figure 3.10e). Such differences may be related to disparate top down processes operating across the bay. During the study period the waters around both islands were subject to experimental fishing closures with Bird Island being closed to fishing during 2012 and 2013 and St Croix being open to fishing during this period. It is possible that removal of fish around St Croix may have masked the natural bio-physical processes here. This phenomenon has been inferred to influence similar associations between oceanography and pelagic fish in the Black Sea (Daskalov 2003) and in the eastern Mediterranean (Katara et al. 2011), albeit over longer time-spans. An alternative hypothesis is that Bird Island is in closer proximity to a more stable source population of pelagic fish that expand their range into the eastern part of the bay more frequently during favourable periods with limited advection into the western part of Algoa Bay. However, this hypothesis is not supported by the results of the regional distribution of small pelagic fish collected by DAFF during the three years of this study (Shabangu et al. 2011, 2012; Mhlongo et al. 2013).

The weak but significant positive relationship between SST and the biomass of fish around St Croix Island closely resembles associations of sardines and SST at coarser scales (Agenbag et al. 2003) and may relate to more sardine schools being present around this island during warmer SST periods. The largest and most dense schools recorded by DAFF in this region between 2010 and 2014 were sardine schools (Figures 2.4b & c) and the presence of these schools during this study is likely to have had a pronounced influence on the range of fish school biomass (TVA) values recorded under different SST scenarios. However, this relationship may also be biased by fishing effects on pelagic fish abundance.

Effects of oceanography on fish dispersal

Aggregation patterns of pelagic fish beyond the level of schools, i.e. from clusters of schools to the population, are believed to be environmentally mediated (Bertrand et al. 2008). Around Bird Island, increased clustering of schools (patchiness) was favoured by decreasing average monthly SST values (Figure 3.5c) and, to some extent, this can be explained by increasing fish abundance under these conditions (Figure 3.6a), viz. an increase in the incidence of upwelling events and associated productivity. However, at s_A values > 1000 m^2 nmi^{-2} there was greater variation in FDI values for Bird Island and fish abundance does little to explain this relationship. Rather, it suggests that cooler average surface temperatures promote the aggregation of fish schools regardless of associated fish abundance. This may be related to the patchy nature of bottom-up processes (notably those influencing zooplankton distribution) during cooler upwelling periods. The patchy nature of community structuring from the bottom-up has been demonstrated in other systems, e.g. Benoit-Bird & McManus (2012) for inshore pelagic habitat in Hawaii and Bertrand et al. (2014) for the upwelling ecosystem off Peru. In both these studies strong environmental forcing could be gauged by the response of higher trophic organisms at scales < 10 km.

Effects of oceanography on the vertical distribution of prey

Aggregated fish altitude (MAI) around St Croix was positively influenced by warming SST conditions and increased stratification, both of these explanatory variables being highly correlated with each other. This suggests that fish moving closer to the surface when there is a marked thermocline, which typically occurs when thermal gradients are accentuated by cooler water from below and a warm mixed surface layer is generated by increased insolation during summer (Schumann et al. 2005). Such conditions favour enrichment of nutrients below the mixed surface layer (Goschen & Schumann 1988) and thus promote responses at higher trophic levels (Cury et al. 2000). Similar influences of SST were evident for the disaggregated model results for St Croix and there was a weak but significant positive influence of chla on school altitude (Figure 3.9a). The latter trend is difficult to interpret given that relative fish abundance was not influenced by this variable but, as with the previous argument related to influences of SST on fish abundance, this may be due to differential species specific preferences with sardines generally occurring at higher altitudes (Lawson et al. 2001) (Figure 3.5a) and generally associating with warmer SSTs (Agenbag et al. 2003).

In contrast to these results there was little influence of thermal stratification and SST on MAI around Bird Island. There were similar peaks in SST and stratification around both sites throughout the study, although periods of increased stratification were more frequent around Bird Island during the last quarter of 2012 corresponding to relatively low SST during these months (Figures 2.10b & c). The only influential covariate for the disaggregated school models for this site was season, with schools being significantly higher in the water column during winter; a trend not apparent for schools around St Croix Island (Figure 3.8b). The relatively low altitude of fish around Bird Island during summer may be attributed to an increase in redeye abundance during this season at this site. Redeye was the only pelagic fish species to be recorded in the east of Algoa Bay in all three November spawner biomass surveys conducted by DAFF between 2011 and 2013 (Shabangu et al. 2011, 2012; Mhlongo et al. 2013) and this species tends to be distributed more inshore during the summer months (Roel & Armstrong 1991) and at relatively low altitudes (Lawson et al. 2001).

Mechanistic drivers of primary production

Low levels of primary production during the 2011/2012 summer were likely related to stronger south-westerly winds during this season (Figure 3.10a). These winds are known to promote mixing of the water column (Lutjeharms et al. 1996) and to suppress upwelling activity in areas south of the prominent capes, such as around Bird Island (Goschen & Schumann 1995). By comparison, stronger north-easterly winds around Bird Island during 2013 and weaker south-westerly winds would have favoured stronger and more frequent upwelling.

The anomalous spike in chla around both islands during April and May 2012 can be attributed to a Natal Pulse (LEM) offshore in the Agulhas Current and the associated influx of cool, upwelled waters into the bay for a few weeks (Figure 3.11). This event is likely to have played an important role in driving primary and secondary processes and ultimately the spike in fish abundance in the two months after the initiation of this event, especially around Bird Island (Figure 3.9). The LEM event during May 2013 also coincided with relatively high chla values, but this event was preceded by even higher chla values in the month leading up to this event (Figure 3.10d), which was probably linked to a combination of wind-induced and shear-edge upwelling events.

Implications of bio-phyisical associations to African Penguins

Results of this research reflect on the complex and highly variable nature of the marine habitat in Algoa Bay. This is significant for the African Penguin population here as two of this species' largest colonies are situated at either ends of this bay. The St Croix Island population is currently the largest globally (8685 pairs, DEA unpublished data) with more than double the population of Bird Island (2837 pairs, DEA unpublished data) yet conditions for their prey are more favourable around Bird Island. Consequently, the probability of density-dependent effects on the St Croix population are likely to be substantially higher and, coupled with increased anthropogenic activities around this island linked to nearby harbours, these factors are likely to increase the vulnerability of this population to further declines. However, one cannot rule out the possibility that bottom-up processes, other than those represented by the proxies for primary productivity used in this study, may be driving a significant proportion of the variation in prey availability here.

Oceanographic influences on the horizontal (FDI) and vertical (AI and MAI) distribution of prey in Algoa Bay are significant in terms of the access and predictability of prey available to African Penguins. Numerous studies have demonstrated the association between seabirds and productive oceanographic features (e.g. Nel et al. 2001; Hyrenbach et al. 2006; Cotté et al. 2007; Cox et al. 2013) and systems that exhibit predictable but patchy community structuring, as has been inferred from these results, are likely to play a significant role in shaping the foraging strategies of these species (e.g. Bon et al. 2015). For diving species, such as penguins, the vertical distribution of prey is a critical determinant of the types of assemblages they target (Zamon et al. 1996; Boyd et al. 2015). My results demonstrate how these parameters vary both in space and time with fish schools around Bird Island occurring at relatively low altitudes during summer and schools around St Croix during the same season being more elevated due to stratified conditions and increased SSTs. One would therefore expect a closer coupling of the at-sea distribution of penguins and their prey around St Croix during these periods, but this remains to be tested.

The findings of this study are important in terms of their use in controlling for natural variation in the prey base when assessing the impact of anthropogenic influences such as purse-seine fishing. Chla is a good predictor of fish abundance around Bird Island and SST and stratification are good predictors of both the vertical and horizontal distribution of fish around St Croix Island. What remains to be tested is whether this variation in prey distribution and abundance has any bearing on the foraging success of African Penguins (see Chapter 4). If this is demonstrated then the findings of this research should prove useful in trying to resolve issues related to the impacts of fishing.

Conclusions

To date, little has been known about the influences of natural variability in pelagic fish distribution and abundance at scales relevant to inshore marine predators in South Africa. In an ecosystem that is increasingly subjected to anthropogenic influences, this information is critical to establish quasi-baseline information to assess the direct impacts of human influences. The situation of the endangered African Penguin is a case in point. During the breeding season this species is confined to within ~40 km of their breeding colonies in waters subjected to periodic purse-seine fishing. The availability of pelagic fish within this range will have a significant bearing on their breeding success and it is therefore essential to understand the physical drivers of pelagic fish assemblages at this scale. To some extent, my results reveal significant processes driving this variability in a region that supports just over half the global population of African Penguins. One shortfall of the methodology used in this study is the lack of species-specific fish data, owing largely to the budgetary and logistical constraints of this project. However, the approach used here is adequate for the ultimate purpose of this study which is to understand the physical drivers to the three dominant fish species from this region, which are the penguins' main prey. Key oceanographic variables revealed by these findings, i.e. chla, SST and stratification, should provide useful covariates for more complex models related directly to African Penguin foraging activities and the influence of purse-seine fishing on this species' activity budgets.

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Table 3.1 Summary statistics of pelagic schooling fish data for 36 surveys conducted between 2011 and 2013 around St Croix and Bird islands in Algoa Bay. Both actual number of schools recorded for each survey and the number of schools corrected for survey length are shown.

Island	Survey date	Transect length (km)	No. fish schools	No. fish schools (corrected)	Relative fish abundace (s_A)	Fish dispersal index (FDI)	Mean school altitude index (MAI)
St Croix	2011-10-21	94.9	14	11	46.1	1.4	0.28
St Croix	2011-11-22	105.6	85	60	195.0	2.7	0.21
Bird Island	2011-11-24	70.5	90	96	250.7	2.8	0.22
Bird Island	2012-01-08	59.5	23	29	134.2	1.9	0.23
St Croix	2012-01-12	60.8	22	27	105.4	2.2	0.29
Bird Island	2012-02-15	62.1	32	39	151.3	3.3	0.08
St Croix	2012-02-16	62.9	19	23	53.1	1.6	0.27
St Croix	2012-03-19	104.7	59	42	102.1	3.6	0.34
Bird Island	2012-03-22	63.9	36	42	99.3	2.6	0.23
Bird Island	2012-04-26	67.1	20	22	41.5	2.8	0.16
Bird Island	2012-05-23	39.9	273	513	6802.8	6.4	0.23
St Croix	2012-05-28	86.7	99	86	221.9	2.9	0.27
Bird Island	2012-06-11	67.6	194	215	1880.2	4.9	0.30
St Croix	2012-06-28	79.3	149	141	576.9	2.8	0.27
St Croix	2012-07-06	70.3	132	141	309.4	4.1	0.19
Bird Island	2012-11-04	68.0	150	165	538.9	6.7	0.14
St Croix	2012-11-07	91.0	85	70	121.6	1.9	0.21
St Croix	2012-12-17	72.7	262	270	1106.7	6.1	0.23
Bird Island	2012-12-20	66.6	288	324	695.6	6.5	0.17
St Croix	2013-02-15	90.1	288	240	812.6	7.1	0.34
Bird Island	2013-02-27	64.6	231	268	2494.0	4.6	0.29
St Croix	2013-03-13	103.2	151	110	1081.5	5.8	0.32
Bird Island	2013-03-22	63.9	157	184	998.0	5.5	0.21
Bird Island	2013-04-06	65.1	78	90	1005.7	5.1	0.23
St Croix	2013-04-13	91.0	341	281	1141.6	5.4	0.21
Bird Island	2013-04-21	64.9	186	215	639.4	4.9	0.14
St Croix	2013-04-25	91.8	103	84	348.0	3.5	0.20
Bird Island	2013-05-05	66.2	318	360	1764.9	4.0	0.26
St Croix	2013-05-12	91.6	140	115	1018.1	3.7	0.30
St Croix	2013-05-22	55.6	105	141	604.2	4.9	0.42
Bird Island	2013-05-29	67.2	178	198	3056.0	5.1	0.21
Bird Island	2013-06-07	66.6	86	97	1301.7	2.9	0.29
Bird Island	2013-06-17	68.9	284	309	2157.4	6.5	0.26
St Croix	2013-06-29	89.9	411	343	498.5	4.7	0.22
St Croix	2013-07-16	97.2	126	97	95.7	4.7	0.18
Bird Island	2013-07-31	66.8	183	205	1356.8	8.6	0.17

Table 3.2 Bivariate model outputs for aggregated pelagic fish school data (by survey) and the influence of oceanographic explanatory variables using three model types: generalised linear models (GLM), generalised additive models (GAM) and linear regression models (LM). For GLM and LM outputs variable coefficients (β) and standard errors (se) are given, and for GAM outputs estimated degrees of freedom (EDF) and referenced degrees of freedom (s) are shown. Goodness-of-fit values (R^2) are maximum likelihood pseudo R^2 values for GLMs, standard multiple R^2 values for LMs and deviance explained for GAM outputs. Variable names: chl60 - chlorophyll a composite over 60 day lag, chl30 - as with chl60 but with 30 day lag, sst30 - sea surface temperature composite over 30 day lag, strat. - stratification (°C), mtemp - mean temperature through the water column (°C). Bold outputs denote significant outcomes at the 5% level.

Explanatory variables	**Response variables**								
	s_A			**FDI**			**MAI**		
	model	**β(se)/EDF(s)**	**R^2**	**model**	**β(se)/EDF(s)**	**R^2**	**model**	**β(se)/EDF(s)**	**R^2**
Bird Island									
chl60	GLM	**0.79** (0.24)**	0.37	GAM	1.89 (2.32)	0.2	LM	0.02 (0.01)	0.1
chl30	GAM	**2.99** (3.48)**	0.44	LM	0.29 (0.39)	0.03	LM	-0.00 (0.01)	0.01
sst30	GLM	-0.27 (0.21)	0.08	LM	**-1.00** (0.27)**	0.5	LM	0.02 (0.01)	0.12
strat.	GLM	-0.39 (0.47)	0.04	LM	-0.44 (0.77)	0.02	LM	-0.01 (0.03)	0.005
mean temp.	GLM	0.25 (0.13)	0.17	LM	-0.11 (0.25)	0.01	LM	0.01 (0.01)	0.17
St Croix Island									
chl60	GLM	0.06 (0.15)	0.008	GLM	-0.06 (0.07)	0.04	GLM	-0.01 (0.05)	0.006
chl30	GLM	0.02 (0.11)	0.002	GLM	-0.06 (0.05)	0.1	GLM	-0.03 (0.04)	0.03
sst30	GLM	0.10 (0.13)	0.02	GLM	0.09 (0.06)	0.1	GLM	**0.12** (0.03)**	0.53
strat.	GLM	-0.18 (0.25)	0.02	GLM	0.07 (0.12)	0.02	GLM	**0.17** (0.05)**	0.38
mean temp.	GLM	-0.12 (0.14)	0.05	GLM	-0.08 (0.07)	0.1	GLM	-0.05 (0.04)	0.12

$^{***}p < 0.001$, $^{**}p < 0.01$, $^{*}p < 0.05$

Table 3.3 Multivariate linear mixed effects models used to determine the influence of oceanographic and temporal covariates on fish school data for surveys conducted around Bird (BI) and St Croix (SC) islands. Akaike's Information criteria (AIC) and the difference in AIC of each model from the lowest AIC for each nested model set (ΔAIC) were used to identify the best fit models following a step wise drop-one selection process. Model abbreviations: TVA - total volumetric abundance of fish (kg), AI - school altitude index; chl30 - chlorophyll a concentration composite over 30 day lag period; sst30 - sea surface temperature (30 day lag); strat - thermal stratification through the water column (°C); mtemp - mean temperature through the water column (°C). For all models survey date was included as a random effect. Shaded rows represent best fit model for each nested set.

Island	Model no.	Model	AIC	ΔAIC
BI	BT1	log(TVA)~chl30+sst30+strat+mtemp+Year+Season	11936.84	17.36
BI	BT2	log(TVA)~chl30+sst30+strat+Year+Season	11932.02	12.54
BI	BT3	log(TVA)~chl30+sst30+Year+Season	11929.82	10.34
BI	BT4	log(TVA)~chl30 +Year+ Season	11925.24	5.76
BI	BT5	log(TVA)~chl30 + Season	11921.6	2.12
BI	BT6	log(TVA)~chl30	11919.48	0
BI	BA1	log(AI)~chl30+sst30+strat+mtemp+Year+Season	3681.1	19.3
BI	BA2	log(AI)~sst30+strat+mtemp+Year+Season	3675.7	13.9
BI	BA3	log(AI)~sst30+strat+mtemp+Season	3671.5	9.7
BI	BA4	log(AI)~sst30+strat+Season	3667.5	5.7
BI	BA5	log(AI)~sst30+Season	3665	3.2
BI	BA6	log(AI)~Season	3661.8	0
SC	ST1	log(TVA)~chl30+sst30+strat+mtemp+Year+Season	10006.48	10.2
SC	ST2	log(TVA)~chl30+sst30+strat+mtemp+Year	10004.14	7.86
SC	ST3	log(TVA)~chl30+sst30+strat+Year	10001.64	5.36
SC	ST4	log(TVA)~chl30+sst30+Year	10001.05	4.77
SC	ST5	log(TVA)~chl30+sst30	9998.75	2.47
SC	ST6	log(TVA)~sst30	9996.28	0
SC	SA1	log(altindex)~chl30+sst30+strat+mtemp+Year+Season	5489.79	20.85
SC	SA2	log(altindex)~chl30+sst30+mtemp+Year+Season	5484.97	16.03
SC	SA3	log(altindex)~chl30+sst30+mtemp+Season	5476.96	8.02
SC	SA4	log(altindex)~chl30+sst30+Season	5471.51	2.57
SC	SA5	log(altindex)~chl30+sst30	5468.94	0

Table 3.4 Best fit model coefficients (β) and standard errors (se) used to determine the influence of oceanographic and temporal covariates on fish school data for surveys conducted around Bird (BI) and St Croix (SC) islands. Variable abbreviations: TVA - total volumetric abundance of fish (kg), AI - school altitude index; chl30 - chlorophyll a concentration composite over 30-day lag period; sst30 - sea surface temperature (30-day lag); Season - summer, winter (W).

	Model number (Response variable)			
Explanatory variables	**BT6 (TVA)** **β (se)**	**BA6 (AI)** **β (se)**	**ST6 (TVA)** **β (se)**	**SA5 (AI)** **β (se)**
chl30	**0.21** (0.07)**			**0.07** (0.03)*
sst30			**0.19** (0.09)*	**0.18** (0.04)***
Season(W)		**0.35** (0.12)**		

$^{***}p < 0.001$, $^{**}p < 0.01$, $^{*}p < 0.05$

Table 3.5 Generalised least square regression coefficients (β) and standard errors (se) for correlations between mean monthly wind values (NE - north-easterly; SW - south-westerly) and chlorophyll a concentrations for Bird and St Croix islands between 2011 and 2013.

	Response (chla)	
Explanatory variables	**Bird Island** **β (se)**	**St Croix Island** **β (se)**
NE wind	0.05 (0.26)	0.35 (0.25)
SW wind	-0.08 (0.11)	-0.17 (0.10)

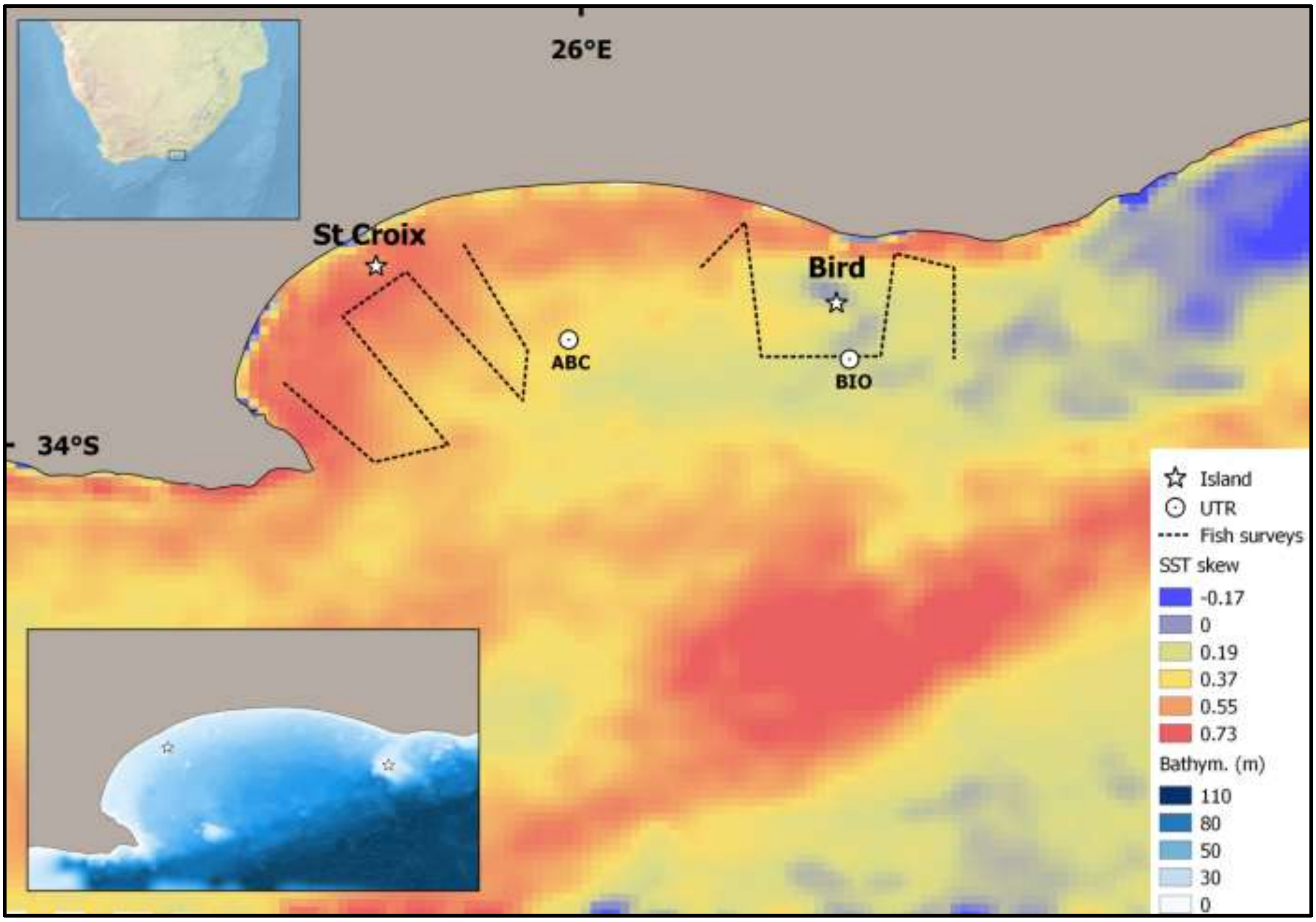

Figure 3.1 Study area in Algoa Bay showing locations of fish survey transects around St Croix and Bird islands, underwater temperature recorders (UTRs): ABC - Algoa Bay Central, BIO - Bird Island Offshore, and sea surface temperature skewness (SST skew) (3 year composite: 2011 - 2013) showing prominent upwelling regions and bathymetry (Bathym.) (insert).

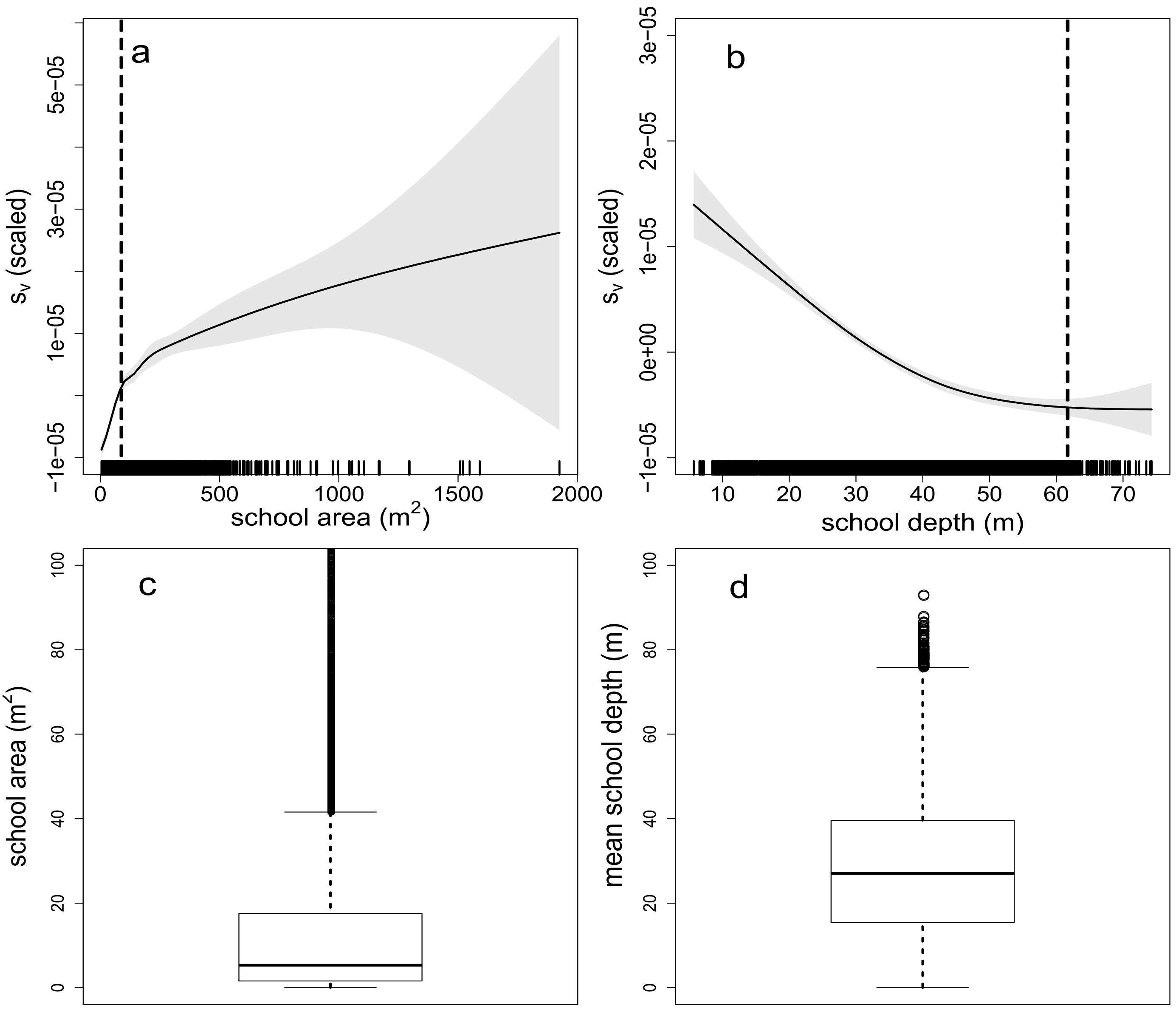

Figure 3.2 Generalised Additive Model (GAM) outputs for forage fish school area (a.) and mean school depth (c.) plotted with their smoother functions against scaled school density (s_v) estimates for schools from Digital outputs. Shaded areas denote 95 % confidence intervals and vertical dotted lines are the 90 % percentiles of corresponding GoPro output values (b. and d.): boxplots showing interquartile (IQR) ranges; whiskers are 1.5 X IQR.

