HAL open science

Small pelagic fish responses to fine-scale oceanographic conditions: implications for the endangered African penguin

Alistair M. Mcinnes, Peter G. Ryan, Miguel Lacerda, Julie Deshayes, Wayne S. Goschen, Lorien Pichegru

To cite this version:

Alistair M. Mcinnes, Peter G. Ryan, Miguel Lacerda, Julie Deshayes, Wayne S. Goschen, et al.. Small pelagic fish responses to fine-scale oceanographic conditions: implications for the endangered African penguin. Marine Ecology Progress Series, 2017, 569, pp.187-203. 10.3354/meps12089 . hal-01630751

HAL Id: hal-01630751

https://hal.science/hal-01630751v1

Submitted on 30 Dec 2023

HAL is a multi-disciplinary open access archive for the deposit and dissemination of scientific research documents, whether they are published or not. The documents may come from teaching and research institutions in France or abroad, or from public or private research centers.

L'archive ouverte pluridisciplinaire **HAL**, est destinée au dépôt et à la diffusion de documents scientifiques de niveau recherche, publiés ou non, émanant des établissements d'enseignement et de recherche français ou étrangers, des laboratoires publics ou privés.

Distributed under a Creative Commons Attribution 4.0 International License

Vol. 569: 187–203, 2017
https://doi.org/10.3354/meps12089

MARINE ECOLOGY PROGRESS SERIES
Mar Ecol Prog Ser

Published April 7

Small pelagic fish responses to fine-scale oceanographic conditions: implications for the endangered African penguin

Alistair M. McInnes[1,*], Peter G. Ryan[1], Miguel Lacerda[2], Julie Deshayes[3], Wayne S. Goschen[4,5], Lorien Pichegru[1,5,6]

[1]DST-NRF Centre of Excellence at the Percy FitzPatrick Institute of African Ornithology, University of Cape Town, Rondebosch 7701, South Africa
[2]Department of Statistical Sciences, University of Cape Town, Rondebosch 7701, South Africa
[3]Sorbonne Universités (UPMC Universités Paris 06) CNRS-IRD-MNHN, Laboratoire LOCEAN/IPSL, Paris 75005, France
[4]South African Environmental Observation Network (SAEON), Elwandle Coastal Node, Port Elizabeth 6031, South Africa
[5]Institute for Coastal and Marine Research, Nelson Mandela Metropolitan University, Summerstrand 6031, South Africa
[6]Department of Zoology, Nelson Mandela Metropolitan University, Summerstrand 6031, South Africa

ABSTRACT: Small pelagic fish play a significant role in regulating the foraging activities and population trends of marine top predators in upwelling ecosystems, yet there is little information on oceanographic drivers of fish assemblages at temporal and spatial scales relevant to their predators. The survival of the Endangered African penguin *Spheniscus demersus* is closely linked to the availability of pelagic fish prey. This study assesses the influence of oceanographic variables on the spatio-temporal dynamics of pelagic fish in Algoa Bay, South Africa, where half of the world population of African penguins breed on 2 islands, St Croix and Bird. Using small-scale acoustic surveys and an array of underwater oceanographic data recorders spread across the bay during 3 yr, we reveal the complex and variable nature of this system, with fish responding differently to physical processes around each island. Chlorophyll *a* concentrations were good predictors of relative fish abundance around Bird Island but had little influence around St Croix Island, possibly due to the masking effect of purse-seine fishing around this site. The horizontal distribution of fish schools around Bird Island was more aggregated under upwelling conditions (cooler sea surface temperatures) and the vertical distribution of fish around both islands was strongly influenced by stratification and mean temperatures. Mechanistic drivers of upwelling included northeasterly winds and offshore Natal pulses, both of which are predicted to have an increasingly more significant effect on the suitability of habitat for pelagic fish and associated predators under the influences of climate change and industrial fishing.

KEY WORDS: Marine top predators · Schooling fish · Oceanographic processes · Acoustic surveys · *Spheniscus demersus* · Benguela upwelling · Predator–prey interaction · Algoa Bay

Resale or republication not permitted without written consent of the publisher

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 seabirds and marine mammals, 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 typically have quantified these relationships at broad geographic scales (Agenbag et al. 2003, Palomera et al.