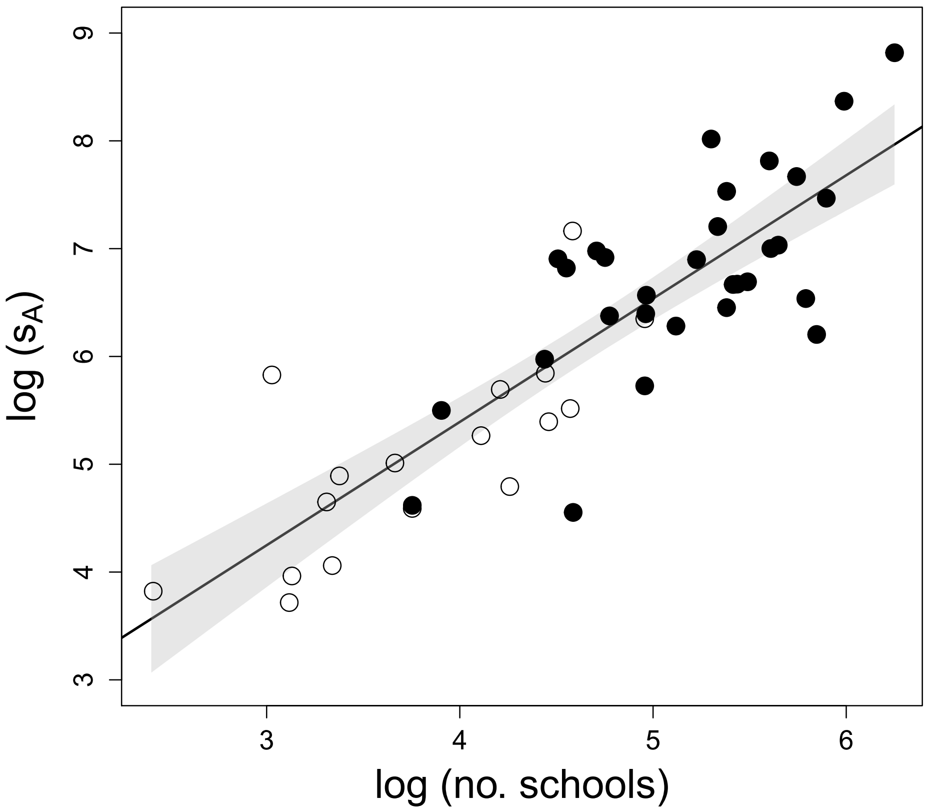

Figure 3.3 Comparisons of the total number of schools recorded for each survey and relative fish abundance estimates (s_A) for surveys recorded using the digital output method (closed symbols) and the GoPro output method (open symbols). The line represents the linear regression model fit for all surveys (both outputs combined), shaded area denote 95 % confidence intervals.

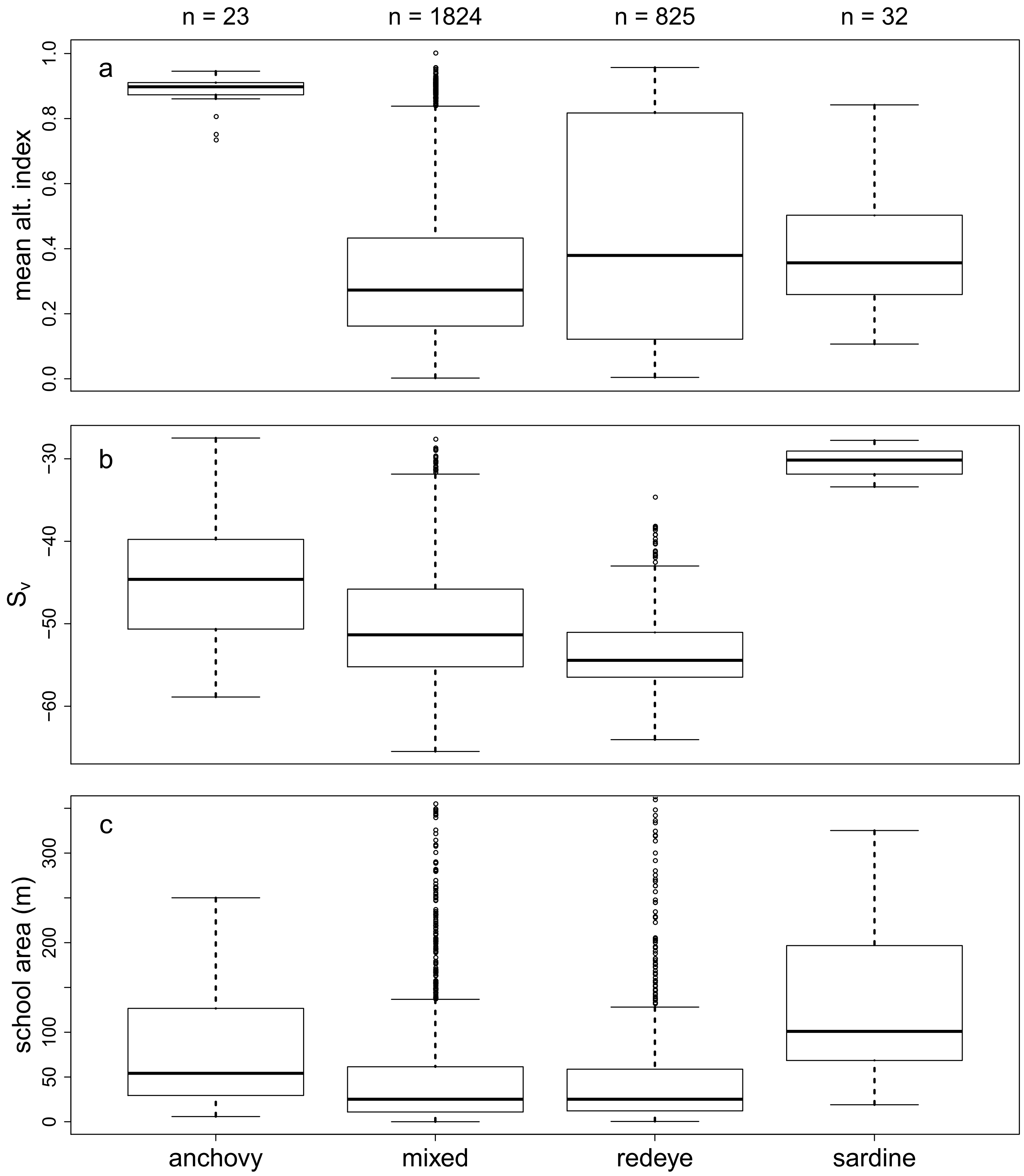

Figure 3.4 Boxplots showing medians and interquartile ranges of three forage fish school parameters, mean school altitude index (a), mean school density using volume backscattering strength (S_v) (b), and school cross-sectional area (c) for four fish school categories: anchovy only, mixed species schools, redeye only and sardine only. Results are from the Department of Agriculture, Forestry and Fisheries' (DAFF) spawner biomass survey data between 2010 and 2014 for Algoa Bay.

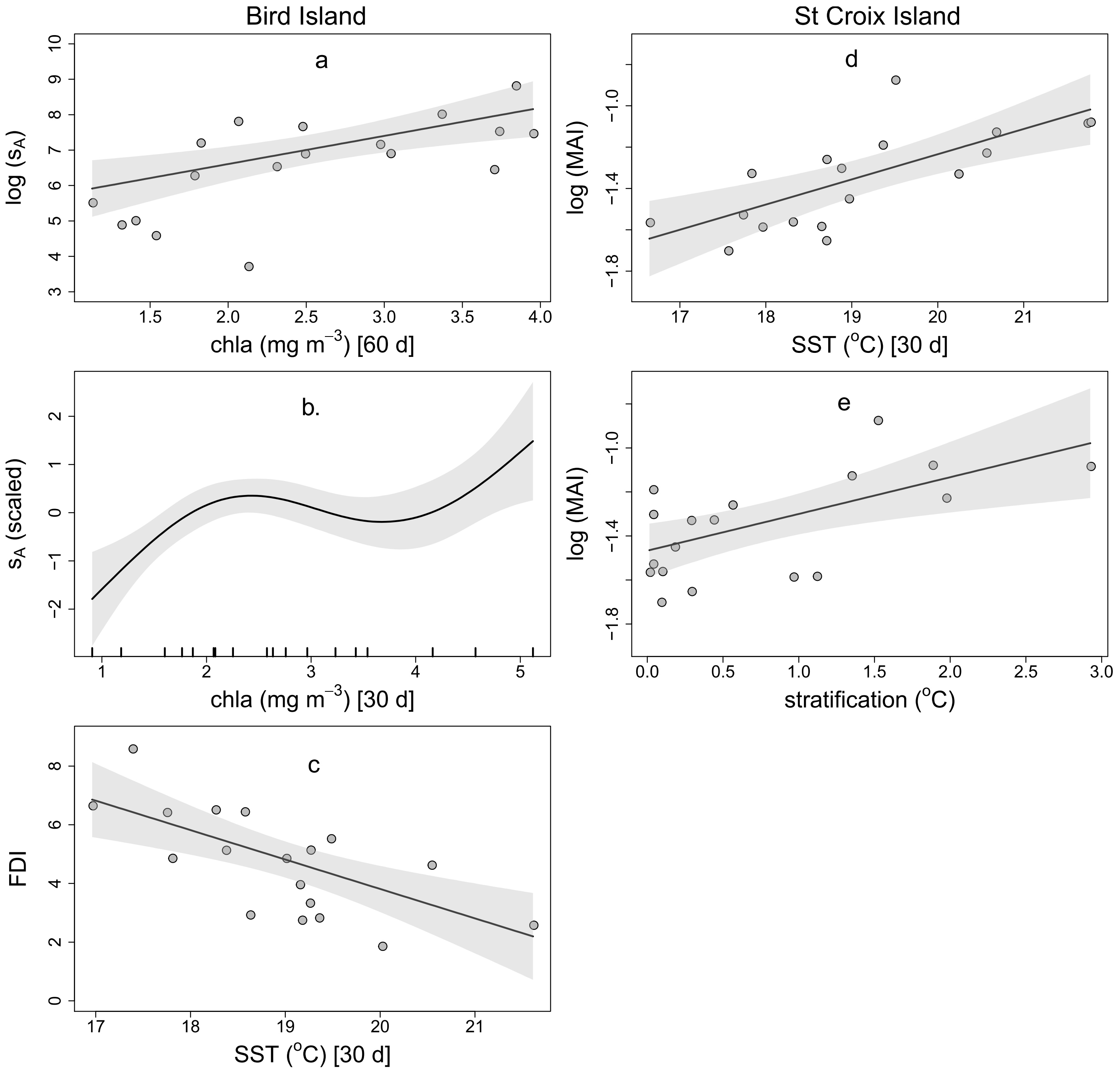

Figure 3.5 Bivariate model prediction plots between aggregated fish data (by survey) and oceanographic variables for surveys conducted around Bird and St Croix islands: a) relative fish abundance using the nautical area scattering coefficient (s_A) vs chlorophyll a concentration (chla) composite over a 60 day lag period; b) s_A vs chla (60 day lag); c) fish dispersal index (FDI) vs sea surface temperature (30 day lag); d) log transformed MAI vs SST (30 day lag); e) log(MAI) vs thermal stratification through the water column. Shaded areas denote 95% confidence intervals and, for Generalised Additive Model (GAM) output (b) , rug plot represent sample effort spread for covariate values.

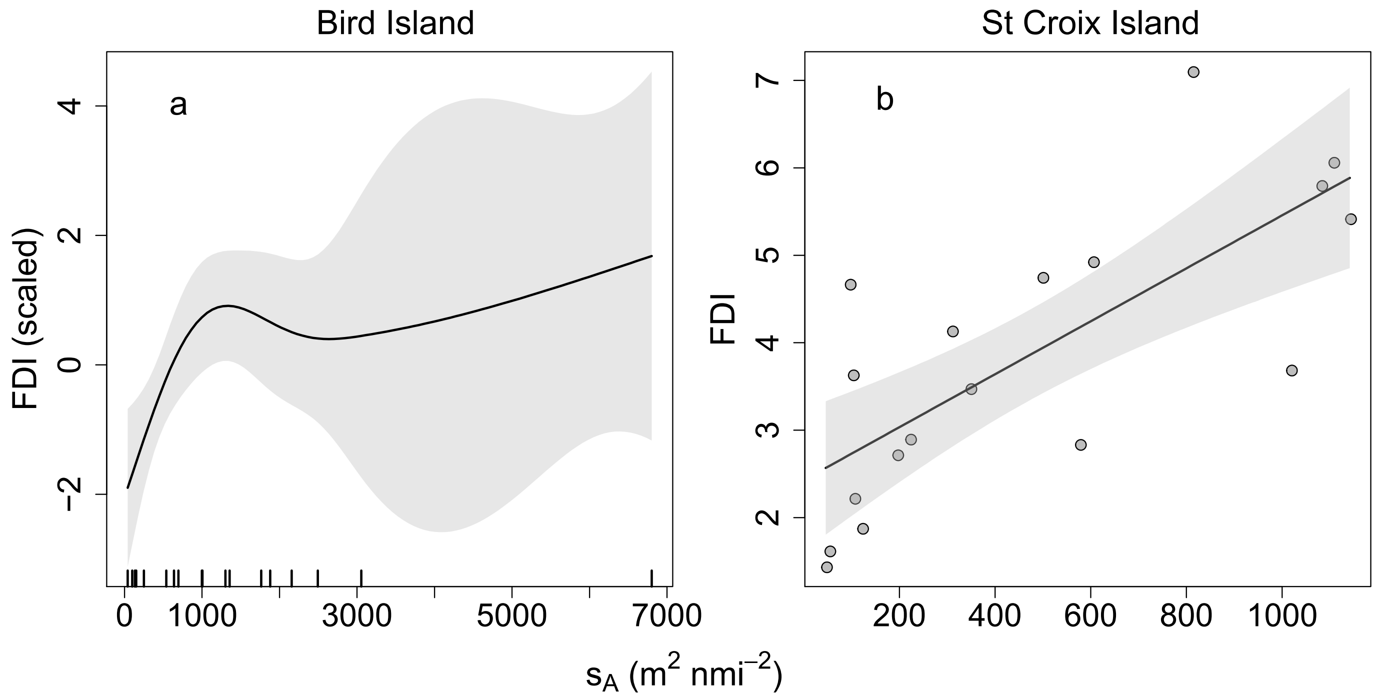

Figure 3.6 Influences of relative fish abundance (s_A) on fish dispersal index (FDI) for fish recorded around Bird (a) and St Croix (b) islands. High FDI values indicate school clustering. For Bird Island a Generalised Additive Model (GAM) was used with the rug plot denoting the sample effort and for St Croix Island a linear regression was used. Shaded areas denote 95% confidence intervals.

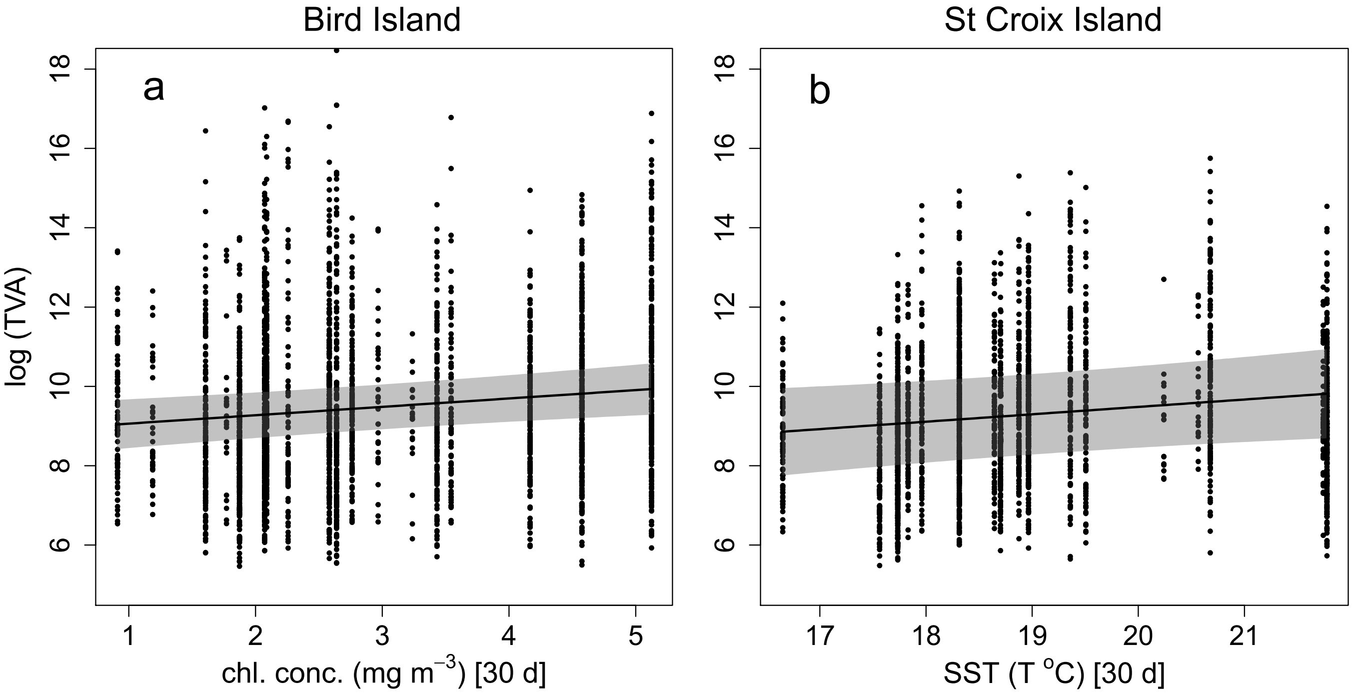

Figure 3.7 Linear mixed-effects model predictions for the influences of 30 day composite lags of chlorophyll a concentration (a) and sea surface temperature (b) on normalised total volumetric fish abundance (TVA) for Bird and St Croix islands, respectively. Grey shaded areas represent 95% confidence intervals.

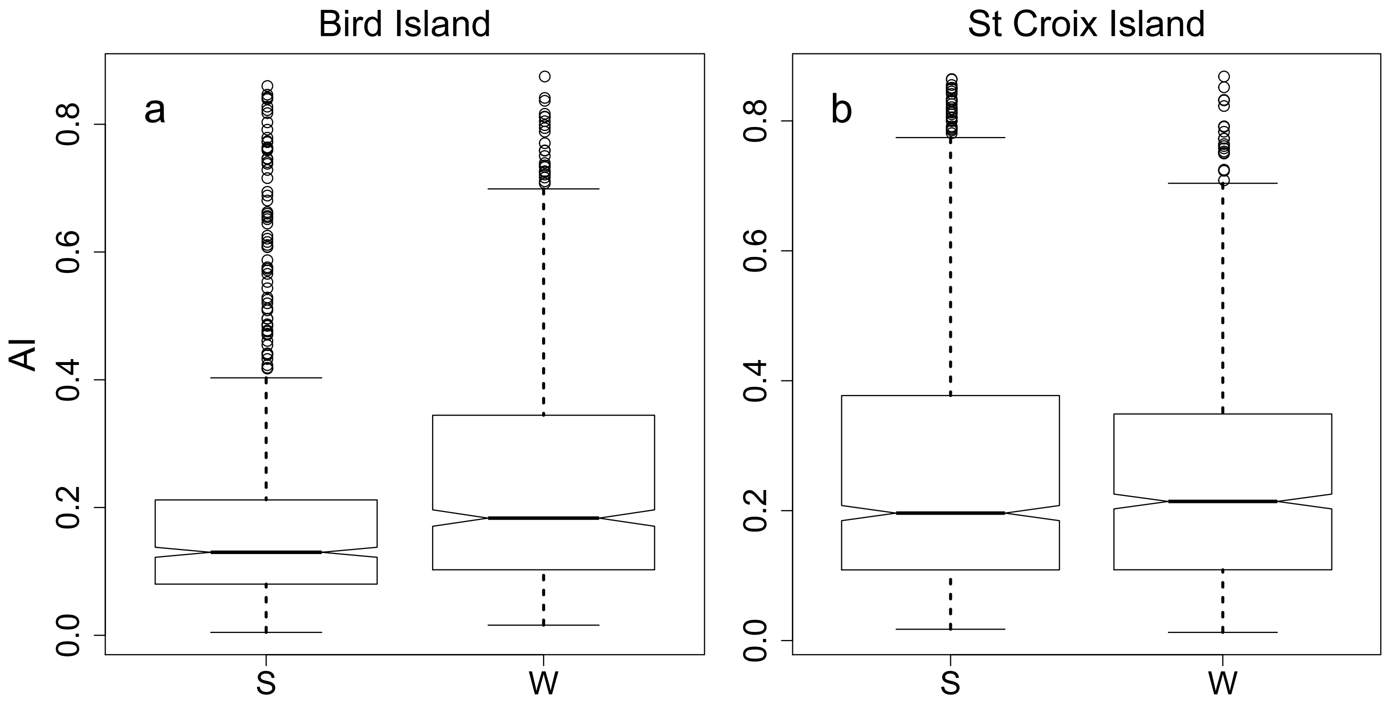

Figure 3.8 Boxplots showing seasonal differences (S - summer, W - winter) in school altitude index values (AI) for pelagic fish schools recorded around Bird (a) and St Croix (b) islands.

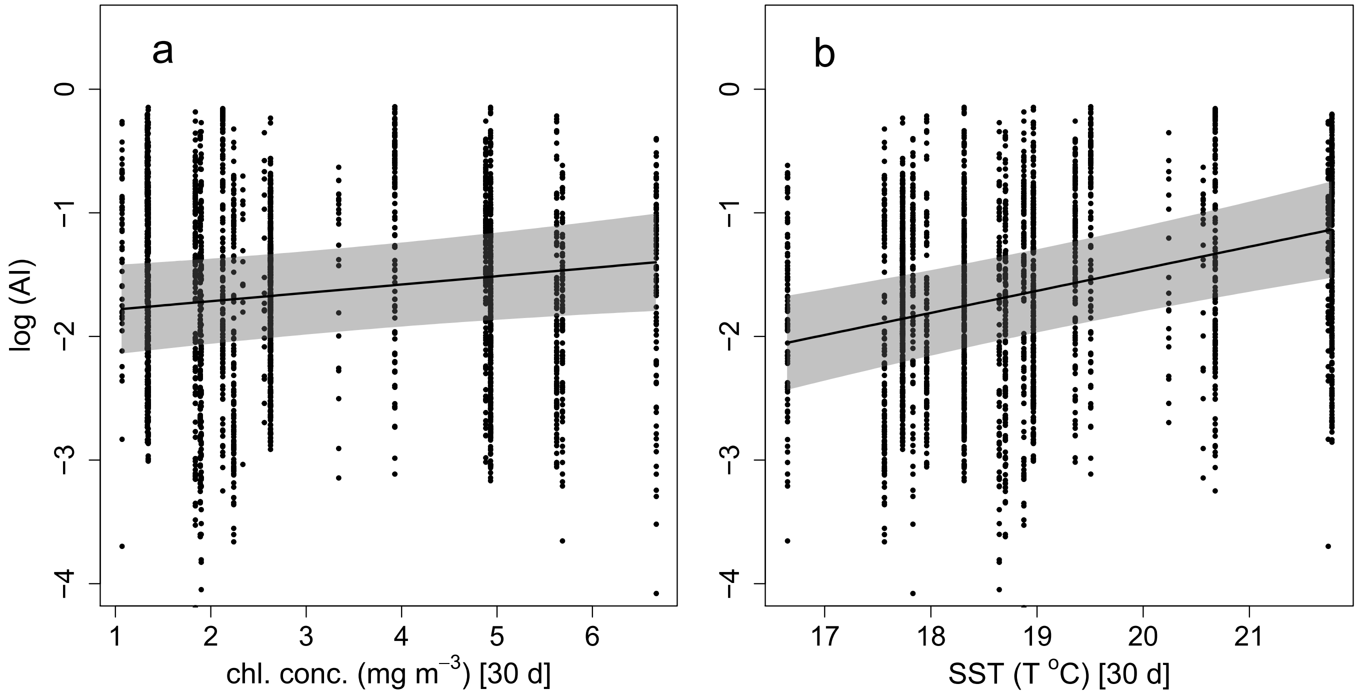

Figure 3.9 Linear mixed-effects model predictions for the influences of 30 day composite lags of chlorophyll a concentration (a) and sea surface temperature (b) on normalised school altitude index values (AI) for St Croix Island. Grey shaded areas represent 95% confidence intervals.

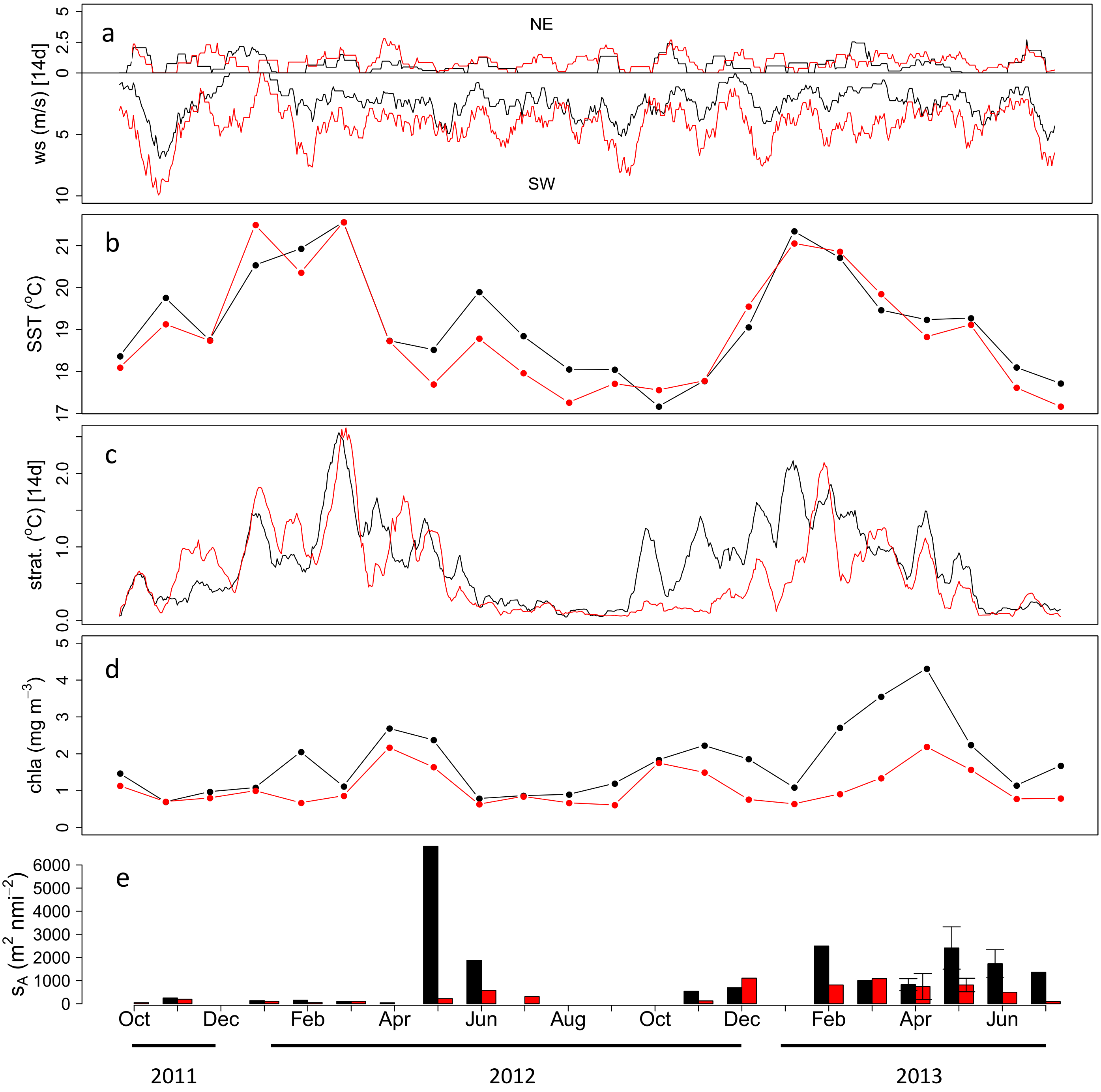

Figure 3.10 Timeseries of oceanographic variables and fish abundance recorded in Algoa Bay between October 2011 and July 2013 for Bird Island (black) and St Croix Island (red): a) wind speed using a 14 day rolling mean for two bearing bins, north-easterly winds (NE, top half of graph) and south-westerly winds (SW, bottom half); b) monthly sea-surface temperature data (SST); c) temperature stratification through the water column using a 14 day rolling mean; d) mean monthly chlorophyll a concentration (chla); e) relative fish abundance (s_A), error bars are standard deviations for months with two surveys.

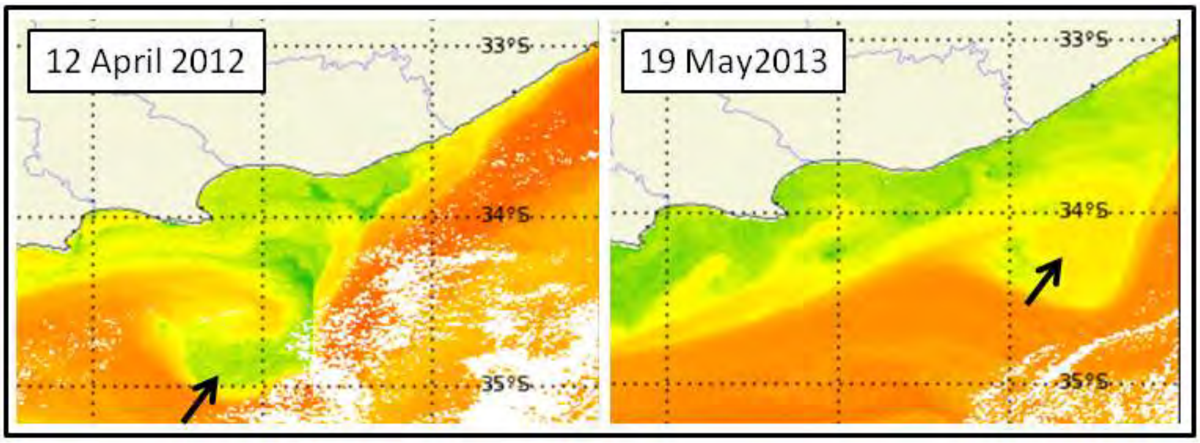

Figure 3.11 Sea surface temperature maps showing two Agulhas meanders, so-called 'Natal Pulse' events, recorded during the study period. Arrows point to the centres of the core meanders with propagating cooler waters shown via plumes inshore in the region of Algoa Bay. White pixels represent cloud cover.

Chapter 4

Meso- and fine-scale associations between pelagic fish aggregations and African Penguins in Algoa Bay, South Africa

Meso- and fine-scale associations between pelagic fish aggregations and African Penguins in Algoa Bay, South Africa

Abstract

Understanding threats to marine top predators is often compromised by limited knowledge on the availability of their prey, especially in upwelling regions where a few species of so-called forage fish dominate mid-level trophic interactions. The recent collapse of African Penguin numbers off South Africa is believed to be strongly linked to the abundance of their pelagic fish prey, anchovy and sardine, which are vulnerable to changes in oceanographic conditions and exploitation by commercial purse-seine fishing. This study investigates the characteristics of prey aggregations targeted by African Penguins to determine how penguins respond to the distribution and abundance of their prey. Research was conducted in Algoa Bay, South Africa, where half of the global population of this endangered penguin now breeds. The at-sea distribution of penguins was modelled against fish distribution and abundance from 47 acoustic surveys conducted within the foraging ranges of penguins from two colonies, St Croix and Bird islands, between October 2011 and April 2014. Penguin distribution at sea was estimated both from direct counts during surveys as well as from the locations of dive bouts inferred from breeding birds tracked using GPS loggers deployed concurrently on 14 survey days. The horizontal distribution of fish within the birds' foraging range had little influence on the location of penguins but they were significantly associated with the vertical distribution of their prey at fine scales (0.5 km) using both at-sea count and tracking data. Model results showed avoidance of fish schools located near the sea bed by penguins at these fine scales potentially related to African Penguin hunting mode and/or the reduced ability to locate these aggregations. The fine-scale location of penguin dive bouts were significantly associated with school depths at two peaks between 20 and 60 m, probably related to annual and seasonal variation in school depths. Foraging metrics of breeding penguins (trip duration, path length and maximum distance travelled from colony) were consistently negatively correlated with fish abundance at mesoscales and these relationships were strengthened when using only targeted fish aggregations (i.e. fish located in the mid- to upper water column). My results provide direct evidence for the negative influence of reduced prey availability on the foraging performance of African Penguins, which has a direct bearing on the species' conservation status. Understanding the external drivers, environmental and anthropogenic, influencing the vertical distribution and abundance of the penguins' prey, is crucial to set appropriate conservation measures for the African Penguin.

Introduction

Research focused on marine predator-prey interactions is crucial to discovering constraints imposed on the availability of prey to predators. In an ocean increasingly vulnerable to the influences of global change phenomena, including overfishing and anthropogenic climate change (Pauly et al. 1998; Jackson et al. 2001; Halpern et al. 2008; Worm & Branch 2012), understanding these links is critical to informing effective management of prey resources. Marine top predators include many seabird species whose populations are known to respond negatively to critical thresholds in prey abundance (Cury et al. 2011). These include threatened species that are in direct competition with commercial fisheries and whose habitats are becoming increasingly susceptible to the influences of global climate change (Grémillet & Boulinier 2009; Croxall et al. 2012; Paleczny et al. 2015). To ameliorate these threats, the specific prey assemblages targeted by different seabird species need to be established so that external influences moderating the availability of these aggregations can be assessed and accounted for in developing ecosystem-focused solutions for maintaining the functional integrity of these systems (Scott et al. 2006).

Seabirds exhibit a diverse range of morphological and physiological adaptations that facilitate location and capture of their prey (Croxall 1987; Shealer 2002). Although diving species, such as penguins, are constrained to smaller home ranges than their flighted counterparts, they have the advantage of being able to target prey over a greater range of depths. Thus, identifying the types of prey assemblages selected by these species requires knowledge of both the vertical and horizontal distribution of their prey (Zamon et al. 1996). Typically, the simultaneous quantification of diving seabirds and their prey involves counting the number of seabirds observed at-sea and overlaying this information with acoustically determined prey distributions (e.g. Piatt 1990; Hunt et al. 1992; Vlietstra 2005). However, depending on the specific foraging mode of the species counted, this approach may be compromised by a lack of knowledge of the behavioural state of individuals counted, i.e. whether they are actively foraging or not, potentially obscuring true predator-prey relationships. The advent of advances in biotelemetry (Wilson et al. 2002; Cooke et al. 2004) have facilitated the remote acquisition of seabird movement data and, using sophisticated modelling techniques, the behavioural state of these birds at each location can be predicted (e.g. Patterson et al. 2008; Gurarie et al. 2009; Dean et al. 2012). Despite this impetus, few studies have compared geo-referenced behavioural state information for seabirds with their prey distributions (Bertrand et al. 2014; Boyd et al. 2015).

Measures of foraging effort provide direct insights into proximate mechanisms influencing population trajectories of seabirds (Lewis et al. 2006). They are useful metrics to test hypotheses related to extrinsic influences on seabird fitness, such as habitat condition (Hennicke & Culik 2005; Kappes et al. 2015) and weather (Pistorius et al. 2015), and frequently have been used in comparative assessments, e.g. inter-colony studies (Radl & Culik 1999; Petersen et al. 2006; Trathan et al. 2006; Pichegru et al. 2007, 2012). Comparing these metrics with concurrent prey data can reveal important thresholds in prey availability that have implications at the population level (Cairns 1987; Harding et al. 2007). This information is vital as the functional link required to calibrate easily obtainable population indices, such as attendance patterns, that can be used as indicators of ecosystem condition (Piatt et al. 2007).

There is strong consensus that a large contributing factor affecting the survival of African Penguins is the influence of prey availability, notably sardine and anchovy (Crawford et al. 2006, 2011; Durant et al. 2010; Weller et al. 2014; Sherley et al. 2015). These forage fish species are targeted by the commercial purse-seine fishery, currently the largest fishery by tonnage in South Africa (Hutchings et al. 2009), and have undergone an eastward range shift in recent years (Roy et al. 2007; Coetzee et al. 2008). Strong positive correlations between pelagic fish stock estimates and breeding penguin numbers have been shown for African Penguins at coarse spatio-temporal scales, i.e. comparing regional differences between groups of colonies against annual fish stock estimates (Crawford et al. 2011). Finer-scale studies of African Penguins and their prey have been limited to inferences of school sizes selected for based on mean dive and pause durations (Heath 1985; Wilson et al. 1988) and hypothesised school encounter rates related to foraging path lengths (Wilson 1985; Wilson & Wilson 1990). To date, no studies have simultaneously quantified African Penguins and their prey at sea. Information on fine-scale associations at sea are crucial to understanding the foraging ecology of this endangered species. Determining the types of fish assemblages selected for by African Penguins and the influence variation in prey availability has on the foraging effort of this species is crucial to assess the impacts of commercial fishing and climate-related changes on this species.

This chapter explores the predator-prey relationships of African Penguins around two of their largest breeding colonies, St Croix and Bird islands, in Algoa Bay, South Africa, currently home to > 50 % of the global population of this species (Crawford et al. 2015). The aims of this chapter are, firstly, to identify prey aggregations selected for by penguins around each colony in terms of the horizontal and vertical prey distributions at fine- to mesoscales. To achieve this, regular acoustic-based pelagic fish surveys were conducted around both colonies. Locations of penguins at sea were recorded through conventional counts and simultaneous multiple deployments of GPS-logged birds from their colonies. Location-based behavioural states were inferred from birds additionally equipped with depth loggers and the derived dive data were used to train a machine learning model to predict behavioural states of positional fixes of all birds. Secondly, using this information, the influence of mesoscale prey variability on the at-sea performance of African Penguins was assessed using path-derived measures of foraging effort.

Methods

Survey procedures

Acoustic pelagic fish surveys were conducted around Bird and St Croix islands between October 2011 and June 2014 (Chapter 3). The relative abundance of African Penguins was estimated by recording all penguins seen within 100 m of a 180° arc from the bow of the boat, with one observer on each side of the vessel. The location and time of observations were recorded from the fish-finder monitor. The influence of observer bias on the probability of encountering penguins was assessed using a logistic regression with explanatory variables including observer group and island to account for the larger population around St Croix Island. I did not factor in the influence of sea state condition on penguin detectability as all surveys were conducted in relatively calm conditions (Chapter 3).

Penguin deployments

On a subset of fish survey days, multiple deployments of GPS loggers were conducted on breeding African Penguins attending chicks < 3 weeks old. Birds were fitted with CatLog-S GPS loggers (30 g, LXWXH: 70 X 40 X 20 mm, Catnip Technologies Ltd, USA), set to record positional fixes at ~ 1 min intervals with an accuracy of ca 10 m. Devices were deployed on the lower backs of penguins using Tesa tape with the entire procedure lasting ca 6 min (Pichegru et al. 2010). In addition, a subset of penguins were fitted with G5 temperature-depth recorders (TDRs; 3 g, CEFAS Technology, Lowestoft, UK) which record depth at 1 s intervals to < 1 m. Deployment nests were monitored for returning birds and after the returned adult had sufficient time to provision its chicks, the device(s) was removed and the data downloaded. Morphometrics of the adults and chicks were recorded to control for influences of sex and brood size (see below).

Foraging effort was estimated using three path metrics: trip duration (minutes), foraging path length (m) and maximum distance travelled from the colony (m). Tracks were filtered to exclude erroneous fixes that exceeded the potential distance covered given their mean maximum speed (12.4 km h^{-1}(Wilson 1985) and only tracks with start and end fixes < 5 km from colonies were used. The path metrics of tracks without start and/or end fixes at the colony were corrected for these gaps by adding distance and duration calculated from the estimated travelling speed of free-swimming African Penguins (4.4 km h^{-1}, Wilson 1985) for foraging path length and trip duration, respectively.

Spatial scale

Selection of appropriate spatial scales for the aggregation of independent and dependent variables for the count and track models was based on the spatial dependencies of two pelagic fish school metrics, school biomass using total volumetric abundance (TVA) and mean school depth (see Chapter 2 for details of these metrics) recorded during surveys along transect 3 east of Bird Island (Figure 4.1). This track was chosen as it traversed the greatest variation in depth. Empirical variograms using the method of moments (Matheron 1965) were used to compute the semivariance of these metrics to a maximum lag distance of 10 km. Scale selection was based on visual inspection of smoothed curves fitted to this data using Nadaraya–Watson kernel regression estimates. All computations were done using the 'geoR' package (Ribeiro & Diggle 2015) in software R (R Core Team 2015). Due to the significant influence of sample size in calculating experimental variograms (Oliver & Webster 2014) this assessment was limited to two surveys with the greatest number of observations along transect 3 adjacent Bird Island, May 2012 and April 2013, both of which had > 40 observations.

Penguin counts and fish schools characteristics

For models assessing the association between the distribution of African Penguins counted at sea and fish school attributes, only sample segments in which both penguins and fish schools were recorded were used. This choice was motivated by excessive zero counts, especially at finer spatial scales, and the inability of zero-inflated models to produce acceptable model diagnostics. A similar filtering approach, i.e. discarding transects with zero counts, was adopted by Logerwell et al. (1998) who investigated seabird-prey correlations using spectral analysis in the Bering Sea. Pelagic fish school metrics selected as potential explanatory variables to describe the variation in penguin counts included a measure of relative fish abundance (TVA), mean school altitude index (MAI) measured as the distance between the seabed and the centre of the school, and mean school depth (MSD) measured as the distance from the sea surface to the mean height of the school. A portion of the surveys conducted included discontinuous sea beds and resulted in erroneous altitude measurements (see Chapter 3 for details). Therefore, two datasets were used, a filtered dataset that included only segments where all three fish variables were recorded accurately and a dataset that included all schools and where only TVA was used as a fish covariate. Distance to island was included as an explanatory variable due to the probability of larger counts of penguins closer to their breeding colonies which may have constituted commuting or resting birds, as well as accounting for some of the spatial dependencies in their distribution. Temporal influences on penguin counts were incorporated into the model as a year/season fixed effect (YS) with season representing African Penguin breeding and non-breeding seasons respectively, i.e. breeding: February - July; non-breeding: August - January.

Generalised additive models for location, scale and shape (GAMLSS) (Rigby & Stasinopoulos 2005) were used, firstly to explore the potential for non-linear associations between the explanatory variables and penguin counts, and secondly because of the flexibility of these models in terms of appropriate family distributions for the response with the conventional exponential family limitations being relaxed. The R package 'gamlss' used penalised splines (piece-wise polynomials) for the smoothing terms based on the default model algorithm, 'RS'. Selection of the appropriate error distribution was achieved using the 'fitDist' function which uses Akaike's Information Criteria (AIC) to select the best fit parametric error distribution.

Behavioural state predicted from track data and fish school characteristics

In order to model the influence of fish school characteristics on penguin locations derived from tracks, it was important to isolate these associations in areas where the penguins were most likely to be foraging, as opposed to the count data where behavioural state could not be determined. Dive data from TDRs deployed on a subset of deployed African Penguins was processed using MTDive software (Jensen Software System). Initially, three dive parameters, i.e. maximum dive depth, pause time at the surface between dives and frequency of dive undulations (wiggles) were used to classify three behavioural states: searching, foraging and commuting. However, track derived predictors, time between fixes, velocity and change in bearing, could not adequately discriminate between foraging (dives with wiggles) and searching dives (dives without wiggles). The classification therefore resorted to two dive parameters, maximum dive depth and pause time at the surface between dives, to quantify diving effort. Dives were mapped to their associated positional fixes using linear interpolation based on fixes within 500 m of the estimated dive locations (no location was assigned to dives that lacked a fix within 500 m). Dive location data were then classified into one of two behavioural states: dive bout or commuting. A dive bout was defined as ≥ 5 consecutive dives after Pichegru et al. (2011), all ≥ 3 m in depth following Wilson & Wilson (1990) and dive intervals ≤ 200 s adapted from Ryan et al. (2007) to incorporate 98 % of all dives from logged birds. All fixes not satisfying these criteria were classified as commuting.

The classified TDR dataset was used as a training set to infer behavioural state from GPS locations using a two-state continuous-time Markov chain fitted to the behavioural state sequences using maximum likelihood. The time steps between fixes were log transformed and modelled with Weibull distributions conditional on the state (again fitted by maximum likelihood). The behavioural states of birds with GPS data only were predicted using a continuous-time hidden Markov model (HMM) with parameters estimated on the training set. The smoothed posterior probabilities of the states at each fix were computed with the forward-backward algorithm and the optimal state sequence was identified with the Viterbi algorithm. The accuracy of state predictions was assessed using a leave-one-out cross validation for all individuals in this sample and calculated as the proportion of states correctly predicted.

Utilisation distributions of foraging African Penguins (UDA) were calculated for each bird from track locations representing the dive bout state only. Kernel density estimates utilising the 50 % range contour were employed for this purpose, using the 'adehabitat' package (Calenge 2006) in R, to limit distributions to where most foraging activity occurred for each bird. For each fish survey day, the corresponding UDAs of birds deployed concurrently were intercepted at the different predetermined scales along the fish survey route and referenced to the associated fish attribute data recorded in each scaled segment. The sum of individual UDAs for each segment was then used as the response variable and modelled against the corresponding fish data.

The modelling approach for this analysis was similar to that of the count data models and used the same fish covariates, although distance to island (used to control for non-foraging aggregations of penguins close to breeding colonies) was excluded. Models used combined data from surveys around both islands, with island set as a fixed effect, due to the limited number of surveys conducted with concurrent penguin track data. Because all surveys were conducted during the breeding season, I replaced the temporal effect of year/season with survey date either as a fixed or random effect depending on the model type. Two modelling approaches were used for the fine- and submeso scales, respectively: GAMLSS with survey date included as a fixed effect, and a generalised additive mixed effects model (GAMM) using survey as a random effect. Selection of appropriate error distributions followed the same procedures for GAMLSS as described for the count models and a Poisson distribution with a log link function was selected as a suitable error distribution for non-Gaussian count data, i.e. in this case the count of UDAs, in the GAMMs. Processing of the GAMM models was done using R package 'mgcv'.

Mesoscale influences of fish abundance on African Penguin foraging effort

To explore potential non-linear influences of prey availability on penguin foraging effort (*sensu* Cairns 1988), I initially used GAMMs with relative prey abundance (s_A) included as a smoothed covariate. If linear trends were apparent the model was re-fitted as a generalised linear mixed effects model (GLMM). A gamma family distribution with a log link function was used for both model types. Sex and brood mass were included as fixed effects due to the potential influence of these variables on foraging effort for African Penguins and other seabird species (Litzow & Piatt 2003; Pichegru et al. 2013). Data from both islands were combined for this analysis due to the limited number of surveys of this nature (i.e. with concurrent penguin deployments) around each island; island was therefore included as a fixed effect. All continuous explanatory variables were standardised to prevent model convergence issues. To account for the expected similarity in measurements on the same day, survey day was included as a random effect. Due to the large variation in sample sizes of penguins deployed on each survey day and the potential bias this could have on the model outcomes, the observations in each model were weighted by the number of penguins deployed for each survey. All models were run in R using packages 'mgcv' and 'lme4' (Bates et al. 2015) for the GAMMs and GLMMs respectively. Unfortunately, metrics of foraging effort from dive data could not be assessed during this study as this data was only available for three months during 2013.

To explore whether the durations of African Penguins' foraging paths were associated with path length and maximum distance travelled from their colonies, I applied least-square linear regressions between these variables for birds from each island. For all models a square-root transformation was applied to meet the assumptions of normality.

Model validation

Cleveland dot plots were used to explore outliers in both the response and explanatory variables. I investigated collinearity amongst the explanatory variables by using variance inflation factors (VIF) (Zuur et al. 2009) with a maximum threshold set to five. For both penguin count and penguin track models a backwards, stepwise selection process was used, dropping variable terms sequentially, to select the model with the most improved performance using Akaike'e information criteria (AIC) and Bayesian information criteria (BIC) indices. For all models, model validation procedures following Zuur et al. (2009) and Zuur et al. (2010) were carried out on the best fitting models for each class. These included visual inspections: for homoscedasticity by plotting the residuals versus the fitted values; for normality by examining Quantile-Quantile plots and for influential observations by plotting the residuals versus the explanatory variables. Spatial autocorrelation in the penguin count and penguin track models were assessed by plotting the semivariance of the model residuals versus the lag distance along the transect for each model. Models with residuals that showed signs of spatial autocorrelation were refitted with latitude and longitude as univariate smooth terms and compared to the original model using AIC and BIC. Moran's I statistic was used to test for spatial autocorrelation.

Results

Spatial scale selection

Results of the fitted smooth curves show a strong nugget effect for the semivariance of TVA values for both surveys indicating finer scale variance not accounted for in these outputs (Figure 4.2). There was little evidence for a prominent sill in the TVA variograms possibly due to an inadequate maximum lag distance but there was a prominent sill related to the semivariance of school depth between 8 and 10 km. Based on these results two scales were selected: 0.5 km (fine scale) as the minimum resolution achievable based on the maximum length of the transect incorporated by one echogram which varied according to depth, i.e. longer segments at increasing depth; and, 10 km (mesoscale) as an approximation of potential spatial independence in samples related to fish school depth values.

Observer bias

Results of potential observer bias using a logistic regression model showed no significant difference of this effect on the detectability of African Penguins counted at sea ($z > 0.56$, $p > 0.4$). The potential for more penguins being counted around St Croix island, given the larger population here, had no appreciable influence on the outcome of this model ($z = -0.18$, $p = 0.86$).

Penguin counts and fish schools characteristics

A total of 47 pelagic surveys was conducted in Algoa Bay between October 2011 and June 2014: 24 around Bird Island (mean ± SD survey length = 64.5 ± 6.6 km) and 23 around St Croix Island (88.1 ± 15 km; Table 4.1). The number of African Penguins counted on each survey ranged from 14 - 528 penguins (mean ± SD = 108 ± 129) for Bird Island and from 22 - 525 penguins (152 ± 145) for St Croix Island. Surveys around both islands produced similar crude penguin density estimates: Bird Island 2 penguins km^{-1} transect; St Croix Island 1.7 penguins km^{-1} transect.

Models

There was no collinearity between covariates selected for the penguin count models at both the 0.5 and 10 km scales for both islands, with all VIF scores < 3. For Bird Island at the finer scale (0.5 km) penguins and fish were recorded in 136 segments of which 62 segments contained schools where depth measurements could not be determined accurately and were excluded for the filtered models; additionally, one outlier segment was removed for an exceptionally high TVA value for models that included all data. For St Croix Island (0.5 km scale) 189 segments contained both penguins and fish data of which five segments contained schools where depth measurements could not be accurately determined and were excluded for the filtered models. A further eight outlier segments were removed, one for an exceptionally high TVA value and seven segments with counts of penguins > 50 birds. For the 10 km scale models, 104 and 139 segments contained both fish and penguins for Bird and St Croix islands, respectively, of which five segments around Bird Island contained schools where depth measurements could not be determined accurately and were discarded from the subsequent analysis for this island.

The best fit family distributions for the penguin count responses included the discrete one parameter logarithmic (LG) distribution for all models using data at the 0.5 km scale, the zero adjusted negative binomial type 1 (ZANBI) distribution for Bird Island count data at the 10 km scale and the Poisson-inverse Gaussian (PIG) distribution for St Croix Island data at the 10 km scale. Comparisons of model performance for both islands at both scales are shown in Table 4.2 and the coefficients for the best fitting models are given in Table 4.3. For Bird Island, the fine scale models (0.5 km) using only filtered data that included school altitude (MAI) and depth (MSD) variables explained 42% of the variation in penguin counts. Models for St Croix Island were less informative with the best fitting fine-scale filtered model explaining 23% of the variation in penguin counts. For both islands, MAI was the most significant covariate but with different influences at each site (Figure 4.3). Around Bird Island, there was a strong positive correlation between the number of penguins counted and school altitude up to MAI values of ca 0.5 but an opposite relationship between these variables for St Croix Island up to MAI values of ca 0.2. Around both islands there were few counts of penguins in segments with MAI values > 0.5, resulting in reduced precision in estimates for this range (Figure 4.3). There was a significant positive correlation between penguins counted and MSD around Bird Island but there was no evidence of this effect around St Croix Island (Table 4.3).

The best fitting models using all fish data but excluding variables MAI and MSD explained 13 % and 27 % of the variation in penguins counted around Bird and St Croix islands, respectively (Table 4.2). For these models at both sites the temporal effect of year/season was included in the best fitting models but was only significantly influential around St Croix Island, with elevated penguin counts during the 2013 breeding season and the subsequent non-breeding season in 2013/2014 (Table 4.3). Relative fish abundance (TVA) had little effect on the number of penguins counted in these models.

Fish covariates did little to explain variation in the number of penguins counted for the mesoscale (10 km) models with year/season being the only significant variable for both islands with elevated counts during the 2013/2014 non-breeding season around Bird Island and during both the non-breeding season of 2012/2013 and the 2013 breeding season around St Croix Island (Table 4.3).

Behavioural state predicted from track data and fish schools characteristics

Behavioural state model predictions

The training data set used to calibrate the HMM model for African Penguin behavioural state predictions included 10 639 dives and track data from 26 birds deployed between April and June 2013 around Bird (n = 17) and St Croix (n = 9) islands. Leave-one-out cross validation revealed high predictive accuracy in the inferred states for all birds (the minimum, maximum, and median proportions of correctly predicted states were: 0.78, 0.99, 0.95, respectively). An example of the model performance for an individual with the median predictive accuracy is illustrated in Figure 4.4 with mostly close correspondence in actual and predicted states being evident. This model was used to predict the behavioural states of African Penguin GPS data (fixes) for the following analyses.

Concurrent surveys

A total of 191 African Penguins (mean ± SD per survey: 14 ± 4) were deployed with GPS loggers during 14 pelagic fish surveys (8 at Bird island and 6 at St Croix Island) between April 2012 and April 2014 (Table 4.1). Penguin tracks using only fixes classified as dive bouts were used to determine the 50% utilisation distribution kernels (UDAs) for each bird and were intercepted with the corresponding fish survey transects at the two spatial scales, 0.5 and 10 km. Ten tracks did not intercept the survey transects and were discarded from the following analyses.

Models

There was no collinearity between variables selected for the penguin track models at both the 0.5 and 10 km scales for both islands with all VIF scores < 3. Data for models at the finer spatial scale (0.5 km) included 1997 segments coming from surveys dissected around both islands and including both presence and absence of penguins and fish. Of these, 907 segments contained schools where depth measurements could not be accurately determined and were excluded for the filtered models. Two segments from the filtered data set and three segments from the unfiltered data set were removed as outliers due to excessively high TVA values. For the 10 km scale models, 93 segments of presence/absence data were used, of which three contained schools where depth measurements could not be accurately determined and one segment was discarded as an outlier due to a high TVA value.

Best fitting family distributions selected for the penguin track data included a negative binomial type 2 (NBII) distribution for filtered data at the 0.5 km scale and a zero-inflated negative binomial type 2 (ZINBII) distribution for unfiltered data at this scale. Variogram outputs of the initial 0.5 km models showed signs of spatial autocorrelation and were subsequently re-fitted with univariate smoothing terms for longitude (x) and latitude (y). For GAMM models at the coarser 10 km scale, a Poisson error distribution was used and survey was added as a random effect. There was no indication of spatial autocorrelation in the residuals of these models (Table 4.4).

The best fitting model for the filtered fine-scale data (0.5 km) included all initial candidate variables as well as the x and y smoothing terms to account for spatial autocorrelation; this model explained 41% of the variation in the number of UDAs intercepted (Table 4.4). Moran's I statistics for spatial autocorrelation were markedly improved after addition of the x and y smoothing terms (Table 4.4). Fish school depth covariates, MAI and MSD, had a strong non-linear influence on the response in this model: diving penguins preferred areas with higher altitude fish schools especially MAI >0.4 (Figure 4.5a), and preference for schools at depths > 20 m associated with two distinct peaks, one at ca 30 m and another at ca 65 m, the latter peak being less precise in its predictive power (Figure 4.5b). As with the filtered model outputs, results of the unfiltered models at this scale showed no appreciable influence of relative fish abundace (TVA) on the presence of foraging penguins, a significant increase in penguin UD encounters around St Croix Island, and similar survey effects; this model explained

34% of the variation in the number of penguin UDAs intercepted (Table 4.5). However, although the inclusion of x and y spatial terms in this model improved both the model fit and the Moran's I statistic (Table 4.4), there was still evidence of spatial autocorrelation and these results need to be treated with caution.

Dropping non-significant terms in the 10 km GAMM made no improvement to the goodness-of-fit scores and the most inclusive model was treated as the optimal candidate (Table 4.4). In this model the only significant covariate was a smoothing term for school depth (MSD) with fewer foraging penguins being present over MSD < ca 28 m (Figure 4.5c).

Mesoscale influences of fish abundance on African Penguin foraging effort

The sample of tracks used for these models was substantially reduced from that of the penguin track models: from the initial 191 birds deployed during concurrent fish surveys, 88 tracks were incomplete for path duration and path length and 37 tracks were could not be used to estimate maximum distance travelled from the colony (Table 4.6). The final number of tracks used in the path duration and path length models ranged from 2 to 16 tracks per survey (mean ± SD: 7 ± 3 tracks) and for the maximum distance models samples ranged from 2 to 18 tracks (11 ± 4 tracks; Table 4.6). Of the tracks selected for the analysis, 18 did not have start fixes on the island and 15 did not have end fixes on the island; these gaps (< 5 km) were interpolated (see Methods). There was a slight tendency to equip more males than females for these analyses (mean ± SD proportion of males for each survey, path length and duration: 0.59 ± 0.26, maximum distance travelled: 0.53 ± 0.18).

Models were fitted using two versions of relative fish abundance (s_A) estimates: all fish schools (s_A [all]) and fish schools with altitude index values ≥ 0.4 (s_A [alt. ≥0.4]). The latter filtered data set was motivated by the apparent avoidance of low altitude fish by African Penguins as shown in the results of the penguin track models (Figure 4.5a). The extremely high estimate of s_A around Bird Island during May 2012 was considered an outlier and all data from this survey were discarded from all models.

Models

Results of all initial GAMM models revealed no evidence of non-linear relationships between penguin path metrics and relative fish abundance; all models were thus fitted as GLMMs. There was a negative influence of relative fish abundance (s_A) on all path metrics modelled but these were only significant for path length when including all fish (s_A [all]) in the estimates and were significant for both path duration and path length when excluding low altitude fish (i.e. s_A [alt. ≥0.4]) (Figure 4.6). Female penguins generally spent more time at sea, had longer path lengths and travelled significantly further from their colonies than males (Table 4.7, Figure 4.6). Brood mass had little influence on the outcome of these models. Penguins deployed at St Croix Island travelled significantly longer, both in terms of path length and maximum distance, than birds from Bird Island, especially for birds deployed toward the end of the breeding season, i.e. June and July, around St Croix (Table 4.7, Appendix 4.1). However, the duration of time spent at sea was similar for birds from both sites with closer concordance in predicted model fits (Figure 4.6).

There was strong positive correlation between the duration and the length of African Penguin tracks around Bird Island ($t = 5.87$, $p < 0.001$) and St Croix Island ($t = 3.87$, $p < 0.001$). Maximum distance travelled from colony and path duration were less strongly associated for both islands: Bird Island ($t = 2$, $p = 0.05$) and St Croix Island ($t = 2.66$, $p = 0.01$) (Figure 4.7).

Discussion

Targeted prey aggregations

The results of this chapter highlight the significance of the depth distribution of pelagic fish schools in determining the location of African Penguins at fine spatial scales. This was evident for both the number of birds observed at sea as well as the foraging locations of penguins inferred from georeferenced dive data. The lack of any pronounced influence of relative fish abundance on the distribution of African Penguins, using count and track data, around Bird and St Croix islands at both fine- (0.5 km) and meso- (10 km) scales is not unusual for seabird-prey interactions (review by Hunt et al. 1999). For instance, optimal scales of association between Macaroni Penguins (*Eudyptes chrysolophus)* and their zooplankton prey, mostly Antarctic krill (*Euphausia superba)*, off Bird Island, South Georgia were in the region of 70 - 100 km with rank correlations < 0.2 for scales < 5 km (Hunt et al. 1992). Several possible explanations have been given for this general lack of fine and meso scale overlap: e.g. preference for sub-optimal prey densities (Woodby 1984); avoidance behaviour by prey species (Fauchald 2009); the influence of overall prey abundance on fine-scale associations (Vlietstra 2005); and inappropriate sampling regimes (Benoit-Bird et al. 2013). Zamon et al. (1996) studied the influence of the three-dimensional prey field of Antarctic krill on foraging Chinstrap Penguins *Pygoscelis antarctica* and showed that spatial coherence between predators and their prey can be masked by ignoring the vertical dimension. They found strong associations between penguins and their prey at depths where penguins most frequently dived but not for prey aggregated throughout the water column. Boyd et al. (2015) using similar methods employed during my study, i.e. concurrent acoustic fish and dive location data, for Peruvian Boobies (*Sula variegata*) and Guanay Cormorants (*Phalacrocorax bougainvilliorum*), found strong associations between dive locations and prey depth and very little influence of prey abundance. I also found that school depth influenced penguin numbers around both islands, particularly at fine spatial scales.

The avoidance of fish near the sea bed may be related to the optimal foraging mode of African Penguins. Based on penguin bite positions on their anchovy prey, Wilson & Duffy (1986) inferred that African Penguins targeted their prey from below. This form of prey capture has been demonstrated for the closely related and ecologically similar Magellanic Penguin (*Spheniscus magellanicus*) with 89% of prey capture events involving passive ascents aided by buoyancy (Wilson et al. 2010). The ability to attack from below is constrained for schools close to the seabed. Also, schools close to the seabed may be harder to locate. The detection probability of a small pelagic fish depends on the relationship between the solar azimuth and the predator's viewing angle, with a greater chance of locating these objects from below or horizontally rather than from above (Johnsen & Sosik 2003). The propensity of V-shaped dives by *Spheniscus* penguins while searching for prey (Wilson & Wilson 1990) would therefore render bottom dwelling fish less detectable. This factor may also explain the paucity of redeye in the diets of African Penguins (Crawford et al. 2011), despite this species being a significant contributor to pelagic fish biomass in the region (Shabangu et al. 2012; Mhlongo et al. 2013), because redeye tend to remain closer to the sea bed than sardine and anchovy during the day (Roel & Armstrong 1991; Lawson et al. 2001; Coetzee et al. 2010).

Intraspecific variation in penguin dive depths has been attributed, at least in part, to vertical prey distribution (Radl & Culik 1999; Taylor et al. 2004; Wilson et al. 2005). The bimodality in mean school depths selected for by African Penguins tracked during this study, i.e. at ca 30 m and ca 65 m (Figure 4.5b), is likely to have been influenced by interannual differences in school depths. The first peak roughly corresponds to the mean dive depths of African Penguins recorded in Algoa Bay during 2009, i.e. 22 - 33 m Pichegru et al. (2013). The second peak is likely an artefact of deeper fish schools recorded during 2012 which was significantly greater than 2013 and 2014 (mean ± SD, 2012: 41.3 ± 15.8 m, 2013/2014: 34.7 ± 13.4 m; T-test, t = 7.5, $p<0.001$) (Figure 4.8). Associations with these deeper fish schools would have been exacerbated by a greater number of penguin tracks (UDAs) intercepted by fish survey transects during April 2012 (Table 4.5, Appendix 4.2) when fish schools were at their greatest depths (Figure 4.8).

Mesoscale influences of fish abundance on African Penguin foraging effort

The negative influence of relative fish abundance on African Penguin foraging metrics lends support to the growing body of research (see Introduction) that highlights the availability of prey as an important factor limiting the survival of this species. Results of these models provide evidence for direct mechanistic links between the mesoscale abundance of pelagic fish and African Penguin foraging effort. Realisation of these functional relationships are crucial to informing resource management strategies aimed at conserving fish stocks at levels that do not inhibit the health of these ecosystems. The effective use of seabirds as biomonitors of healthy fish stocks depends on quantitative data connecting population indices with prey stocks (Furness & Camphuysen 1997; Piatt et al. 2007). This information can be used to calibrate remotely-acquired long-term activity budget data such as attendance patterns of breeding birds (Rishworth et al. 2014) with the potential to provide an efficient and relatively accurate means of monitoring prey stocks. The functional response of African Penguins to varying prey stocks, as documented here, supports the use of this species as a biomonitor of prey stocks in Algoa Bay, provided this data can be collected with minimal disturbance to this threatened species.

The negative correlation between the time spent by breeding African Penguins at sea and fish found at higher altitudes emphasises the importance of the depth distributions of fish schools in influencing penguin time budgets. Oceanographic features that favour elevated fish assemblages in Algoa Bay include increased thermal stratification and high levels of primary production, conditions typical of the Benguela Upwelling system in this region during summer (Goschen & Schumann 2011). The Agulhas Current plays a significant, albeit infrequent, role in mediating both temperature and thermal stratification in Algoa Bay, mainly though mechanisms associated with meander-driven plumes and eddies (Schumann et al. 1988; Goschen & Schumann 1994; Roberts 2010; Goschen et al. 2015). These events have different impacts on fish altitude depending on the thermal qualities of the waters advected by these meanders into the bay: cold bottom waters increase productivity and favour elevated fish assemblages, whereas warm surface waters have the opposite effect, driving fish to lower altitudes or out of the system entirely (Chapter 3). Climate change predictions for the Agulhas Current includes an increase in episodic meander events (Lutjeharms & de Ruijter 1996). Indeed, this current has intensified and warmed in recent years (Rouault et al. 2010) and these changes are likely to play an increasingly more prominent role in the ecology of pelagic fish and associated predators in this region. In a recent study, van Eeden et al. (2016) documented deeper dives by African Penguins during warm intrusion events and shallower dives near the thermocline during stratified conditions around Bird Island. These findings highlight the significance of the thermal properties of waters in Algoa Bay to the performance of African Penguins, concomitant with the depth dependencies of their prey as documented here, and emphasise the vulnerability of these systems to thermal perturbations. This is of crucial significance to marine spatial planners when designating important habitat for African Penguins and other predators reliant on these assemblages.

Inter-colony differences in path length and maximum distances travelled have been previously documented for African Penguins in Algoa Bay and have been attributed to disparate influences of prey availability associated with commercial fishing operations (Pichegru et al. 2010, 2012). Penguins from St Croix Island travelled significantly further from their colony than those from Bird Island and this distance was significantly correlated with the time they spent away from the colony (Figure 4.7). The relationship between path duration and maximum distance travelled was weaker for penguins from Bird Island probably because of the closer proximity to suitable habitat and density dependent effects alleviating pressure on resources; prey densities were generally higher around Bird Island during this study (Table 4.1) and the Bird Island population is only about one third the size of the St Croix colony (DEA unpublished data). Furthermore, the different bathymetric profiles around each island (Figure 4.1) ensures a greater volume of water closer to Bird Island potentially providing a greater variety of foraging opportunities under different oceanographic conditions. Inter-colony differences in foraging ranges have been documented for African Penguins between mainland and island based colonies off the Western Cape (Petersen et al. 2006) and for colonies throughout the range of the congeneric Magellanic Penguin (Wilson et al. 2005) and have been inferred to be associated with variance in habitat and prey availability. My study shows that the use of foraging range (i.e. maximum distance travelled) as a measure of foraging effort for African Penguins needs to be used with caution and should be assessed in light of colony-specific attributes.

Conclusions

This chapter presents the first account of the fine-scale characteristics of prey assemblages targeted by African Penguins, and highlights the significance of the vertical distribution of their prey. It comprises one of only a few studies that have attempted to directly quantify the functional links between seabird foraging metrics and concurrent measures of prey, and provides evidence for negative influences of prey abundance on foraging effort by African Penguins. The lack of any apparent non-linear effects showing distinctive thresholds in prey abundance below which energy expenditure is compromised (*sensu* Cairns 1988) may be related to the relatively small sample of survey days not being adequately representative of the true variance in prey abundance, and there is clearly a need for more sampling effort in this regard. Results given here can be applied to current research into the influences of purse-seine fishing pressure on the survival of African Penguins by refining and calibrating current models employed for this purpose. This chapter also highlights the vulnerability of African Penguins to changing oceanographic conditions through impacts on prey aggregations.

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Table 4.1 Summary statistics of fish and penguin data collected during fish surveys conducted between 2011 and 2014 around St Croix and Bird islands, Algoa Bay. Penguins counts are corrected for survey length.

			Fish		Penguins	
Island	**Date**	**Transect length (km)**	**S_A (m^2 nmi^{-2})**	**FDI**	**total counted**	**total tracks**
St Croix	2011/10/21	94927.2	46.1	1.4	40	0
St Croix	2011/11/22	105629.4	195.0	2.7	151	0
Bird Island	2011/11/24	70494.2	250.7	2.8	73	0
Bird Island	2012/01/08	59482.7	134.2	1.9	21	0
St Croix	2012/01/12	60813.2	105.4	2.2	36	0
Bird Island	2012/02/15	62098.1	151.3	3.3	32	0
St Croix	2012/02/16	62850.8	53.1	1.6	77	0
St Croix	2012/03/19	104652.4	102.1	3.6	128	0
Bird Island	2012/03/22	63872.0	99.3	2.6	64	0
Bird Island	2012/04/26	67064.9	41.5	2.8	29	12
Bird Island	2012/05/23	39895.2	6802.8	6.4	16	14
St Croix	2012/05/28	86664.9	221.9	2.9	22	0
Bird Island	2012/06/11	67622.5	1880.2	4.9	14	19
St Croix	2012/06/28	79341.9	576.9	2.8	39	0
St Croix	2012/07/06	70304.8	309.4	4.1	65	11
Bird Island	2012/11/04	67968.3	538.9	6.7	33	0
St Croix	2012/11/07	91032.7	121.6	1.9	134	0
St Croix	2012/12/17	72655.0	1106.7	6.1	145	0
Bird Island	2012/12/20	66639.5	695.6	6.5	219	0
St Croix	2013/02/15	90090.7	812.6	7.1	28	0
Bird Island	2013/02/27	64555.8	2494.0	4.6	41	0
St Croix	2013/03/13	103184.4	1081.5	5.8	525	14
Bird Island	2013/03/22	63943.6	998.0	5.5	234	8
Bird Island	2013/04/06	65104.7	1005.7	5.1	124	12
St Croix	2013/04/13	90977.0	1141.6	5.4	510	0
Bird Island	2013/04/21	64855.1	639.4	4.9	24	0
St Croix	2013/04/25	91761.4	348.0	3.5	310	11
Bird Island	2013/05/05	66174.6	1764.9	4.0	404	14
St Croix	2013/05/12	91573.2	1018.1	3.7	113	0
St Croix	2013/05/22	55636.1	604.2	4.9	129	19
Bird Island	2013/05/29	67223.9	3056.0	5.1	76	0
Bird Island	2013/06/07	66553.0	1301.7	2.9	39	0
Bird Island	2013/06/17	68924.2	2157.4	6.5	192	21
St Croix	2013/06/29	89903.9	498.5	4.7	34	15
St Croix	2013/07/16	97191.0	95.7	4.7	341	0
Bird Island	2013/07/31	66810.7	1356.8	8.6	146	0
Bird Island	2013/11/04	67061.1	396.3	3.8	124	0
St Croix	2013/11/13	92691.0	795.1	4.9	187	0
Bird Island	2014/01/24	69764.2	792.7	4.5	528	0
St Croix	2014/01/27	115904.3	299.3	3.0	51	0
St Croix	2014/03/23	91374.3	592.0	4.1	78	0
Bird Island	2014/03/28	67105.9	58.4	3.1	26	0
Bird Island	2014/04/05	67135.9	246.4	4.0	49	15
St Croix	2014/04/10	91716.6	342.4	3.1	93	6
St Croix	2014/05/15	95471.5	4339.1	4.7	267	0
Bird Island	2014/05/23	67120.0	923.4	6.2	61	0
Bird Island	2014/06/12	50694.3	717.4	7.2	21	0

Table 4.2 GAMLSS models used to determine the influence of fish and temporal covariates on African Penguin counts aggregated at two scales around Bird and St Croix islands. Two data sets were modelled at the 0.5 km scale: filtered data using all covariates but excluding segments with erroneous fish depth data, and; all data using only TVA as a fish covariate. Akaike's information criteria (AIC), Bayesian information criteria (BIC) and the difference in AIC of each model from the lowest AIC for each nested model set (ΔAIC) were used to identify the best fitting models following a step wise drop-one selection process. Family abbreviations: LG - logarithmic; ZANBI - zero-adjusted negative binomial type 1; PIG - Poisson-inverse Gaussian. Model term abbreviations: TVA - total volumetric abundance of fish (kg), MAI -mean school altitude index; MSD - mean school depth; ISDIST - distance from island; YS - year/season; s() - smoother (additive) term.

Data	Scale (km)	Family	Model	BIC	AIC	ΔAIC	R^2
Bird Island							
filt.	0.5	LG	count~TVA+s(MAI)+MSD+ISDIST+YS	345.4	315.7	2.8	0.49
filt.	0.5	LG	count~TVA+s(MAI)+MSD+YS	341.9	314.4	1.5	0.48
filt.	0.5	LG	count~TVA+s(MAI)+MSD	328.9	312.9	0	0.42
all	0.5	LG	count~TVA+ISDIST+YS	647.2	613.1	2.4	0.14
all	0.5	LG	count~ISDIST+YS	643.2	611.2	0.5	0.14
all	0.5	LG	count~YS	639.8	610.7	0	0.13
filt.	10	ZANBI	count~TVA+MAI+MSD+ISDIST+YS	704.6	675.9	6.6	0.36
filt.	10	ZANBI	count~TVA+MAI+ISDIST+YS	700.2	673.9	4.6	0.36
filt.	10	ZANBI	count~MAI+ISDIST+YS	696	672	2.7	0.35
filt.	10	ZANBI	count~ISDIST+YS	691.8	670.2	0.9	0.35
filt.	10	ZANBI	count~YS	688.4	669.3	0	0.34
St Croix Island							
filt.	0.5	LG	count~TVA+s(MAI)+s(MSD)+s(ISDIST)+YS	622	580.1	6.8	0.23
filt.	0.5	LG	count~TVA+s(MAI)+s(ISDIST)+YS	617.2	576.7	3.4	0.24
filt.	0.5	LG	count~s(MAI)+s(ISDIST)+YS	605.7	573.3	0	0.23
all	0.5	LG	count~s(TVA)+ISDIST+YS	786.6	754.3	2	0.27
all	0.5	LG	count~s(TVA)+YS	781.3	752.3	0	0.27
all	10	PIG	count~TVA+MAI+s(MSD)+ISDIST+YS	1301.6	1260.5	5.4	0.17
all	10	PIG	count~TVA+MAI+s(MSD)+YS	1296.7	1258.6	3.5	0.17
all	10	PIG	count~TVA+MAI+YS	1281.6	1255.1	0	0.15

Table 4.3 Best-fitting model coefficient estimates (β) ± standard errors (se) for the influence of fish and temporal covariates on penguin counts aggregated at two scales around Bird and St Croix islands. Two data sets were modelled at the 0.5 km scale: filtered data using all covariates but excluding segments with erroneous fish depth data, and; all data using only TVA as a fish covariate. Model term abbreviations: TVA - total volumetric abundance of fish (kg), MAI -mean school altitude index; MSD - mean school depth; ISDIST - distance from island; YS - year/season. For smoother (additive) terms the estimated degrees of freedom (sdf) are given.

	filtered (0.5 km)		**all (0.5 km)**		**all (10 km)**
Explanatory variables	**sdf**	**β (se)**	**sdf**	**β (se)**	**β (se)**
Bird Island					
TVA	-	-5x10^{-7} (5x10^{-5})	-	-	-
MAI	3	**15.28 (3.01)***	-	-	-
MSD	-	**0.11 (0.04)***	-	-	-
ISDIST	-	-	-	-	-
YS: 12B	-	-	-	-1.28 (1.12)	-0.6 (0.44)
YS: 1213NB	-	-	-	1.37 (1.15)	0.09 (0.5)
YS: 13B	-	-	-	0.77 (1.08)	0.76 (0.45)
YS: 1314NB	-	-	-	1.28 (1.11)	**1.61 (0.5)****
YS: 14B	-	-	-	1.16 (1.29)	-0.22 (0.46)
St Croix Island					
TVA	-	**-**	2	2x10^{-6} (1x10^{-5})	2x10^{-8} (1x10^{-8})
MAI	2	**2.36 (0.91)***	-	-	1.86 (1.01)
MSD	-	-	-	-	-
ISDIST	2	-4x10^{-5} (4x10^{-5})	-	-	-
YS: 12B	-	-0.39 (0.91)	-	-036 (0.85)	6.19 (3.62)
YS: 1213NB	-	0.53 (0.93)	-	0.86 (0.87)	**1.12 (0.35)****
YS: 13B	-	-0.34 (0.91)	-	**1.98 (0.84)***	**1.09 (0.31)*****
YS: 1314NB	-	1.26 (1.06)	-	**2.97 (0.99)****	1.06 (0.31)
YS: 14B	-	0.76 (0.92)	-	1.05 (0.85)	0.45 (0.43)

$^{***}p < 0.001$, $^{**}p < 0.01$, $^{*}p < 0.05$

Table 4.4 GAMLSS and GAMM models used to determine the influence of fish and temporal covariates on the number of intercepted penguin utilisation distributions at two scales around Bird and St Croix islands. Two data sets were modelled at the 0.5 km scale: filtered data using all covariates but excluding segments with erroneous fish depth data, and; all data using only TVA as a fish covariate. Akaike's information criteria (AIC), Bayesian information criteria (BIC) and the difference in AIC of each model from the lowest AIC for each nested model set (ΔAIC) were used to identify the best fit models following a step wise drop-one selection process. Moran's I statistics are given with bold entries showing evidence for spatial autocorrelation. Family abbreviations: NBII - negative binomial type 2; ZINBI - zero-inflated negative binomial type 2. Model term abbreviations: TVA - total volumetric abundance of fish (kg), MAI -mean school altitude index; MSD - mean school depth; s() - smoother (additive) term.

Data	Scale (km)	Model	Family	Model	BIC	AIC	ΔAIC	R^2	Moran's I
filt.	0.5	GAMLSS	NBII	count~TVA+s(MAI)+s(MSD)+ island+survey	2558.7	2196.3	6.7	0.24	**0.09*******
filt.	0.5	GAMLSS	NBII	count~TVA+s(MAI)+s(MSD)+ s(x)+s(y)+island+survey	2454.9	2189.6	0	0.41	0.001
all	0.5	GAMLSS	ZINBI	count~TVA+s(x)+s(y)+island+survey	4681.3	4438.7	0	0.34	**0.02*******
all	0.5	GAMLSS	ZINBI	count~TVA+island+survey	5026	4930.9	492.1	0.13	**0.08*******
filt.	10	GAMM	Poisson	count~TVA+MAI+s(MSD)+island	-	-	-	0.11	0.07
filt.	10	GAMM	Poisson	count~MAI+s(MSD)+island	-	-	-	0.09	0.07
filt.	10	GAMM	Poisson	count~s(MSD)+island	-	-	-	0.07	0.07

$^{***}p < 0.001$

Table 4.5 Best-fitting model coefficient estimates (β) ± standard errors (se) for the influence of fish and temporal covariates on the number of intercepted penguin utilisation distributions at two scales for Bird and St Croix islands. Two data sets were modelled at the 0.5 km scale: filtered data using all covariates but excluding segments with erroneous fish depth data, and; all data using only TVA as a fish covariate. Model term abbreviations: TVA - total volumetric abundance of fish (kg), MAI -mean school altitude index; MSD - mean school depth; ISDIST - distance from island; YS - year/season. For smoother (additive) terms the estimated degrees of freedom (sdf) are given. For the GAMM model coefficient MSD the F statistic is given.

	GAMLSS				**GAMM**	
	filtered (0.5 km)		**all (0.5 km)**		**all (10 km)**	
Explanatory variables	**sdf**	**β (se)**	**sdf**	**β (se)**	**sdf**	**β (se)**
TVA	-	$5x10^{-8}$ ($3x10^{-7}$)	-	$5x10^{-9}$ ($2x10^{-8}$)	-	$-2x10^{-8}$ ($1x10^{-8}$)
MSALTI	5	**2.66 (0.29)*****	-	-	-	1.71 (0.94)
MSDPTH	6	**0.03 (0.005)*****	-	-	2.6	**6.35***^{a}
island: SC	-	**2.07 (0.33)*****	-	**5.97 (0.22)*****		-0.5 (0.28)
x	7	**$-9x10^{-5}$ ($1x10^{-5}$)*****	7	**1e04 (5e-06)*****	-	-
y	7	**$7x10^{-5}$ ($7x10^{-6}$)*****	7	**-1e-04 (6e-06)*****	-	-
survey:						
May2012BI	-	**-0.4 (0.02)***	-	0.02(0.14)	-	-
June2012BI	-	-0.02 (0.2)	-	**-0.29 (0.14)***	-	-
July2012SC	-	**-0.2482**	-	**-1.81 (0.16)*****	-	-
March2013BI	-	**-0.86 (0.23)*****	-	**-0.93 (0.12)*****	-	-
March2013SC	-	**-0.75 (0.14)*****	-	**-1.03 (0.12)*****	-	-
April2013BI	-	**-1.17 (0.23)*****	-	**-1.01 (0.16)*****	-	-
April2013SC	-	**-1.11 (0.17)*****	-	**-1.4 (0.16)*****	-	-
May2013BI	-	**-0.45 (0.16)****	-	-0.12 (0.14)	-	-
June2013BI	-	**-1.3 (0.19)*****	-	-0.05 (0.11)	-	-
June2013SC	-	**-0.94 (0.15)*****	-	**-0.84 (0.12)*****	-	-
April2014BI	-	-0.77 (0.39)	-	**-0.76 (0.17)*****	-	-
April2014SC	-	**-2.3 (0.47)*****	-	**-1.53 (0.18)*****	-	-

$^{***}p < 0.001$, $^{**}p < 0.01$, $^{*}p < 0.05$, ^{a} - F-statistic.

Table 4.6 Summary statistics of 14 pelagic fish acoustic surveys and concurrent multiple African Penguin deployments around Bird and St Croix islands between April 2012 and April 2014. Estimates of relative fish abundance (S_A) using all schools and only schools with altitude index values ≥ 0.4 are given. For penguins the total number of tracks deployed (n tracks) is given and the filtered number (n) of tracks used for each activity budget showing the number of males and females (m, f) used for each survey.

		Fish S_A		**Penguins**									
					activity budgets								
					path duration (h)			**path length (km)**			**max. distance (km)**		
Island	**Date**	**all**	**alt. ≥ 0.4**	**n tracks**	**n (m, f)**	**mean**	**sd**	**n (m, f)**	**mean**	**sd**	**n (m, f)**	**mean**	**sd**
Bird Island	2012/04/26	41.5	4.6	12	4 (4, 0)	18.7	1.1	4 (4, 0)	52.7	10.5	12(6, 6)	13.8	4.1
Bird Island	2012/05/23	6802.8	584.0	14	11 (6, 5)	21.4	9.7	11 (6, 5)	52.0	9.5	14 (7, 7)	12.8	2.8
Bird Island	2012/06/11	1880.2	454.2	19	16 (4, 12)	21.4	7.4	16 (4, 12)	58.1	11.9	18 (5, 3)	16.4	2.2
St Croix	2012/07/06	309.4	31.7	11	9 (4, 5)	22.4	2.7	9 (4, 5)	83.4	14.7	9 (4, 5)	34.4	8.9
St Croix	2013/03/13	1081.5	201.7	14	6 (4, 2)	19.2	4.1	6 (4, 2)	66.8	13.8	14 (8, 6)	27.1	7.2
Bird Island	2013/03/22	998.0	116.4	8	8 (4, 4)	22.8	10.4	8 (4, 4)	52.2	15.8	8 (4, 4)	12.2	1.5
Bird Island	2013/04/06	1005.7	60.3	12	9 (7, 2)	22.5	11.0	9 (7, 2)	38.7	21.3	12 (9, 3)	10.0	3.1
St Croix	2013/04/25	348.0	69.9	11	7 (3, 4)	21.2	4.0	7 (3, 4)	64.7	13.4	10 (4, 6)	22.3	7.0
Bird Island	2013/05/05	1764.9	509.1	14	5 (4, 1)	14.8	4.2	5 (4, 1)	39.4	7.6	12 (6, 6)	12.6	3.9
St Croix	2013/05/22	604.2	469.4	19	8 (1, 7)	17.8	4.9	8 (1, 7)	57.9	10.8	11 (2, 9)	23.1	5.9
Bird Island	2013/06/17	2157.4	379.3	21	6 (3, 3)	13.4	9.8	6 (3, 3)	32.8	21.2	9 (4, 5)	10.1	2.3
St Croix	2013/06/29	498.5	66.8	15	7 (3, 4)	22.3	6.8	7 (3, 4)	83.8	18.6	12 (6, 6)	34.9	6.6
Bird Island	2014/04/05	246.4	79.8	15	5 (4, 1)	20.4	9.5	5 (4, 1)	61.7	21.9	11 (6, 5)	18.8	8.9
St Croix	2014/04/10	342.4	274.5	6	2 (2, 0)	17.2	0.0	2 (2, 0)	59.0	16.8	2 (2, 0)	22.6	10.2

Table 4.7 Generalised linear mixed effects model (GLMM) coefficients for the influences of relative fish abundance (s_A), using all fish and only fish schools with altitude index values ≥ 0.4, on African Penguin activity budgets using path metrics: duration, length and maximum distance from colony. All models include controls for fixed effects: sex, brood mass and island and survey day was added as a random effect. Values for continuous covariates are standardised values.

	Penguin activity budgets		
	path duration	**path length**	**max. distance**
Explanatory variables	**β (se)**	**β (se)**	**β (se)**
all fish			
SA	-0.10 (0.05)	**-0.13 (0.06)***	-0.09 (0.08)
sex (M)	-0.03 (0.03)	-0.01 (0.02)	**-0.08 (0.01)*****
brood mass	0.01 (0.02)	0.01 (0.01)	0.01 (0.01)
island (SC)	-0.00 (0.11)	**0.28 (0.12)***	**0.63 (0.15)*****
fish altitude index ≥ 0.4			
SA	**-0.13 (0.04)****	**-0.13 (0.06)***	-0.08 (0.08)
sex (M)	-0.03 (0.03)	-0.01 (0.02)	**-0.08 (0.01)*****
brood mass	0.01 (0.02)	0.01 (0.01)	0.01 (0.01)
island (SC)	0.00 (0.08)	**0.31 (0.11)****	**0.68 (0.14)*****

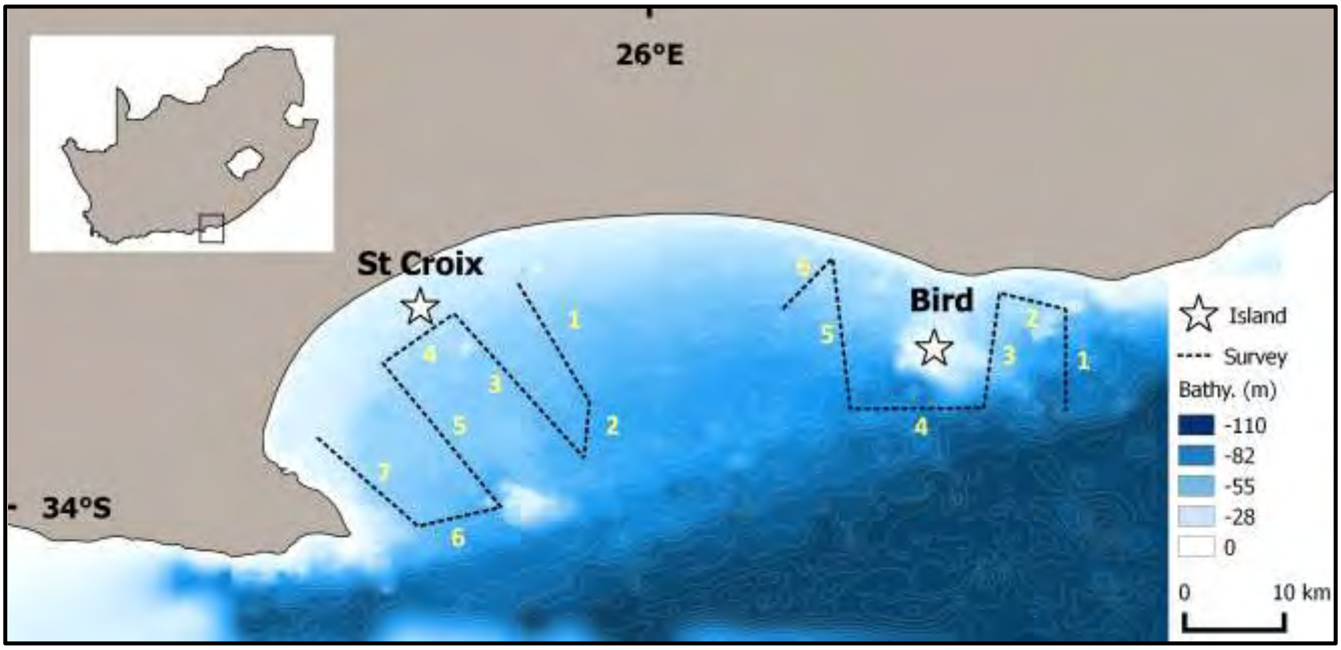


Figure 4.1 Study area showing the fish survey routes around two African Penguin breeding colonies in Algoa Bay, St Croix and Bird islands. Numbers denote survey sections and contours overlaying the bathymetry model are spaced at 5 m.

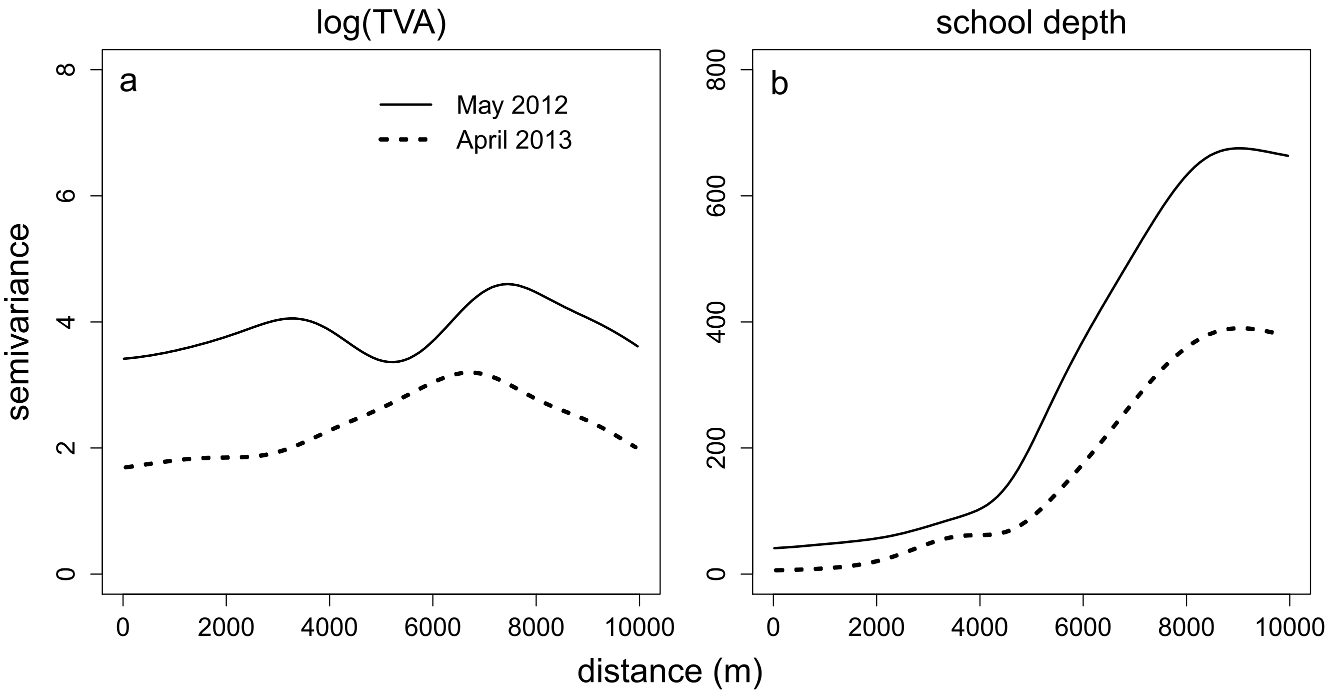


Figure 4.2 Smoothed variograms showing the spatial dependencies of two pelagic fish metrics: a) relative fish abundance calculated as total volumetric abundance (TVA, kg) of fish schools; b) mean school depth. Variograms are for data from section 3 along the Bird Island survey route during two survey days.

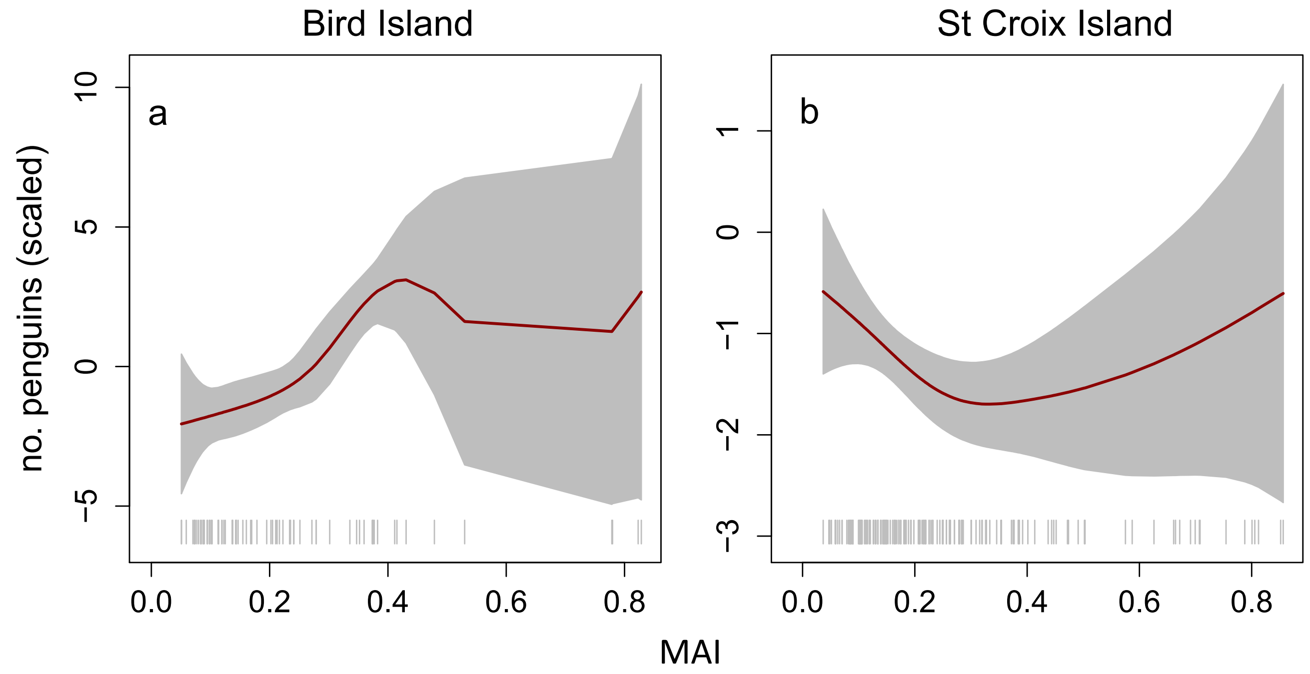


Figure 4.3 Generalised additive models for location, scale and shape (GAMLSS) outputs for African Penguin count models around Bird (a) and St Croix (b) islands showing the predicted influences of mean school altitude index (MAI) on the number of penguins counted. Rug plots show the sampling effort on the x-axis and shaded areas denote 95 % confidence intervals.

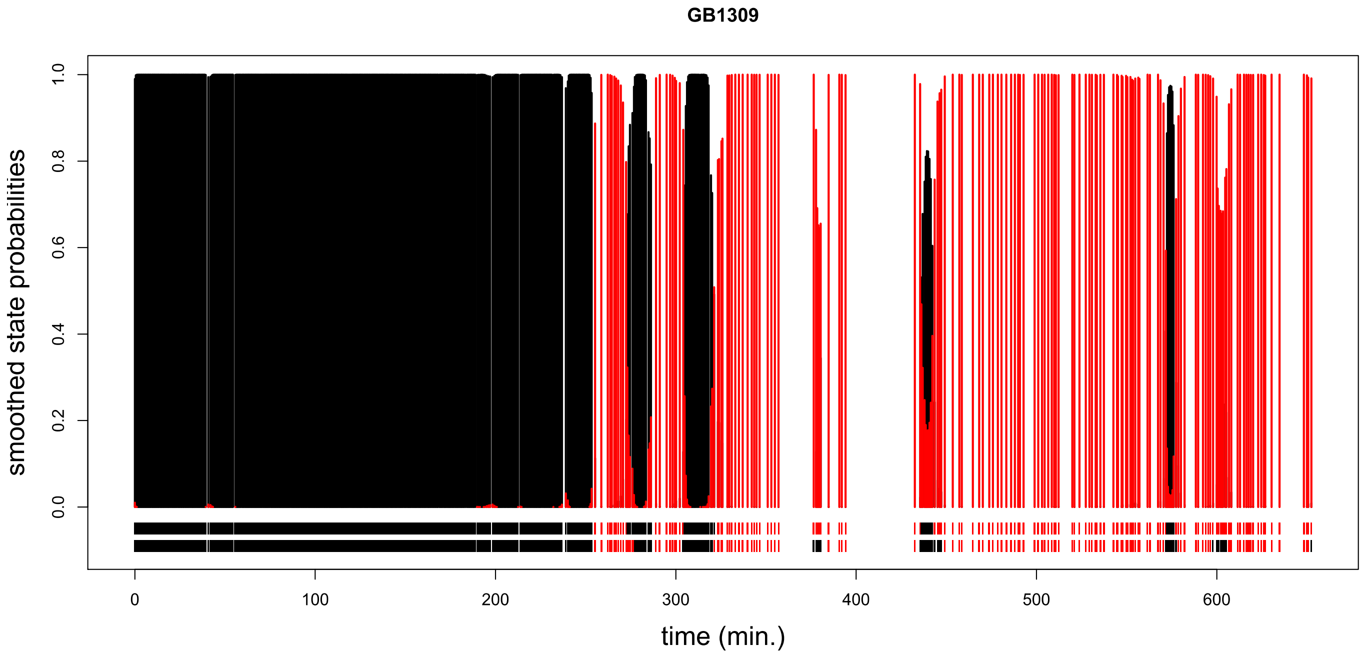


Figure 4.4 Smoothed state probabilities (commuting in black; dive bouts in red) of an African Penguin track at sea during the course of a daily foraging trip (time since departing from colony on x-axis). States were predicted using a Hidden Markov Model (see Methods for details). The narrow bars at the base of the plots represent the predicted (top) and actual states (bottom) with closer alignment of these phases being indicative of improved model performance.

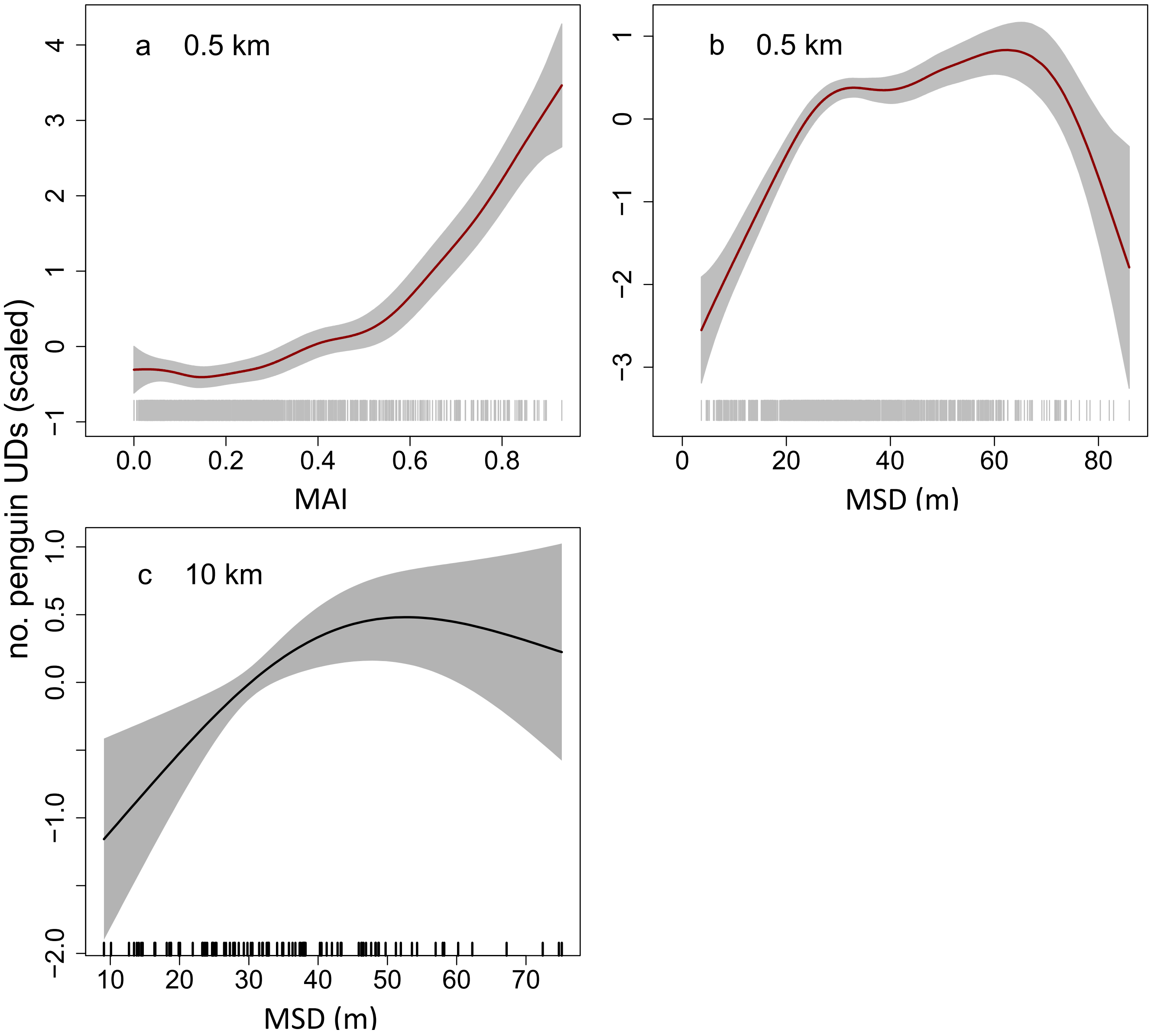


Figure 4.5 Generalised additive models for location, scale and shape (GAMLSS) showing the predicted influences of: a) pelagic fish mean school altitude index (MAI) and b & c) mean school depth (MSD) on the number of intercepted penguin utilisation distributions summed over two scales, 0.5 km (a & b) and 10 km (c). Rug plots show the sampling effort on the x-axis and shaded areas denote 95 % confidence intervals.

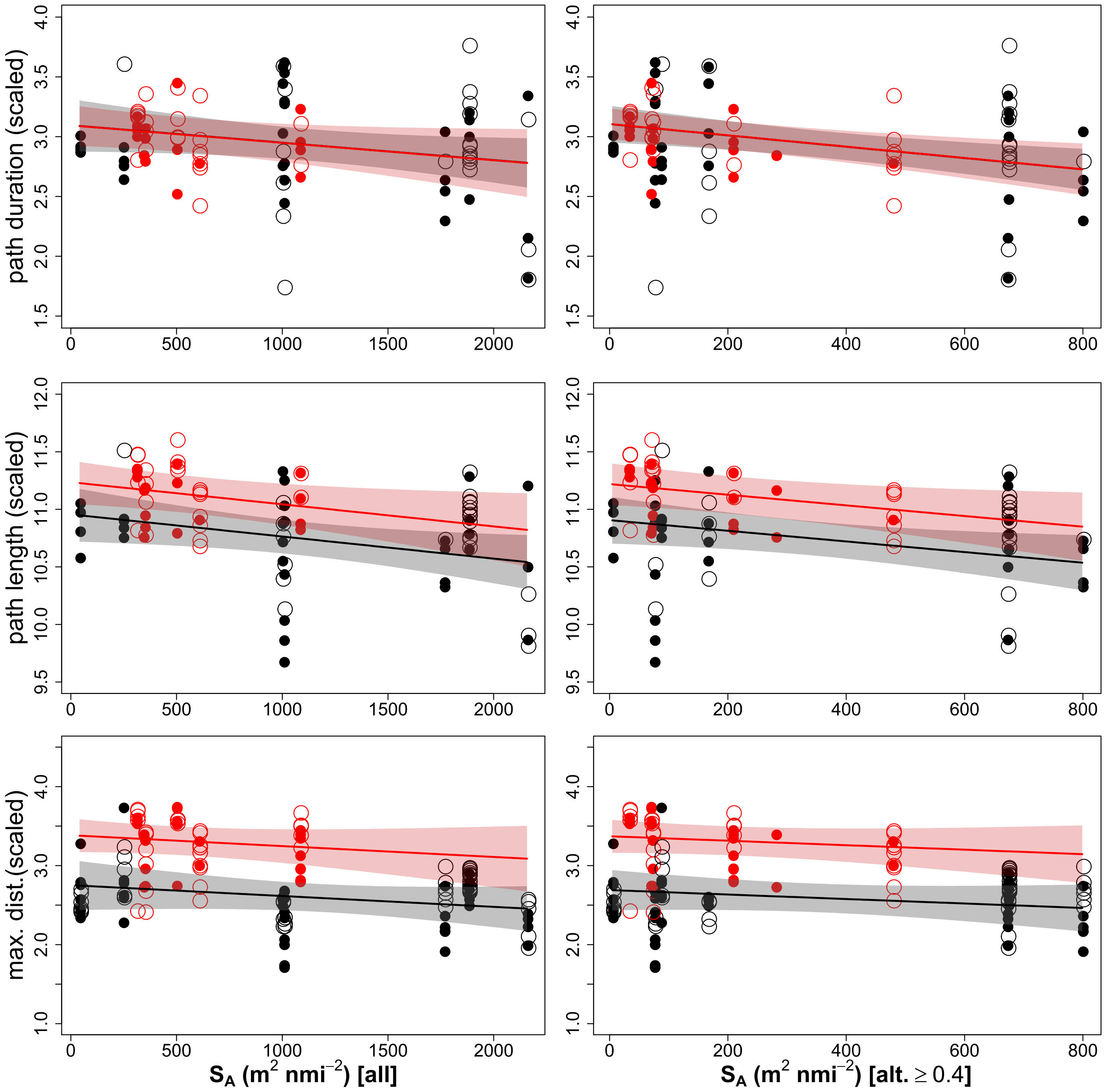


Figure 4.6 Generalised linear mixed effects model (GLMM) outputs for breeding African Penguin activity budgets in Algoa Bay using three path metrics: path duration, path length and maximum distance travelled from the colony. Plots show the predicted effects of relative fish abundance (s_A) using all fish and only fish schools with altitude index values ≥ 0.4. Additional covariates include site (black: Bird Island, red: St Croix Island) and sex (small filled circles = males, large open circles = females). Shaded areas denote 95 % confidence intervals for fixed effects for St Croix and Bird islands.

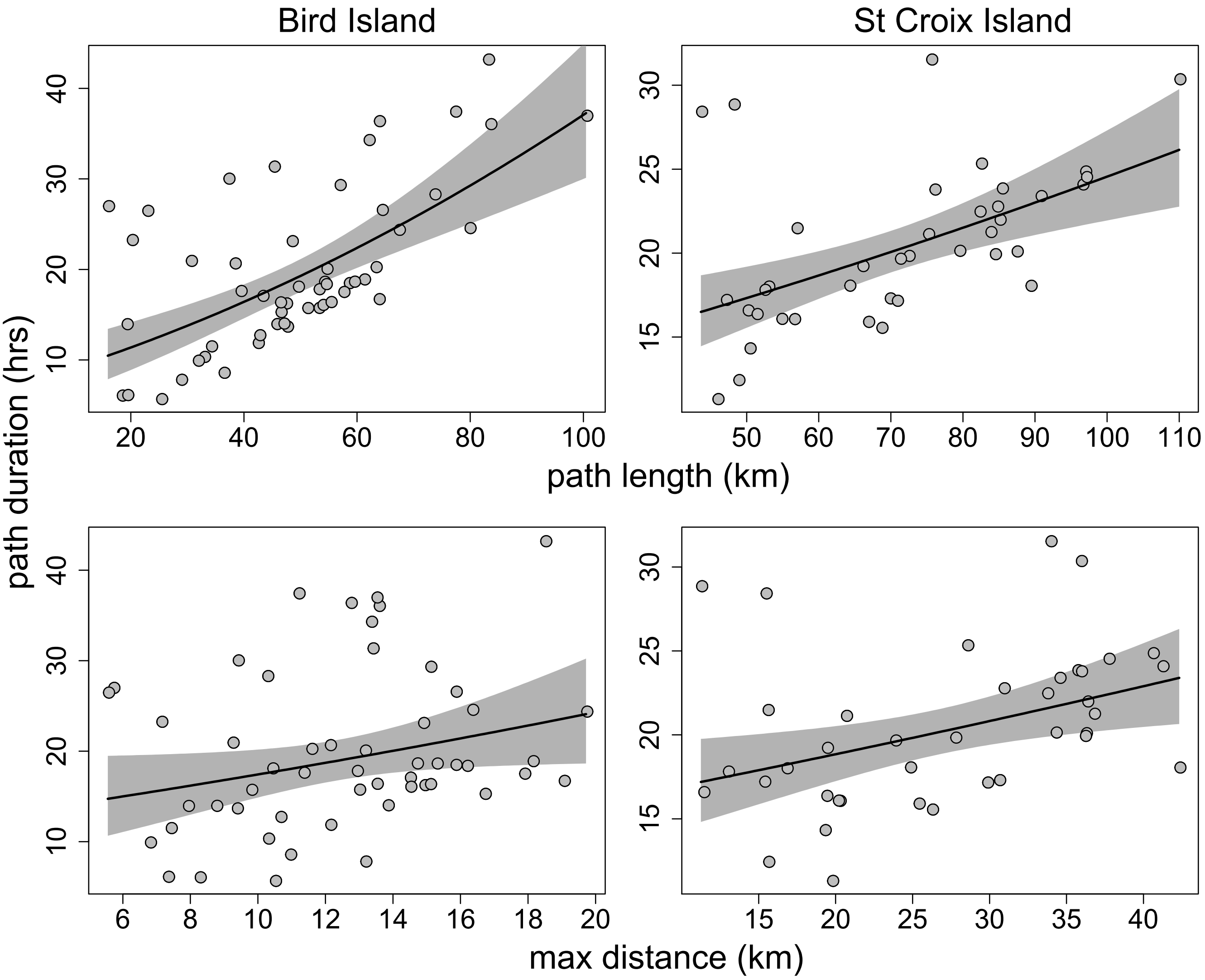


Figure 4.7 Least-square linear regressions showing the influences of path metrics (length and maximum distance from the colony) of daily time budgets (path duration) of African Penguins tracked around St Croix and Bird Islands. Shaded areas denote the 95% confidence intervals.

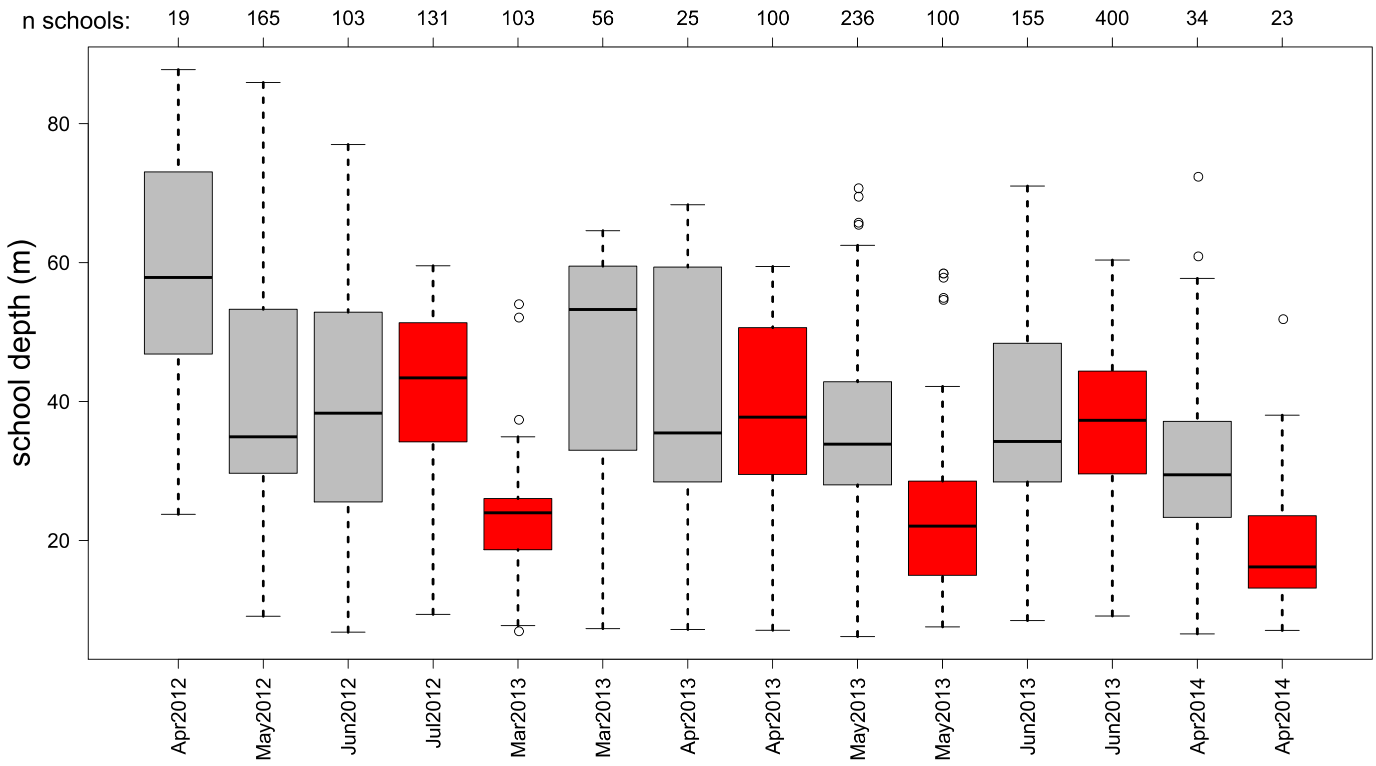
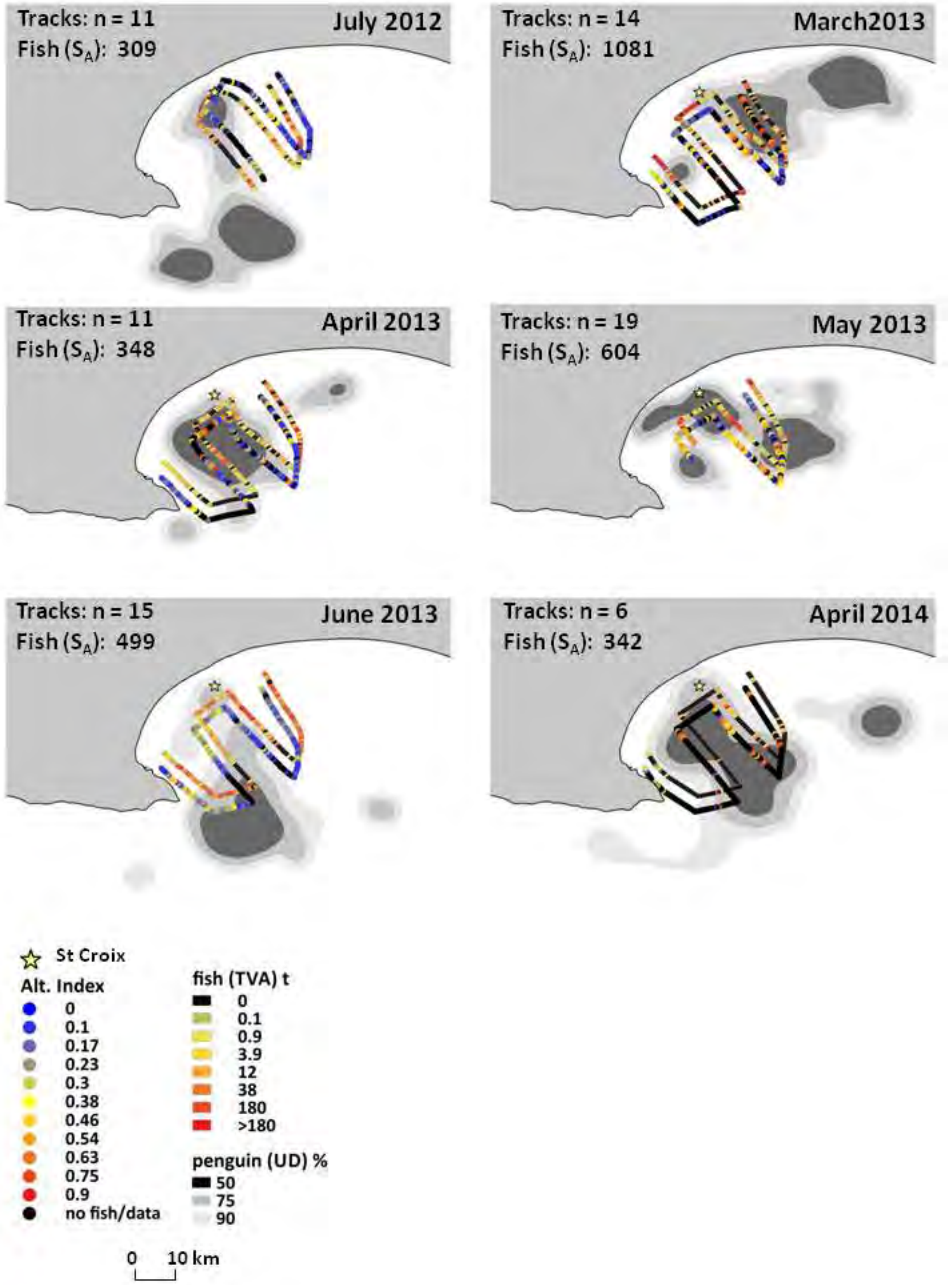
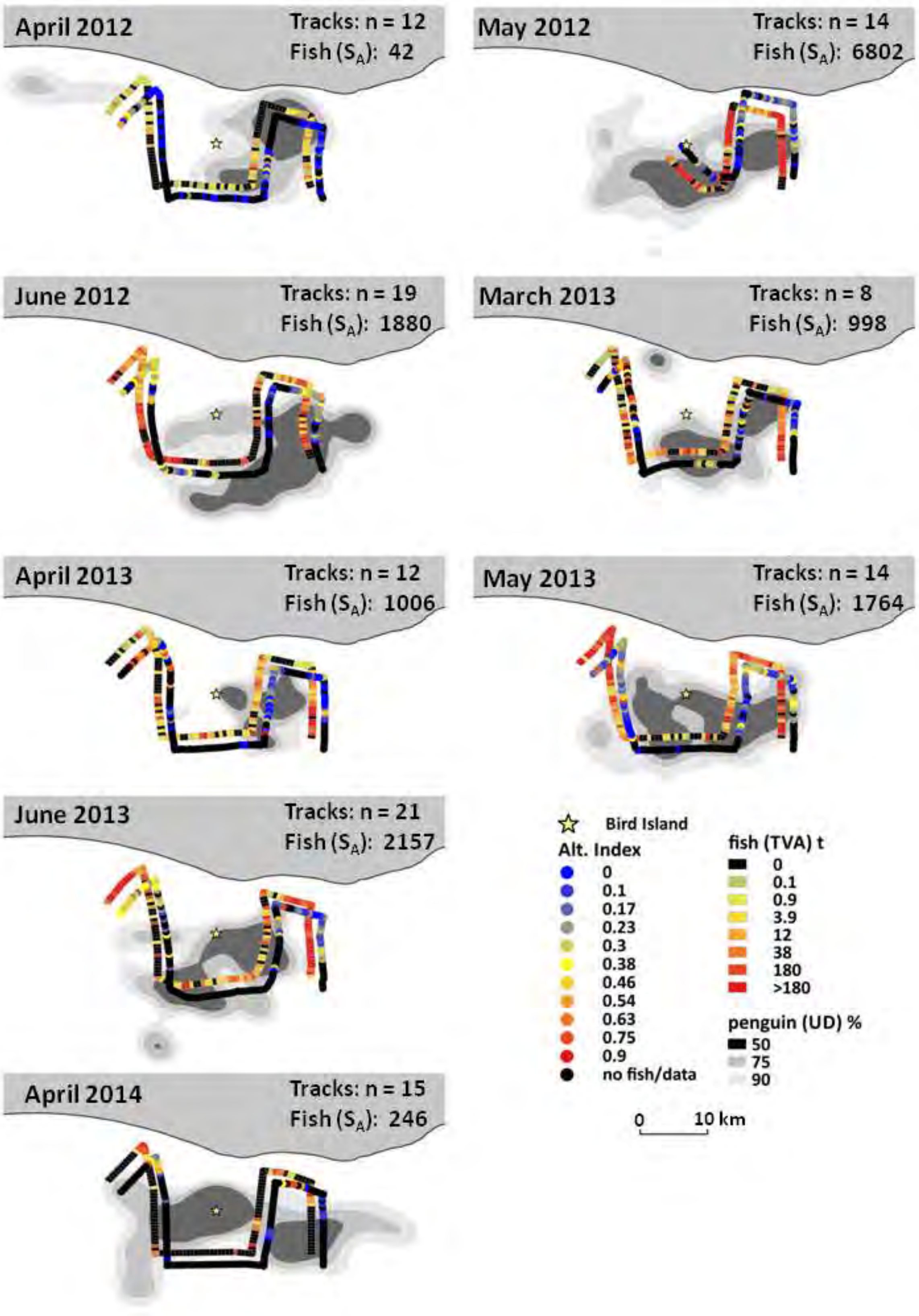


Figure 4.8 Box plots showing the medians and inter-quartile ranges of fish school depths recorded around Bird (grey) and St Croix (red) islands during 14 pelagic fish surveys conducted concurrently with multiple penguin deployments. Top axis denotes the number of fish schools used to calculate the box plot statistics for each survey.



Appendix 4.1 Spatial summary maps of concurrent fish survey and African Penguin GPS deployment days around St Croix Island showing combined utilisation distribution (percentiles) of all penguins deployed on each day, the total volumetric abundance (TVA) (aligned to actual survey route) and the mean altitude index (offset from survey route) of fish recorded at a scale of 0.5 km.



Appendix 4.2 Spatial summary maps of concurrent fish survey and African Penguin GPS deployment days around Bird Island showing combined utilisation distributions (percentiles) of all penguins deployed on each day, the total volumetric abundance (TVA) kg (aligned to actual survey route) and the mean altitude index (offset from survey route) of fish recorded at a scale of 0.5 km.

Chapter 5

Controlling for natural variation in prey abundance to infer responses of African Penguins to competition by purse-seine fishing in Algoa Bay, South Africa

Controlling for natural variation in prey abundance to infer responses of African Penguins to competition by purse-seine fishing in Algoa Bay, South Africa

Abstract

Establishing impacts that fisheries have on seabird populations that compete for the same resource is complicated by confounding processes, such as oceanographic conditions and trophic interactions, that mediate the availability of prey. Survival of the endangered African Penguin is closely linked to the variation in pelagic fish biomass that is also targeted by the purse-seine fisheries, but mechanisms underlying potential competition between these consumers have yet to be established. To investigate potential causation in negative penguin-fishery interactions, localised depletion of pelagic fish stocks were assessed in 2012 and 2013 when the waters around the largest breeding colony of African Penguins, St Croix Island, were opened to fishing. The interaction of primary production (chla), as a proxy for natural prey variation, and geo-referenced cumulative catch data was modelled against foraging metrics from 119 African Penguins provisioning chicks between 2011 and 2013. Localised depletion of fish stocks was evident during both years, with most catches initially occurring close to port in 2012 but becoming more dispersed once the bulk of catches had accumulated, and in 2013 by the negative association of cumulative catches on acoustically derived estimates of fish abundance. Path lengths and foraging ranges of African Penguins were significantly reduced when there was little fishing effort within 30 to 90 days of these deployments and during higher levels of primary production. The results highlight the negative consequences of direct competition by purse-seine fisheries on the foraging effort of breeding African Penguins. These findings have an important bearing on current resource management initiatives, such as motivation required to implement no-take zones around African Penguin breeding colonies.

Introduction

Establishing the impacts that fisheries have on seabird populations that compete for the same resource is complicated by confounding processes such as oceanographic conditions and trophic interactions that mediate the abundance and distribution of these forage fish species, i.e. factors that determine recruitment success and optimal habitat conditions (Tasker et al. 2000; Arnott & Ruxton 2002; Daskalov 2003; Bertrand et al. 2004; Frederiksen et al. 2004, Engelhard et al. 2014). Signals of fishing effects on seabird survival parameters may only be reflected during periods of limited forage fish availability such as the thresholds postulated by Cury et al. (2011) to influence seabird breeding success. Consequently, during periods of relatively high fish biomass, there may even be positive correlations between catches and seabird survival indices (Furness 2002, 2003). Determining cause and effect in seabird-fishery interactions is further complicated by difficulties in demonstrating fishery-induced localised fish depletions largely due to the dynamic nature of fish movements and the allocation of a suitable spatio-temporal window to test these effects (Bertrand et al. 2012, Rogers et al. 2013).

Small pelagic purse-seine fisheries contribute to the largest fish catches in terms of biomass globally (FAO 2014). Within eastern boundary upwelling regions where a large proportion of this fish is caught, many seabird species are largely reliant on these same fish stocks for their survival (Chavez & Messié 2009). Population trends of these seabird species are closely correlated with the abundance of their prey (Jahncke & Rivas 1998; Crawford 2007), which fluctuates according to prevailing oceanographic conditions at different spatio-temporal scales (Cury & Roy 1989; Jahncke et al. 2004; Shannon et al. 2008). The large-scale harvesting of small pelagic fish can have devastating consequences to seabird populations during periods of unfavourable oceanographic conditions. For instance, population crashes of guano producing seabirds were recorded off Peru during El Niño conditions in the early 1970s concomitant with some of the highest historical fish landings there (Duffy 1983; Jahncke et al. 2004). Incidentally, during the same period in the northern Benguela upwelling region, sardine stocks crashed following the largest harvests of this species off Namibia, resulting in dramatic reductions in both Cape Gannet and African Penguin populations (Crawford & Shelton 1978; Cury & Shannon 2004; Roux et al. 2013).

Advances in fish monitoring programmes have alleviated excessive harvesting in the southern Benguela upwelling region (Hutchings et al. 2009; Jarre et al. 2013) but the populations of seabirds reliant on small pelagic fish continue to decline and there is growing concern that competition by purse-seine fisheries may be contributing to this predicament (Crawford 2007; Pichegru et al. 2009; Trathan et al. 2015; Grémillet et al. 2016). The conservation status of African Penguins has been upgraded to 'endangered' following >60 % decrease in their population during the first decade of this century largely due to a reduction in the abundance of their principle prey species, anchovy and sardine (Crawford et al. 2011). To gauge the impacts of purse-seine fishing harvests on survival indices of African Penguins, an island closure feasibility study was initiated in 2008 around four of their largest colonies in South Africa with alternating open and closed periods to fishing. Two of these colonies, Bird and St Croix islands, are situated at the eastern most distribution range of this species and, despite being relatively isolated, together hold approximately 50% of the global breeding population of African Penguins (Crawford et al. 2015). Recent studies involving these experimental no-take zones around these two islands have shown evidence for decreased foraging effort of African Penguins during closures (Pichegru et al. 2010, 2012). However, these results have been disputed due to a lack of control for natural variation in prey availability (Coetzee 2010).

This chapter investigates the impacts of purse-seine fishing activities on the at-sea performance of African Penguins in Algoa Bay. To establish cause and effect, evidence for localised fish depletions due to purse-seine harvests were investigated by examining both the influence of cumulative catches on estimates of acoustically determined fish biomass, where survey frequency permitted, and, indirectly, by assessing the distances fishing vessels travelled from port (*sensu* Cardinale et al. 2011) as the fishing season progressed. The latter method is based on the assumption that fishermen prioritise catches closer to port when the distribution of available fish biomass permits to minimise fuel costs and time spent at sea, and move progressively further from port as fish stocks become locally depleted. Effects of fishing activities, i.e. geo-referenced catch biomass, were then modelled against path-derived measures of foraging effort of breeding African Penguins while controlling for natural variation in prey availability using previously demonstrated oceanographic predictors of prey abundance and distribution in this region (Chapter 3).

Methods

Data sources

For indices of primary productivity, 30 day composites of chlorophyll a concentration (chl30) were extracted from the Moderate Resolution Imaging Spectroradiometer (MODIS) satellite array from the NASA ocean colour group (Chapter 3). This variable had the greatest influence on the variability in pelagic fish distribution and abundance around Bird Island where potential confounding influences of commercial fishing were absent during the course of this study (Chapter 3). Chl30 was aggregated within a 20 km radius of Bird and St Croix islands with mean values calculated for 30 days prior to the date of each response.

Pelagic fish school data were quantified from surveys conducted around St Croix Island following the methods described in Chapter 3. For survey level comparisons of relative abundance, two estimates of the nautical area scattering coefficient were used: estimates based on all pelagic schools recorded (s_A); and, estimates using only schools targeted for by African Penguins, i.e. with mean school altitude index values (MAI) ≥ 0.4 (s_A [alt. ≥ 0.4]) (Figure 4.5a).

Purse-seine fishery catch data of sardines administered by the Department of Agriculture, Forestry and Fisheries (DAFF) were extracted for each vessel operating in Algoa Bay between 2011 and 2013. GPS locations, date and the mass of sardines were provided for each haul.

Deployment procedures for bio-logged African Penguins and details of the methods used to determine path-derived measures of foraging effort are described in Chapter 4. For the purposes of this chapter an additional sample of penguin track data from birds deployed during 2011 was used to bolster the sample size. These deployments used GPS-TD loggers (70 g, LXWXH: 96 × 39 × 26.5 mm, Earth & Ocean Technologies, Germany) housed in streamlined fibre-composite containers and which recorded GPS localities at the same frequency and accuracy as loggers used in subsequent years (fixes every 1 minute; spatial accuracy < 10 m).

Foraging effort and primary production

The influence of primary production (using chl30) on African Penguin foraging metrics was modelled to evaluate the suitability of using primary production indices as proxies for prey availability for African Penguins. This approach was deemed appropriate given the significant influence chla had on both the vertical distribution of fish and relative fish abundance in Algoa Bay (Chapter 3). To omit potential confounding anthropogenic influences on this relationship I only used data from around Bird Island where there was virtually no fishing pressure during the study period (Figure 5.1).

Mixed effects models were used to account for correlated measurements on each deployment day. To account for potential non-linear associations between chl30 and the three penguin foraging metrics (path length, path duration and maximum distance travelled from the colony), generalised additive mixed effects models (GAMM) were initially used. If the inferred degrees of freedom suggested a linear model, generalised linear mixed effects models (GLMM) were used instead. Due to the skewness of the response variables, a Gamma error distribution with a log link function was used in all models. The relationship between each of the response variables and chl30 was modelled in the GAMM with a penalised regression spline with at most three degrees of freedom to allow for the negative, nonlinear relationship that has been previously demonstrated for seabird activity budget-prey interactions (Cairns 1987; Harding et al. 2007). Sex and brood mass were included as fixed effects due to the potential influence of these variables on foraging effort for African Penguins and other seabird species (Litzow & Piatt 2003; Pichegru et al. 2013). All observations in the models were weighted by the number of grid cells used to estimate the 30 day lagged composites for chlorophyll a (chl30) which varied according to the amount of cloud cover during a given composite period. Models were fitted using the R software (R Core Team 2015) with packages 'mgcv' (Wood 2006) and 'lmer4' (Bates et al. 2015) used for the GAMMs and GLMMs respectively. Model validation procedures followed those of Zuur et al. (2010) (see Chapters 3 and 4 for details).

Seasonal differences

Bio-physical seasonal variation in oceanographic conditions, pelagic fish attributes, purse-seine fish catches and African Penguin acforaging effort were assessed to contextualise inter-annual differences in these variables over the course of this study period. Seasonal periods were allocated based on known diverging oceanographic conditions in Algoa Bay in the months leading up to and including the African Penguin breeding season (February – July). Two periods were included: Biophysical season 1 (BPS1), January - April, when elevated stratification and frequent wind-driven upwelling events predominate, and BPS2, May - July, when more mixed water conditions predominate in the bay (Goschen & Schumann 2011, Figure 3.10). Non-parametric tests were used to ascertain significant differences between years for oceanographic, fish and penguin data, where sample sizes permitted, using Kruskal-Wallis tests for comparisons between all three years, and Mann-Whitney tests for comparisons between two years.

Localised depletion of fish

Evidence for localised fish depletion was assessed using two methods. Firstly, in 2012 and 2013, when fishing was permitted around St Croix Island, the distance of each geo-referenced catch from Port Elizabeth harbour was modelled against the temporal progression of the fishing season (Jan to July) – corresponding to the period when most catches were made in both years and coinciding with the African Penguin breeding season. The purpose of this analysis was to establish whether catches were located at increasing distances from port as the season progressed, implying that fish were locally depleted. Only catches within 50 km of St Croix Island were used for this analysis. The expected non-linear nature of this association was modelled using generalised additive models (GAM; Wood 2006) which use smoothing terms to approximate non-linear influences of explanatory variables on the response. Separate models were used for each year using distance of catch from port as the response and days elapsed since the start of the fishing season as the explanatory variable. The number of knots used in the smoothing terms for both GAMs were limited to six to prevent over-fitting of the models while still representing the prominent trends. Due to the skewness of the response, a Gamma error distribution and a log link function were used. All computations were conducted in R using the package 'mgcv'.

The second method involved direct comparisons between cumulative fish catches and estimates of pelagic fish biomass using s_A [alt. ≥ 0.4]. This filtered abundance estimate was deemed most appropriate as being representative of fish assemblages targeted for by both African Penguins and purse-seine fishers. The latter assertion is supported by higher altitude values for sardine schools in Algoa Bay, recorded by DAFF (Figure 3.4), and the probability of improved responses by the distribution and abundance of elevated assemblages to purse-seine fishing activities . For this analysis, only catches within 20 km of St Croix Island were used so as to assess potential depletion effects within the range of the acoustic fish surveys (Figure 5.1). This comparison involved visual inspection of overlaid time-series and was only done for data collected during 2013 when fish surveys were conducted more frequently. The prevailing levels of primary production using chl30 were included as a control for natural prey conditions.

Catch/oceanography interaction models

The purpose of the catch/oceanography interaction models was to investigate the effects of cumulative purse-seine fishery catches under varying oceanographic conditions on African Penguin foraging effort. Due to the small number of catches around Bird Island, only data for St Croix Island were used in these analyses. Catches were aggregated to within 20 km of St Croix Island following the prescribed temporary closure regimes by the Island Closure Task Team (ICTT, see General Introduction for details). GLMMs were used with penguin deployment date treated as a random effect. A model was fitted for each of the three penguin foraging response variables: path length, path duration and maximum distance travelled from colony. For non-Gaussian responses, Gamma error distributions with a log link function were applied to either the non-transformed data or log-transformed data, as determined by examining the model residuals.

An interaction term between chl30 and catch level was included in each model. Three separate models were fitted for each response variable with cumulative catches covering 30, 60 and 90 days. Sex and brood mass were included as fixed effects in all models (see above). All continuous explanatory variables were standardised to prevent model convergence issues. For all models, two versions were fitted, one with all observations weighted by the number of grid cells used in calculating chl30 (see above), and a non-weighted version.

To test the significance of interaction terms, the performance of models with significant interaction outcomes were compared to equivalent models without interactions using analysis of variance tests (ANOVA) with three additional model validation criteria, Akaike's information criteria (AIC, Akaike 1973), Bayesian information criteria (BIC) and likelihood ratio tests. Package 'lme4' was used in R and model validation procedures followed Zuur et al. (2010) (see Chapters 3 and 4 for details).

Results

Foraging effort and primary production

A total of 192 African Penguins were deployed with GPS loggers between 26 April 2011 and 29 June 2013 on Bird Island. After applying filtering procedures for erroneous fixes and incomplete tracks, 113 penguin tracks were used in models with path length or path duration as a response and 177 tracks were included in the model of maximum distance from the colony. One track was removed from the path length model due to an excessively long trip (181 km) and two tracks that had maximum distances travelled > 50 km were excluded from models.

Penguin path lengths and maximum distances travelled from the colony were negatively associated with primary production (Table 5.1). For the GAMM model, using path length as a response, there was a strong non-linear association with chl30 ($p=0.5$) with a sharp negative correlation between path length and chl30 at chla < 4 mg m^{-3} (Figure 5.3a). Brood mass had little influence on the outcome of these models but sex was influential, with female penguins travelling significantly further than males (maximum distance travelled from Bird Island; Table 5.1, Figure 5.3b).

Seasonal differences

During BPS1 primary production (chla) differed among years, with 2011 being the most productive, 2012 least productive, and 2013 intermediate (Table 5.2). There was no significant difference in BPS2 chla values among years. Fish were substantially more abundant during both BPS1 and BPS2 in

2013 than 2012; these differences were particularly pronounced during BPS1 for all pelagic fish schools (s_A; Table 5.2). In contrast to these trends, most purse-seine catches took place during BPS1 in 2012 with 1.3 times as many hauls and 1.5 times as much biomass taken during this season in 2012 than 2013. Catches were substantially reduced during BPS2 in both years. Purse seine fishing operations were mostly absent around St Croix Island during the 2011 penguin breeding season due to the 20 km no-take zone there in this year (Figure 5.1).

Foraging metrics were not recorded for African Penguins during BPS1 in 2012 but estimates of all three path-metrics for this species in 2011 and 2013 were very similar (Table 5.2). Inter-annual comparisons of foraging metrics during the BPS2 season showed that birds in 2012 travelled significantly further and for longer distances than birds in 2011 and 2013.

Localised depletion of fish

Fishing catch data used to test whether distance from port increased over the season included 231 hauls (4756 tonnes of sardine) from eight vessels within 50 km of St Croix Island between 21 January and 25 July 2012, and 169 hauls (3041 tonnes of sardine) from eight vessels between 17 January and 31 July 2013. Results for both GAMs were highly significant (2012: $F = 13.36$, $p < 0.001$; 2013: $F = 5.6$, $p < 0.001$) but the relationships between distance to port and time elapsed show markedly different trends between years (Figure 5.4). During 2012, most catches were made < 10 km from port and became abruptly more dispersed toward the end of March after the bulk of the annual catch was landed. By comparison, most catches in 2013 were dispersed at varying distances from the port throughout the fishing season.

Fishing catch data used to test the effect of cumulative fish catches on acoustic estimates of pelagic fish biomass included 123 hauls (2274 tonnes of sardine) from eight vessels within 20 km of St Croix Island between 21 January and 31 July 2013. Acoustic estimates of targeted fish abundance decreased from 355.6 m^2 nmi^{-2} on 15 February when 49 % of catches were taken to 69.9 m^2 nmi^{-2} on 25 April when 91 % of the total catch had been taken (i.e. an 80 % reduction in acoustic estimates over this period) (Figure 5.5). Fish abundance increased during May, when there were few catches, and there was elevated chl30 since March (Figure 5.5).

Catch effects on penguin foraging effort

Tracks from 119 African Penguins provisioning small chicks at St Croix Island between 25 April 2011 and 29 June 2013 were filtered to exclude erroneous fixes and incomplete tracks. The filtered sample included 69 individual tracks for models using path length and path duration and 104 tracks for models using maximum distance from the colony. Results for both weighted and un-weighted model versions were very similar with no differences in significance levels for all predictors; only the results of the un-weighted models are presented here. There were highly significant interaction effects of chl30 and catch at both 60 and 90 day cumulative catch periods in models that used penguin path length as the response variable (Table 5.3). Variables included in all models for path duration did little to explain the variance in this response. For maximum distance travelled from the colony, there were significant interaction effects for chl30 with both 30 and 60 day cumulative catches (Table 5.3). Brood mass had a significantly positive influence on the maximum distance from the colony for the model including an interaction effect of chl30 and catch30.

All models with significant interaction terms performed significantly better than models lacking interactions (Table 5.4). Figure 5.6 illustrates the influences of the chl30 interaction terms with various levels of catches for path length and maximum distance travelled. At both the 60- and 90-day cumulative catch levels, penguin travelled significantly shorter distances when catches were low and at high chl30 levels (Figures 5.6a & b). These trends were reversed under high fishing pressure, especially at 60 days of cumulative catches where penguins travelled significantly longer at both high catch and chl30 levels (Figure 5.6a). At both 30 and 60 days of cumulative catches the maximum distance penguins travelled from St Croix Island peaked at high catch and chl30 levels (Figures 5.6c & d).

Discussion

Primary production as a proxy for prey availability

Primary production is inextricably linked to the maintenance of pelagic fish stocks in upwelling areas due to the short food chains connecting plankton to fish in these systems (Pauly & Christensen 1995; Cury et al. 2000; Chavez & Messié 2009). It plays a significant role in determining the abundance and distribution of fish in Algoa Bay, being the most influential oceanographic variable affecting relative fish abundance around Bird Island (Chapter 3). Indices of primary production have been used as proxies to establish habitat selection preferences in a diverse range of seabird species (e.g. for Northern Gannets (*Morus bassanus*) (Scales et al. 2014), Common Guillemots (*Uria aalge*) (Bellier et al. 2010) and White-chinned Petrels (*Procellaria aequinoctialis*) (Péron et al. 2010)), and are important determinants of breeding success and population growth of seabird species reliant on pelagic fish in the upwelling system off Peru (Jahncke et al. 2004). My results highlight the disparity in the influence of primary production on foraging metrics of African Penguins around Bird and St Croix islands (Figures 5.3 & 5.6). For Bird Island, where fishery catches were negligible, the negative curvilinear response of penguin path length to chl30 reflects Cairns' (1988) hypothesised non-linear response of seabird activity budgets to varying prey availability with unproductive periods forcing penguins to work harder to find their prey. However, around St Croix Island, associations of chl30 and path lengths travelled by penguins were masked by the influence of cumulative purse-seine fishing catches (Figures 5.6a & b) such that, under reduced cumulative catches of between 60 and 90 days, these bio-physical relationships approximate those of Bird Island, i.e. the expected natural response (Figure 5.3a).

Localised depletion of fish

Determining localised depletions of forage fish stocks due to competition by fisheries is complicated by fish movements, making it difficult to define a suitable spatio-temporal window to test these depletion effects (Rogers et al. 2013). Localised and serial depletions have been demonstrated for unregulated stocks of pelagic fish off Indonesia by assessing catch effort as a function of the temporal span of distances travelled by fishing vessels from their ports (Cardinale et al. 2011). These authors used distance to port as a proxy for effort as it relates to both time and fuel costs and showed that the most profitable species close to port were the most sought after and were the first to be depleted.

When fishing was permitted around St Croix Island during 2012 and 2013, most catches were taken between January and March, in the pre- and early breeding season of African Penguins (Figure 5.2, Table 5.2). In 2012, most catches occurred within 10 km of Port Elizabeth harbour, becoming progressively more dispersed as the cumulative catch levelled off in April (Figure 5.4). The abrupt nature of this change in the spatial distribution of fishing vessels provides some support for local depletion during this time. During the first quarter of 2013, the distribution of catches was more dispersed providing no evidence to support localised depletion of fish. However, despite reduced fishing intensity coupled with relatively high estimates of pelagic fish abundance in comparison to 2012, relative fish abundance was negatively correlated with accumulated catches between February and April 2013. Fish abundance decreased toward the end of the peak catch season and remained low until April despite improved oceanographic conditions during this time (Figure 5.5). When fishing subsided (there were no catches between 6 April and 4 July) fish stocks increased again and subsequently fish abundance was closely related to prevailing levels of primary productivity.

Knowledge on fine-scale movements of sardine and other pelagic fish in the Algoa Bay region are lacking, although sardines have been recorded at relatively high densities during winter and summer, when all major life-stages have been recorded (Beckley 1986; Armstrong et al. 1991; Barange & Hampton 1997; Beckley & van der Lingen 1999; Coetzee et al. 2010). Although I cannot rule out the potential influence of localised sardine movements on the outcomes of these results, it is unlikely that this phenomenon was the major driver of fish distributions because oceanographic conditions remained stable (2012) and even improved (2013) when depletion effects were evident.

Impacts of fishing on penguin foraging effort

The study period was spread over a diversity of oceanographic conditions and discordant levels of fishing pressure, providing a unique opportunity to investigate the influence of these interactions on the at-sea performance of African Penguins. Contrasted catches were enhanced by the island closure experiment, with very little fishing occurring during 2011. Levels of primary production also showed significant variability, notably in the period leading up to and at the onset of the African Penguin breeding season, an important stage for seabirds as they improve body condition to cope with the approaching breeding effort (Drent & Daan 1980; Sorensen et al. 2009). In fact the lowest levels of primary production coincided with the largest fish catches during this time, concomitant with almost an order of magnitude reduction in estimated relative fish abundance when compared to the same period during 2013 (Table 5.2). It was during 2012 that African Penguin foraging effort was greatest, with birds travelling the longest distances further from the colony and spending more time at sea (Table 5.2). 2012 also saw a 15-20 % decrease in the numbers of breeding pairs of African Penguins on St Croix Island compared to 2011 and 2013 (2011 = 8500 pairs; 2012 = 6625; 2013 = 7657; DEA unpub. data).

The at-sea performance of African Penguins improved significantly during periods of up to three months of no fishing and when primary productivity levels were greatest (Figure 5.6). The best conditions were during May 2013 when penguin foraging metrics were at their lowest, and this corresponded to a decrease in fishing pressure and subsequent increase in acoustic estimates of fish abundance associated with increased primary production (Figure 5.5). In the preceding two months when fishing catches were greatest, birds had to work significantly harder to get enough food to sustain themselves and their chicks and this situation persisted for over a month after fishing activities were suspended despite improving oceanographic conditions (Figures 5.2 & 5.5).

In Algoa Bay, during the latter half of the African Penguin breeding season, sea-surface temperatures typically drop and thermal stratification is reduced (Goschen & Schumann 2011). During this season pelagic fish tend to occur deeper (Figure 4.8) closer to the seabed, when they are less available to African Penguins (Figure 4.5a). Penguins from St Croix Island adapt to these conditions by foraging further offshore (see deployment data for July 2012 and June 2013; Appendix 4.1). Despite similar oceanographic conditions during these deployments, birds travelled significantly further, both in terms of range and path length, during 2012 when localised depletion of sardine stocks were greatest, than in 2013 (Table 5.2).

Evidence for competition between small pelagic fisheries and seabird populations has been inferred from studies using correlated time-series of forage fish abundance, fish catches and seabird populations (e.g. Duffy 1983; Crawford et al. 1987; Cury et al. 2000; Österblom et al. 2006; Crawford & Whittington 2009). However, it has been hard to demonstrate the mechanisms underlying this competition, largely due to the complicated nature of these systems. Confounding processes that obscure causal signals include seasonal differences in seabird foraging ranges and associated discontinuities in their overlap with fisheries (Duffy et al. 1987) or compromised natural trophic interactions due to removal of competing predators (Furness 2002). As far as I know, only one study (Bertrand et al. 2012) clearly establishes cause and effect with regards to resource competition in seabird-fishery systems. Bertrand et al. (2012) demonstrated the negative effects of local depletion of anchovy (*Engraulis ringens*) stocks on the foraging distributions of Peruvian Boobies (*Sula variegata*) by recording the movements of birds and fishing vessels as the fishing season progressed off Peru. My results from Algoa Bay provide further support for the negative influences of purse-seine fisheries on seabirds that compete for the same resources. Predictions of the interaction models emphasise the importance of controlling for natural variation in prey abundance and shed light on the temporal lag of fishing effects after catches have subsided.

Conclusions

Penguins (Spheniscidae) comprise some of the most threatened seabird species globally (Croxall et al. 2012). Resource competition is seen as a significant threat to three of the four *Spheniscus* penguin species and is thought to be the most significant threat to African Penguins (Trathan et al. 2015). Given its obligations to adopt a more ecosystem-based approach to fisheries management, DAFF initiated island closure experiments in 2008 to gauge the benefits of periodically closing African Penguin foraging territories to fishing during their breeding seasons. To date results coming from the two western colonies, Robben and Dassen islands, have been largely inconclusive although there is support for benefits of closures on chick survival around Robben Island (Sherley et al. 2015). Results of temporary closures around penguin colonies in Algoa Bay have demonstrated potential benefits of closures in terms of improved foraging performance of African Penguins (Pichegru et al. 2010, 2012) but, as discussed in the introduction, this evidence was disputed due to a lack of control for natural prey variation (Coetzee 2010). My study provides evidence for localised depletion of fish abundance in both years when fishing was permitted around St Croix Island, despite modest catches, and demonstrates the negative consequences of fishing on the foraging effort of breeding African Penguins when most fishing occurred, especially during periods of low primary productivity. Importantly, outputs of the interaction models show that effects of fishing pressure are cumulative and that persistent fishing under adverse conditions can have serious consequences for breeding African Penguins. These results are significant in terms of current resource management initiatives, such as assessing the feasibility of island closures and the need to manage fish stocks over local spatio-temporal scales that are appropriate for conserving penguins.

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Table 5.1 Coefficients (β) and standard errors (se) of the influence of primary production using 30 day composites of chlorophyll a concentrations (chls30) on African Penguin activity budgets around Bird Island between 2011 and 2013. For models using path duration and maximum distance travelled as responses, Generalised linear mixed effects models (GLMM) were used, and for path length a Generalised additive mixed effect model (GAMM) was used. GAMM outputs are F statistics (F) and p-values (p).

	Penguin activity budgets			
	path duration		**path length**	**max. distance**
Explanatory variables	**β (se)**	**edf**	**β (se) / F (p)[a]**	**β (se)**
chl30	-0.06 (0.07)	1.8	**4.8 (0.05)[a]**	-0.09 (0.06)
sex (M)	-0.03 (0.09)		-3.28 (3.24)	**-0.11 (0.04)****
brood mass	0.05 (0.05)		0.003 (0.003)	0.02 (0.02)

*p<0.05, **p<0.01, [a] GAMM output

Table 5.2 Inter-annual comparisons within bio-physical seasons (see methods for details) showing medians (m) and inter-quartile ranges (IQR) of data used in the analyses for St Croix Island. Test statistics are given for adequate samples: χ^2 - Kruskal-Wallis tests for three year comparisons; W - Mann-Whitney tests for two year comparisons. For catch data, total catch is denoted by the annual sums^s.

	Biophysical season 1 (BPS1) January - April								**Biophysical season 2 (BPS2) May - July**							
	2011		**2012**		**2013**				**2011**		**2012**		**2013**			
	n	**m (IQR)**	**n**	**m (IQR)^s**	**n**	**m (IQR)^s**	**χ^2 / W**	**p**	**n**	**m (IQR)**	**n**	**m (IQR)^s**	**n**	**m (IQR)^s**	**χ^2 / W**	**p**
Oceanography																
chl*a* (mg m^{-3})	82	2.9 (4.2)	66	1.4 (2.4)	82	2 (2.5)	17.7	**<0.001**	58	1.9 (2)	55	1.9 (1.3)	54	1.9 (1.2)	0.1	0.9
Fish																
fish (s_A)	-	-	3	102.1 (26.2)	4	947.1 (400.1)	-	-	-	-	3	309.4 (177.5)	4	551.4 (309.9)	-	-
fish(s_A [alt.≥ 0.4])	-	-	3	36.5 (16.8)	4	172.5 (115.2)	-	-	-	-	3	60.5 (45.1)	4	185.7 (291.2)	-	-
Catches																
haul (t)	-	-	145	20 (16.8)	108	17.3 (13.9)	8611.5	0.18	-	-	24	11 (10.1)	15	13.1 (11.3)	195	0.68
total catch (t)	-	-	-	3121.3^s	-	2098.9^s	-	-	-	-	-	348.1^s	-	175.8^s	-	-
Penguins																
path length (km)	7	69.9 (21)	-	-	20	62.3 (23.7)	75	0.81	10	69.9 (19.4)	17	85.4 (15.1)	15	68.7 (30)	12	**0.003**
path duration (h)	7	22 (4.9)	-	-	20	19.1 (5.9)	75	0.81	10	21.3 (8)	17	23.8 (3.3)	15	18.1 (5.5)	5.5	0.06
max. distance (km)	9	28.8 (12.2)	-	-	41	27.8 (14)	172	0.77	10	20.9 (7.5)	20	37 (5.3)	24	31 (14.3)	22.1	**<0.001**

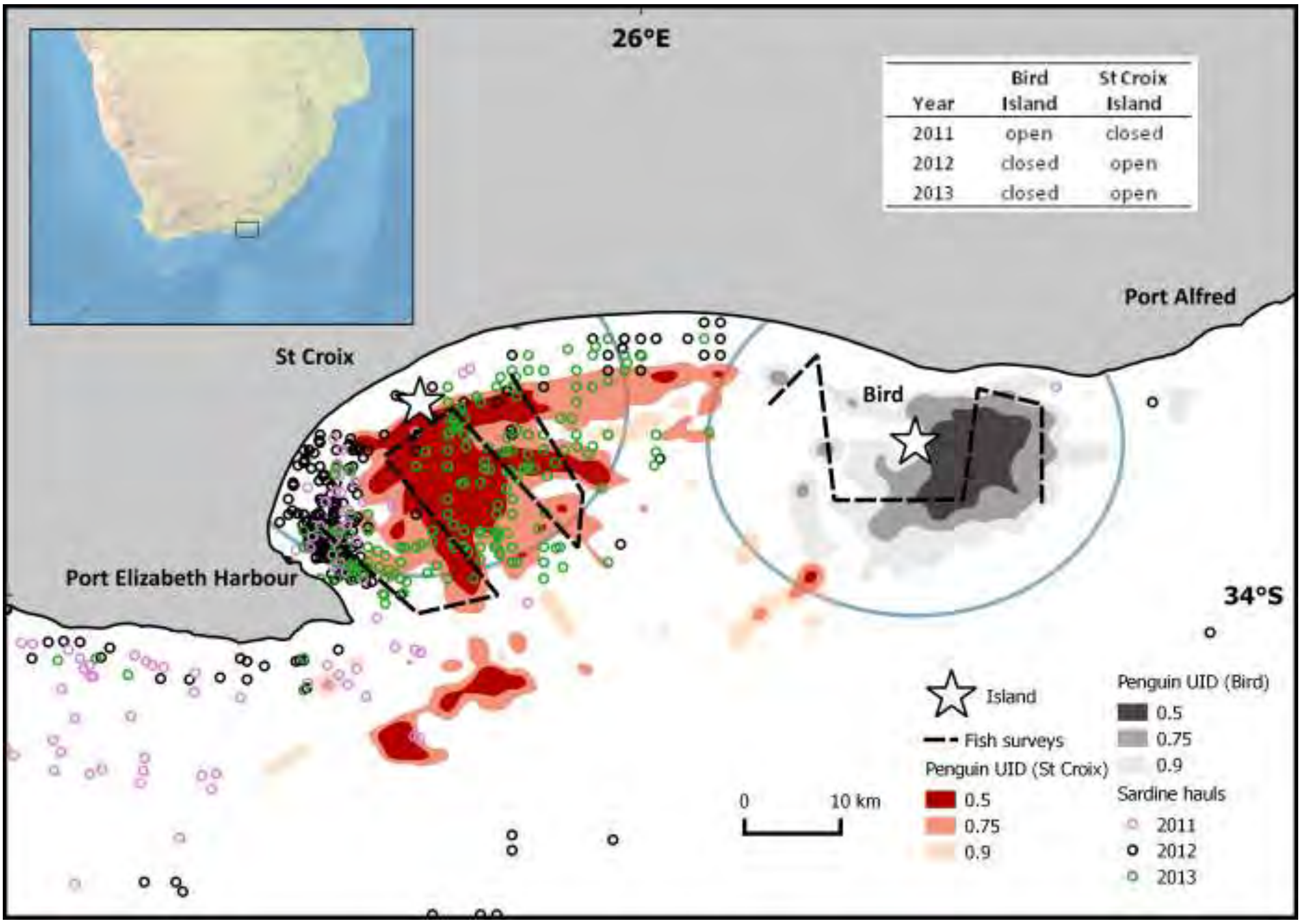
Table 5.3 Coefficients (β) and standard errors (se) of mixed effects models showing the influence of 30 day composites of chlorophyll a concentrations (chls30) and fishing catches, using three cumulative periods (30, 60, 90 days), as well as interactions of these variables, on the activity budgets of African Penguins. Coefficients from continuous variables represent standardised values, except for brood mass used as covariates for the responses: path distance and path duration.

	Penguin activity budgets								
	path distance β (se)			**path duration β (se)**			**max distance β (se)**		
Explanatory variables	**catch30**	**catch60**	**catch90**	**catch30**	**catch60**	**catch90**	**catch30**	**catch60**	**catch90**
chl30	-4.06 (4.58)	**-7.43** (1.82)***	**-10.37** (2.12)***	-2.82 (1.82)	-1.08 (0.96)	-1.23 (0.99)	0.12 (0.15)	0.04 (0.12)	-0.08 (0.10)
catch	4.49 (7.81)	1.42 (2.53)	-2.43 (1.79)	-3.76 (2.95)	-0.63 (1.14)	-0.73 (0.77)	0.25 (0.17)	0.12 (0.10)	0.01 (0.07)
sex (M)	-0.80 (3.65)	-0.99 (3.55)	-0.71 (3.59)	-0.96 (1.25)	-1.07 (1.24)	-1.09 (1.24)	0.01 (0.06)	0.01 (0.06)	0.01 (0.06)
brood mass	0.005 (0.003)	0.006 (0.003)	0.004 (0.003)	-0.002 (0.001)	-0.002 (0.001)	-0.002 (0.001)	**0.07** (0.03)*	0.06 (0.03)	0.06 (0.03)
chl30*catch	13.66 (9.80)	**10.84** (3.37)**	**6.71** (1.95)***	-3.55 (3.69)	0.79 (1.65)	1.03 (0.94)	**0.52** (0.21)*	**0.34** (0.16)*	0.14 (0.11)

*p<0.05, **p<0.01, ***p<0.001

Table 5.4 Model performance comparisons to test significance of interaction terms for African Penguin activity budget models. Tests are performed for each group which includes a comparison between the interaction effect and the equivalent model with the interaction removed. Terms: AIC - Akaike's Information Criteria, BIC - Bayesian Information Criteria, LogLik - log likelihood test.

Group	**Model**	**AIC**	**BIC**	**LogLik**	**χ^2**	**p**
1	maxdist~ chl30* catch30+sex+ brood mass	746	767.1	-365	4.7	**0.03**
1	maxdist~ chl30+ catch30+sex+ brood mass	748.7	767.2	-367.3	-	-
2	pathlength~ chl30* catch60+sex+brood mass	566.7	584.5	-275.3	10.5	**0.001**
2	pathlength~ chl30+ catch60+sex+brood mass	575.1	590.8	-280.6	-	-
3	maxdist~ chl30* catch60+sex+ brood mass	748.4	769.5	-366.2	4	**0.045**
3	maxdist~ chl30+ catch60+sex+ brood mass	750.4	768.9	-368.2	-	-
4	pathlength~ chl30* catch90+sex+brood mass	568.3	586.1	-276.1	11.5	**<0.001**
4	pathlength~ chl30+ catch90+sex+brood mass	577.7	593.4	-281.9	-	-



Year	Bird Island	St Croix Island
2011	open	closed
2012	closed	open
2013	closed	open

Figure 5.1 Study area showing locations of pelagic fish survey routes, location of sardine hauls and the utilisation distributions of African Penguins (quantiled kernels) calculated from GPS logger fixes from birds breeding on Bird and St Croix islands between 2011 and 2013. The temporary 20 km fishing exclusion zones are shown as blue circles. Table insert is fishing closure schedule for each island.

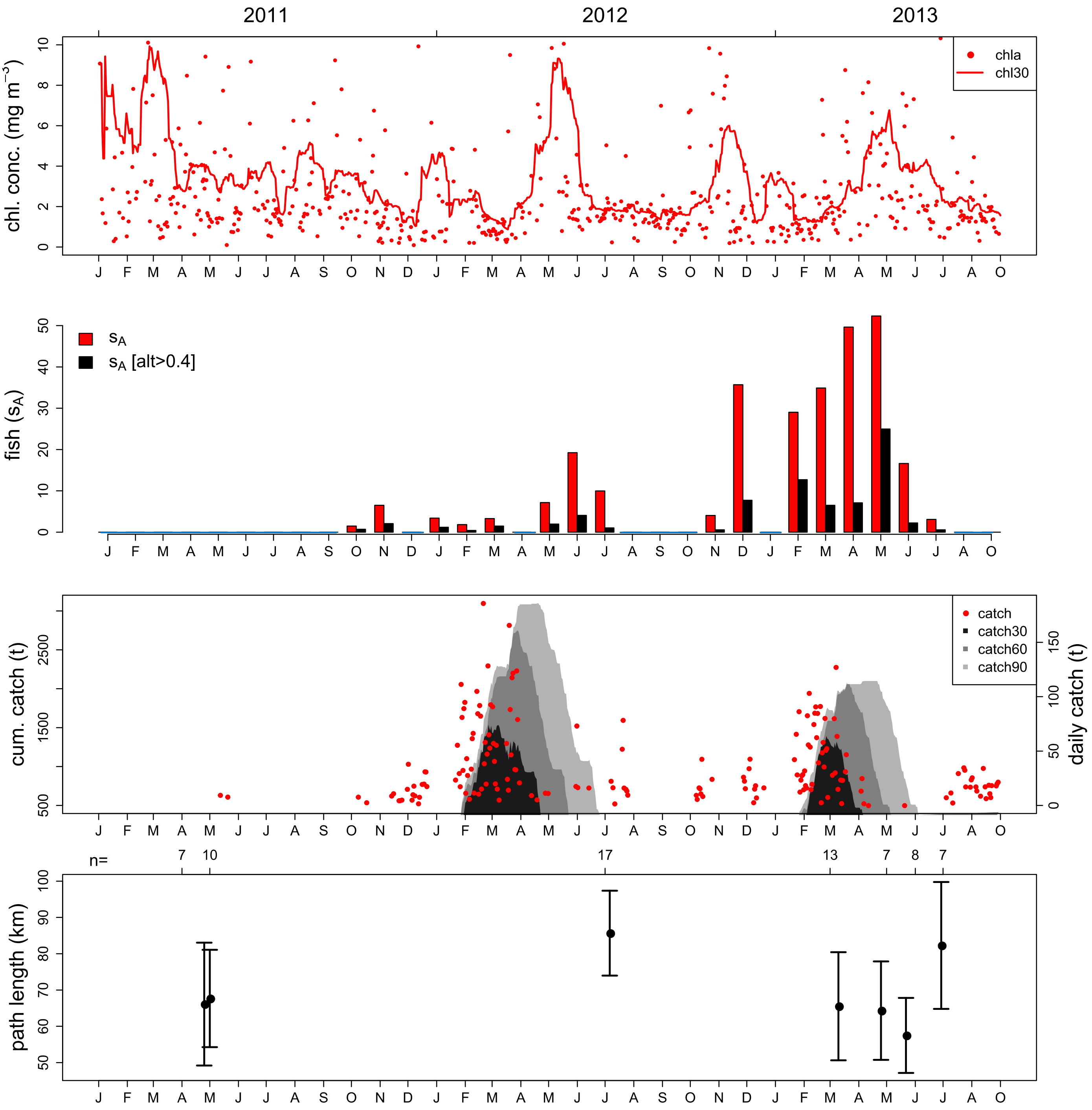


Figure 5.2 Time series of data used in the analyses for pelagic habitat around St Croix Island: a) oceanographic variables, chlorophyll a concentration and sea-surface temperature (SST) showing raw data (points) and 30-day composite rolling means; b) relative fish abundance using the nautical area scattering coefficient (s_A) for all pelagic schooling fish (s_A) and for targeted fish assemblages with altitude index values ≥ 0.4 (s_A [alt. ≥ 0.4]), blue lines represent no data; c) sardine catches within 20 km of St Croix Island showing all catches (points) and 1 - 3 month cumulative catches (catch30, catch60, catch90); d) one of three penguin foraging metrics used in the analyses, path length averaged over the month within which the birds were deployed (whiskers denote standard deviations and sample sizes are included on the top axis).

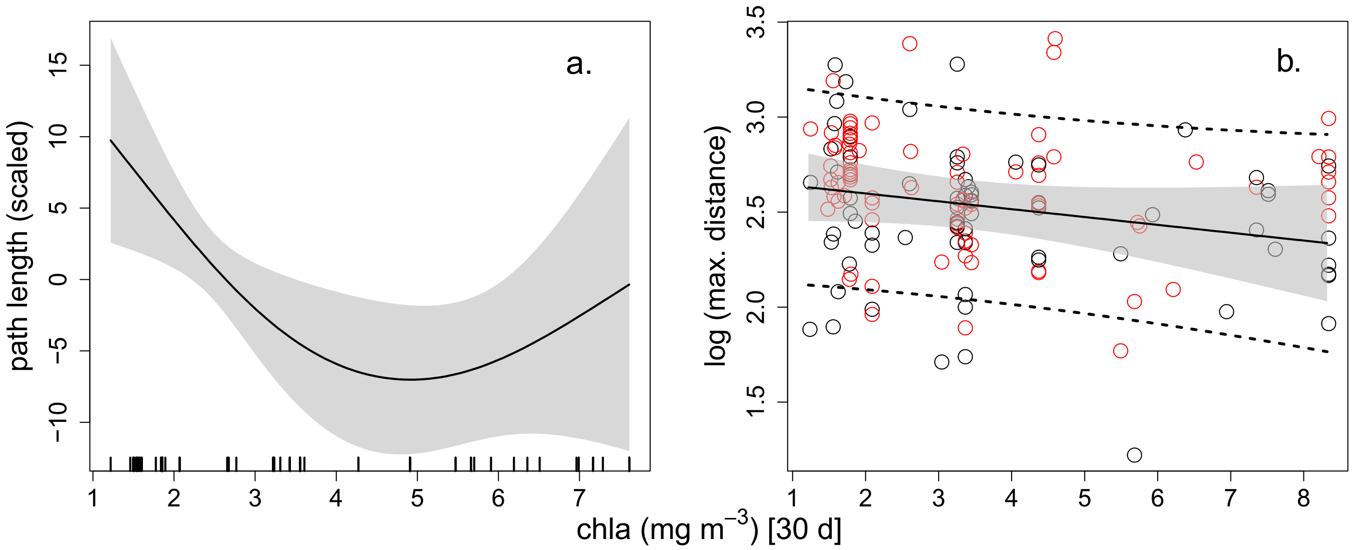


Figure 5.3 Mixed effects model outputs showing the influence of 30-day lagged composites of chlorophyll a concentrations on African Penguin foraging metrics around Bird Island: a) scaled foraging path length, and b) log transformed maximum distance travelled from colony for females (red) and males (black). Rug plots show sampling effort relative to the x-axis, shaded areas denote 95 % confidence intervals and hatched lines show influences of random effects.

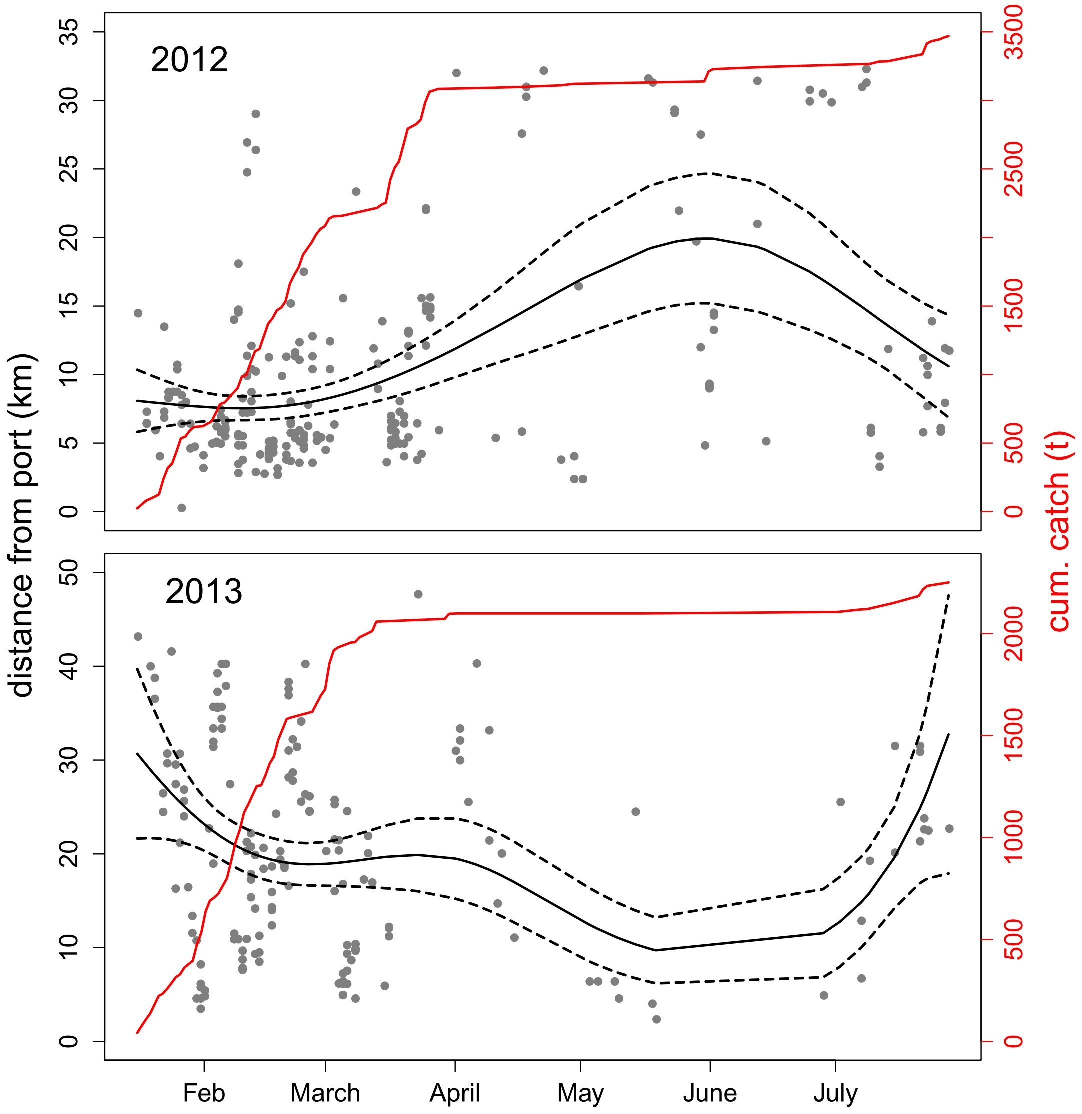


Figure 5.4 Time series of progressive distances of catch localities of purse-seine fishing vessels from Port Elizabeth Harbour throughout the most intensive fishing periods in 2012 and 2013. Overlaid to the raw data is the smoothed generalised additive model (GAM) predictions with hatched lines representing 95% confidence limits. Cumulative catches of sardine are shown as red lines.

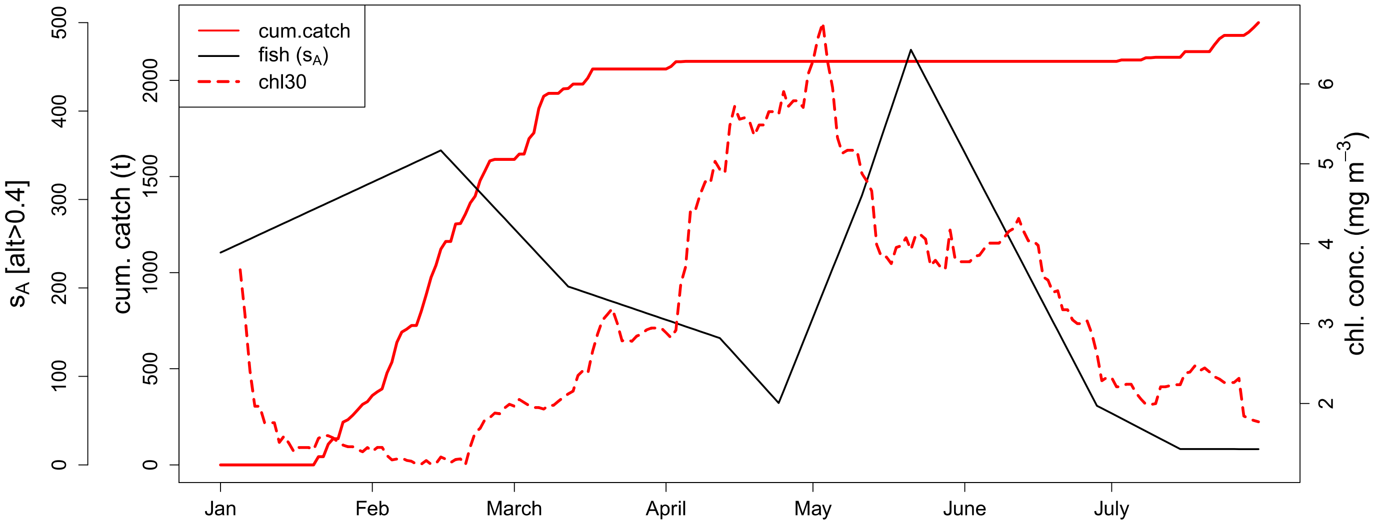


Figure 5.5 Time series of cumulative sardine catches (red line), acoustically determined fish abundance using the nautical area scattering coefficient (s_A) of pelagic fish schools recorded at mean altitude index values > 0.4 (black line), and 30-day composites of chlorophyll a concentrations (hatched red line) during 2013 around St Croix Island.

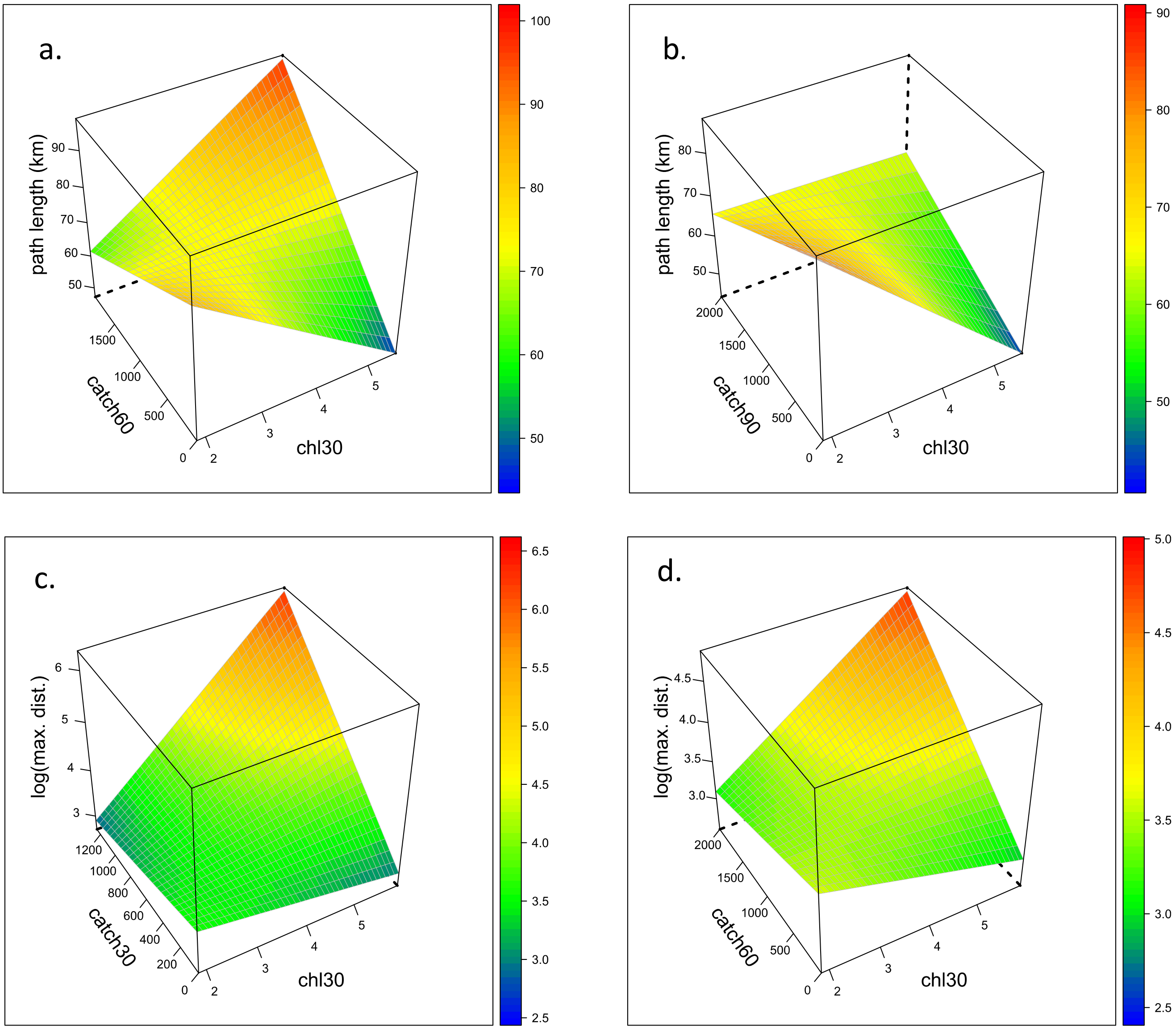


Figure 5.6 Interaction effects of cumulative purse-seine fish catches in tonnes and 30-day lagged composites of chlorophyll a concentration in mg m^{-3} (chl30) on predicted African Penguin foraging metrics around St Croix Island: a) path length at 60 days cumulative catches; b) path length at 90 days cumulative catches; c) log transformed maximum distance travelled at 30 days cumulative catches; and d) log transformed maximum distance travelled at 60 days cumulative catches. Predictions are from mixed effects models shown on the z-axis and the colour scale bar.

Chapter 6

Synthesis

Synthesis

Understanding interactions between top predators and their prey is a central theme in marine ecology studies. Due to the difficulty of observing these associations directly, technological advancements in acquiring information on predator movements and behaviour (Wilson et al. 2002; Cooke et al. 2004; Hays et al. 2016), the location and spatial distribution of their prey (MacLennan 1990; Misund 1997; Chu 2011) and the physical drivers of their environment (Kerr & Ostrovsky 2003; Turner et al. 2003) have assisted biologists in tapping into this relatively unexplored domain. These tools have enabled scientists to test hypotheses that, until relatively recently, have been unattainable by conventional methodologies. This thesis identified factors that influence the foraging ecology of African Penguins by utilising a combination of these tools and, where quantification of fish is concerned, developing these tools, to infer hitherto unknown aspects of the penguin's foraging ecology. The main motivation for this research was the African Penguin’s recent population decrease, which is believed to be related to local reductions in the availability of the penguin’s prey, small pelagic fish species (Crawford et al. 2011; Weller et al. 2014). The thesis is concerned with the fine-scale processes affecting the foraging performance of African Penguins during the breeding season, a crucial stage in the life-history of seabirds (Hamer et al. 2002). To accomplish this, I looked at predator-prey interactions in the context of bottom-up and top-down processes that are likely to limit the availability of prey to African Penguins in Algoa Bay, South Africa, a region that now holds approximately half the global population (Crawford et al. 2015). The results have shown important associations between small pelagic fish prey and the physical processes that influence their abundance and distribution. For the first time direct comparisons between the at-sea location and behaviour of African Penguins are compared to concurrent prey data. Results highlight the significance of the vertical distribution of prey to African Penguins and provide the first evidence for functional links between African Penguin foraging effort and prey abundance and availability. The final chapter draws on these findings to test if purse-seine fishing activities compete with African Penguins for the same prey resource and provides convincing evidence for competition around St Croix Island when fishing was permitted here during 2012 and 2013. The following account elaborates on these key findings and provides suggestions for future research to advance our understanding of the ecology of African Penguins and their prey. Finally, the application of these results to marine resource management are discussed with reference to an ecosystem approach to fisheries management.

Finding fish inexpensively

Applications of acoustic technologies to the marine environment include mapping benthic habitats (e.g. Anderson et al. 2008; Brown et al. 2011) and vegetation (e.g. Komatsu et al. 2003), measuring sediment processes (e.g. Thorne & Hanes 2002), and analysing the distribution, abundance and behaviour of zooplankton (e.g. Pieper & Holliday 1984; Holliday et al. 1989) and fish (reviews in Misund 1997 and Simmonds & MacLennan 2005). Since the 1930s, echo-sounders have been used extensively to locate fish for both commercial and scientific purposes (see history by Simmonds & MacLennan 2005). Given its economic importance, a large amount of work has gone into the determination of fish target strength (TS), an acoustically-calibrated representation of a species at different caudal lengths, and the translation of this value into mass. Advances in fishery science have been closely linked to improvements in acoustic technology from single beam devices through to dual- and, more recently, split beam echo-sounders and multi-beam sonars (Metcalfe et al. 2008; Chu 2011). Yet access to these technologies for non-fishery related applications have been limited due to the specialised nature of this science and have contributed to a paucity of dedicated fine-scale predator-prey interaction studies. As demonstrated in Chapter 2, recreational fish-finders (RFF) can be used to fill this void at a substantially reduced cost with relatively little expertise required. There are limitations to using this method, most notably the reduced dynamic range, which affects the ability to estimate school densities. Nevertheless, the calibration experiment conducted during this study showed that RFFs are effective in determining relative fish abundance, providing accurate estimates of school size and depth. Interestingly, the results of Chapter 4 highlight the significance of school depth to the distribution of foraging African Penguins as has been shown in the few studies that have used scientific echo-sounders to determine the predator-prey relationships of diving seabirds (Zamon et al. 1996; Boyd et al. 2015).

Notwithstanding their technological limitations, RFFs offer much promise for similar applications where budgetary and logistical constraints prevent detailed, longer-term predator-prey studies. The software FISH developed for this study has only been coded for the specific RFF used for this research but the source code has been published as open access to facilitate customisation to other systems. As with scientific echo-sounders, RFFs have undergone vast technological improvements in recent years. For instance, Compressed High-Intensity Radiated Pulse (CHIRP) technology enables multiple frequencies to be broadcast simultaneously, giving much improved resolution of echo-returns. It is likely that these systems will have superior dynamic range capabilities than the RFF used in this study and calibration of these systems with scientific echo-sounders is recommended. The versatility of these devices enables users to operate them on very small vessels, e.g. kayaks, with the potential to explore habitats inaccessible to larger vessels.

Physical drivers of the distribution and abundance of African Penguin prey

This thesis demonstrates the first associations between physical marine processes and the abundance and distribution of small pelagic fish in the Benguela region at spatio-temporal scales relevant to African Penguins. Chapter 3 highlights the significance of primary production on habitat for pelagic fish within 1-2 month lags. Although this influence was more apparent for Bird Island than St Croix, the negative relationship between African Penguin foraging path length and primary production under low levels of fishing pressure (Chapter 5) provide support for the hypothesis that these relationships were masked by purse-seine fishing activities around St Croix Island. Consequently, variation in primary productivity in Algoa Bay and ultimately the physical processes responsible for this variation appear to be key drivers of habitat suitability for foraging African Penguins.

The frequency and intensity of the underlying physical drivers of primary production observed during this study, i.e. wind-induced upwelling and large episodic meanders (LEM), are likely to play an increasingly significant role in moderating habitat suitability under the influences of global climate change phenomena (Lutjeharms & de Ruijter 1996; Sydeman et al. 2014). To improve our understanding of the potential effects of future climate changes on this ecosystem, it would be beneficial to analyse a longer time series of wind records and LEMs against African Penguin population indices to gauge the longer-term influences of these processes on African Penguins at a population level. Long-term count data at breeding colonies administered by the Department of Environmental Affairs can be used to facilitate this research. Any apparent trends coming from a study of this nature can then be used to forecast African Penguin population trajectories under various climate change scenarios.

Chapter 3 also demonstrated the significance of sea-surface temperature (SST) and associated water stratification in moderating the vertical distribution of fish prey around St Croix Island with positive correlations between fish school altitude and both stratification and SST, conditions typical of summer in this region (Goschen & Schumann 2011). An increase in sardine abundance due their preference for higher SSTs (Agenbag et al. 2003) was postulated as potential reason for these associations. This assumption is supported by the high incidence of sardine catches around St Croix Island during during 2012 and 2013 (Chapter 5). However, these results may have been exacerbated by localised depletion of sardine stocks due to fishing coinciding with winter conditions where SSTs decreased and stratification was suppressed. Hypothesised fishing effects on these relationships can be tested by comparing fish and oceanographic data collected from around St Croix Island during periods of reduced or absent fishing effort.

The African Penguin 'preyscape'

Prior to the 1980s, information on the at-sea behaviour of African Penguins was limited to knowledge derived from observations of penguins at-sea when there was no known means of observing entire tracks or diving behaviour (Siegfried et al. 1975). It wasn't until the seminal work by Wilson (1985a) using autoradiographic speed-distance and dive depth meters that we began to understand what penguins were doing throughout an entire foraging trip. Since this time, biotelemetry technologies have substantially improved our understanding of the distribution and foraging effort of African Penguins from different breeding colonies (Petersen et al. 2006a; Pichegru et al. 2010, 2012; van Eeden et al. 2016), and more recently, using satellite transmitter and GPS tags, information is available on the movements of non-breeding adults (Harding 2013, Roberts 2016) and fledglings (Sherley et al. 2013). Despite this improvement in our understanding, research on the prey field targeted by African Penguins has been limited to studies on diet (Randall 1983; Wilson 1985b; Randall & Randall 1986; Crawford et al. 2011) and inference from bite marks on fish prey (Wilson & Duffy 1986). My results provide the first simultaneous quantification of foraging African Penguins and their prey using both direct counts and concurrent logger deployment data. Few studies globally have contemporaneous data on prey and seabird movements (Hays et al. 2016) and this appears to be the first study to regularly quantify these interactions on multiple dates over more than one breeding season. Key findings of this analysis include the significance of the depth distribution of fish to African Penguins especially at fine-scales (0.5 km) with strong avoidance of areas with bottom dwelling fish (Chapter 4). This is likely a consequence of the hunting mode of African Penguins mainly attacking fish from below (Wilson & Duffy 1986) and potential limitations imposed on the detection of reflective prey, such as small pelagic fish. These hypotheses can be tested using bird-borne video recorders to quantify the frequency and approximate angles of head movements, relative to the approximate solar azimuth, during searching behaviour and modelling these variables as functions of subsequent prey detection probabilities. A study of this nature could also reveal the portion of the water column in which African Penguins are able to locate their prey in under a range of visibility conditions.

The research conducted in Chapter 4 to determine the locations of African Penguins at sea used two methods, count data from birds observed while conducting pelagic fish surveys and remotely acquired track data from bio-logged birds. The sampling period of these two datasets differed with penguin deployments only being achieved on a subset of fish survey days. The results of both sets of analyses were similar, highlighting the significance of the vertical distribution of fish to the at-sea distribution of penguins. However, an impediment to utilising counts of seabirds at-sea to infer predator-prey interactions is the lack of knowledge on the behavioural state of the species in question unless they are observed actively foraging. Many count-based studies classify birds on the sea-surface as representing foraging birds (e.g. Piatt 1990; Swartzman & Hunt 2000; Vlietstra 2005) and, as discussed in Chapter 4, this has the potential to bias the results by including potentially non-foraging birds, i.e. birds resting (Ropert-Coudert et al. 2004) or, for non-flighted species, birds commuting between sites, in these assessments (Hunt et al. 1996). The dataset collected as part of this research provides an opportunity to test potential biases associated with these different methodologies by comparing the results only from days when both methods were used. This may provide useful insights into potential limitations or validation of using either method in future predator-prey studies.

Functional links between African Penguin foraging effort and prey availability

Chapter 4 provides the first evidence for functional responses of African Penguin foraging effort to varying prey abundance estimates. This analysis was done for fish abundance estimated from all fish schools as well as for those prey assemblages targeted by penguins, showing the significance of the latter schools in influencing the duration of African Penguin foraging trips while provisioning chicks. This result emphasises the importance of resolving the specific characteristics of fish schools targeted when investigating these relationships with the potential for misleading results when including abundance estimates of all potential prey species. Measures of prey abundance have been shown to influence seabird activity budgets that are measured at the colony, e.g. nest attendance patterns (Litzow & Piatt 2003; Harding et al. 2007), but studies showing their influence on foraging effort, i.e. using path-derived descriptors or dive data, are less common (Bertrand et al. 2012; Hays et al. 2016). The influence of prey availability on differential path metrics has been inferred for studies that have compared the movements of *Spheniscus* penguins, including African Penguins, between different colonies (Radl & Culik 1999; Petersen et al. 2006b; Boersma & Rebstock 2009, Pichegru et al. 2010). The functional responses demonstrated for African Penguins during this study, i.e. related to penguin path duration and path length, lends support to the inferences suggested in these studies. However, each site is likely to have its own peculiarities, such as density-dependent effects, that may influence these hypothesised outcomes and it will be prudent to repeat the analyses, as conducted in this thesis, to test these assumptions for different penguin populations.

As discussed in Chapter 4, the lack of any exponential responses of African Penguin foraging effort to variances in prey abundance, as hypothesised by Cairns (1987), is likely an artefact of the limited sample of fish survey days used in this study. This is supported by the results of Chapter 5 when a larger sample of deployment days was used to assess the influence of primary productivity, as a proxy for prey abundance, on foraging effort and where the expected non-linear trend was apparent for penguin path length. A continuation of this research is therefore recommended to bolster the sampling effort so that more meaningful thresholds in prey abundance can be determined and applied to resource management initiatives.

Evidence for competition with fisheries

Competition between African Penguins and fisheries has long been suspected (Westphal & Rowan 1969) but the mechanisms underlying this competition have proved difficult to demonstrate (Duffy et al. 1987). Despite convincing circumstantial evidence to show the benefits of no-take zones to purse-seine fishing operations as formulated by the Island Closure Task Team (ICTT) (Pichegru et al. 2010, 2012; Sherley et al. 2015), the results of these experiments have been controversial owing, in part, to a lack of control for natural prey variability (Coetzee 2010; Cherry 2014). My research provides direct evidence for competition effects by this fishery on the foraging effort of African Penguins using primary production as a control for natural prey variability. Chapter 5 clearly shows the influences of cumulative catches under different oceanographic regimes with favourable conditions inducing increased penguin foraging effort. Evidence for fish depletion provides the causal mechanism driving increased foraging effort and the significantly reduced number of breeding attempts during 2012, when fishing pressure was at its peak, provides additional circumstantial evidence to support these claims. The results of this study compliment broader scale assessments of the negative impacts of industrial fisheries on fish stocks over large temporal scales (Pinsky & Byler 2015, Essington et al. 2015).

The evidence presented here provides strong motivation for the implementation of permanent no-take zones around African Penguin colonies both prior to and during the breeding season as long as the population remains depleted. A similar strategy to conserve North Sea populations of Black-legged Kittiwakes (*Risa tridactyla*) by preventing industrial fishing during periods of adverse lesser sandeel (*Ammodytes marinus*) abundance proved beneficial to the breeding success of these seabirds at the turn of the 20th century (Lewis et al. 2001, Frederiksen et al . 2004).

African Penguins included in an ecosystem-based management approach to fisheries

Growing evidence of the damaging impacts that traditional “single target species” approaches to fishery management are having on marine ecosystems (e.g. Worm et al. 2006) led to the exploration of alternatives centred on the ecosystem rather than economically viable stocks, so-called ecosystem-based management (EBM) (Garcia et al. 2003). EBM is a complex endeavour given the many inter-connected facets of both the ecological and socio-economic systems involved and associated obstacles to consensus and implementation (Garcia et al. 2003; Browman & Stergiou 2005). A global evaluation of progress in implementing EBM in fisheries revealed better performance by undeveloped countries, including South Africa and Peru, than many developed countries but overall poor levels of implementation amongst most countries assessed (Pitcher et al. 2009). Limitations in adopting this approach include the identification of suitable ecological indicators, the formulation of defensible methods to monitor and interpret these indicators, and the budgetary and logistical constraints linked to such operations. Examples of ecological indicators include top predator species, such as seabirds, which can provide useful insights into the state of marine ecosystems and can be useful proxies to gauge impacts of commercial fishing on marine systems (Crawford et al. 2006; Furness 2007; Bertrand et al. 2012; Pichegru et al. 2012). Quantification of specific indices to measure the response of indicator species to environmental fluctuations includes population censuses, breeding success parameters and activity budgets. However, determining influences of fishing on survival indices is often conjectural if there is no control for natural variation in the food base (Einoder 2009). My results provide support for using African Penguins as indicators of small pelagic fish abundance in the southern Benguela ecosystem and, potentially, other marine top predators that feed on these prey. The results of this thesis demonstrate functional relationships between measures of African Penguin foraging effort and the abundance of small pelagic fish, how these pelagic fish are influenced by natural physical processes, and how competition with fisheries impacts the performance of African Penguins at sea. This provides a unique framework to guide implementation of a long-term monitoring programme of this species where near real-time calibrated responses of African Penguin foraging effort and prevailing oceanographic conditions can be used to flag periods of adverse conditions and adapt the spatial management of resource extraction accordingly. One way of potentially achieving this would be to calibrate colony based activity budgets (e.g. nest attendance patterns) with the same functional responses used in this thesis, i.e. at-sea path metrics. The monitoring of nest attendance patterns can be done remotely (Rishworth et al. 2014) with pit tag transponders which are currently being used to monitor African Penguin population demographics. A project of this nature would need the support of local and regional resource management authorities who are currently mandated to align their policies and practices with the principles of an ecosystem centred approach to the management of marine resources (Shannon et al. 2006).

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