*Corresponding author: amcinnes3@gmail.com

© Inter-Research 2017 · www.int-res.com

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 small pelagic fish species, which contributed 19% of global marine and freshwater fishery catches by mass in 2012 (FAO 2014), and the need to investigate causes of population-level variability. Studies of the interactions between physical processes and small pelagic fish at finer spatiotemporal 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 local variations in prey abundance. Top predators include seabird species endemic to these upwelling areas that have undergone significant decreases in their populations over the last few decades and have therefore become the focus of research to determine 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 4 major eastern-boundary upwelling ecosystems globally (Chavez & Messié 2009). Three threatened seabird species endemic to the BUR are largely reliant on small pelagic fish species for their survival: Cape gannet *Morus capensis*, Cape cormorant *Phalacrocorax capensis* and African penguin *Spheniscus demersus* (Crawford & Jahncke 1999). These species differ in terms of their foraging ranges, with the African penguin, the only non-flighted species, having the most limited foraging 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' (BirdLife International 2016) following a >60% decrease in its population during the first decade of the 21st century, which is believed to be largely driven by local decreases in the availability of their principal prey, anchovy *Engraulis encrasicolus* and sardine *Sardinops sagax* (Crawford et al. 2011, Sherley et al. 2013, Weller et al. 2014). Understanding the natural variability in the availability of these prey species 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. These include spatial scales that incorporate their mean foraging range during the breeding season, <45 km (Petersen et al. 2006, Pichegru et al. 2012), and at temporal frequencies that can potentially signal variation in processes aligned to the penguin's phenology, notably periods leading up to and including the breeding season. Determining biophysical associations at these scales is crucial to informing 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, on the St Croix and Bird island groups, which together are home to >50% of the global population (Crawford et al. 2014). During their breeding season (February–August), adult penguins from Algoa Bay mostly forage within 32 km of their colonies where they predominantly dive to depths between 22 and 34 m with a maximum recorded dive depth of 93 m (Pichegru et al. 2012, 2013). The distribution of African penguins during the non-breeding season has only been assessed for penguins caught on Bird Island and was found to be surprisingly similar to breeding birds, i.e. mostly recorded within 35 km of the island (Harding 2013). Diet samples of breeding penguins provisioning chicks showed that the majority of prey consumed (>82% by mass) constituted 3 small pelagic fish species: anchovy (56–97%), sardine (5–23%) and redeye *Etrumeus whiteheadi* (5%) (Randall & Randall 1986, Pichegru et al. 2012). More recently, chokka squid *Loligo reynaudii* has been identified as an important self-provisioning prey item for African penguins in this region (Connan et al. 2016). The bay also supports the largest breeding colony of gannets globally (Crawford et al. 2007) and large numbers of Indo-Pacific bottlenose dolphins *Tursiops aduncus* (Reisinger & Karczmarski 2010), both of which largely feed on small pelagic fish.

Algoa Bay is influenced by a diverse array of physical processes that influence productivity, including frequent, short-term (3–7 d) wind-induced upwelling associated with northeasterly winds during summer (Schumann et al. 1982, 2005, Goschen & Schumann 2011, 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 (averaging 2 events per year) but more persistent (10–40 d) and widespread upwelling events associated with 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. Stratification predominantly occurs during summer, with the thermocline situated at 20–30 m, while a well-mixed water column typically occurs during winter (Goschen 1991, Goschen &

Schumann 2011). Bird and St Croix islands are situated at opposite ends of the Bay, and thus often experience contrasting oceanographic conditions.

This study assesses the extent to which oceanographic factors influence forage fish assemblages at a response scale relevant to African penguin foraging activity and hence, potentially, their survival. To achieve this, both *in situ* sea temperature and wind data, and satellite-derived sea surface temperature (SST) and chlorophyll *a* (chl *a*) concentrations are compared to acoustic-derived pelagic fish survey data in the core foraging ranges of African penguins from the Bird and St Croix island groups. We examine fish parameters that are known to influence predator responses: relative fish abundance (Cairns 1987, Piatt 1990, Cury et al. 2011), spatial co-location of schools (i.e. clustered versus dispersed school aggregations) (Wilson 1985, Fauchald 2009) and vertical distribution (Zamon et al. 1996, Boyd et al. 2015). Oceanographic data include indicators of primary production and vertical thermal structure (i.e. SST, profiled temperature data and thermal stratification), 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). Two sets of models are used: the first uses all fish aggregated for each survey, and the second uses measurements of individual schools to gauge the influence of environmental processes on the variability of different school attributes. The influences of mechanistic forces, i.e. wind and mesoscale offshore processes, on proxies for primary production, i.e. chl *a* concentrations and SSTs, are investigated to better understand the underlying drivers of productivity within the context of pelagic fish habitat in this region. The outcomes of these analyses are assessed in terms of their relevance to the current biogeographical location of Algoa Bay, i.e. at the eastern range limit of many BUR endemics, and the significance this may have on future changes to this system.

METHODS

Oceanographic data

SST and chl *a* data were obtained from the NASA ocean colour group's Moderate Resolution Imaging Spectroradiometer (MODIS) satellite array, quantified into 1 × 1 km grid cells and extracted for the period October 2011 to July 2013. These data were sampled over a 20 km radius around each island group (excluding land areas) to encompass the full extent of the acoustic survey routes (Fig. 1). Due to spatially incomplete datasets on days with cloud cover, 30 d mean composite spans were used to ensure adequate coverage of the study area: hereafter denoted as SST30 and CHL30. SST30 was used as an indication of upwelling intensity and CHL30 as a proxy for primary production. The lag times associ-

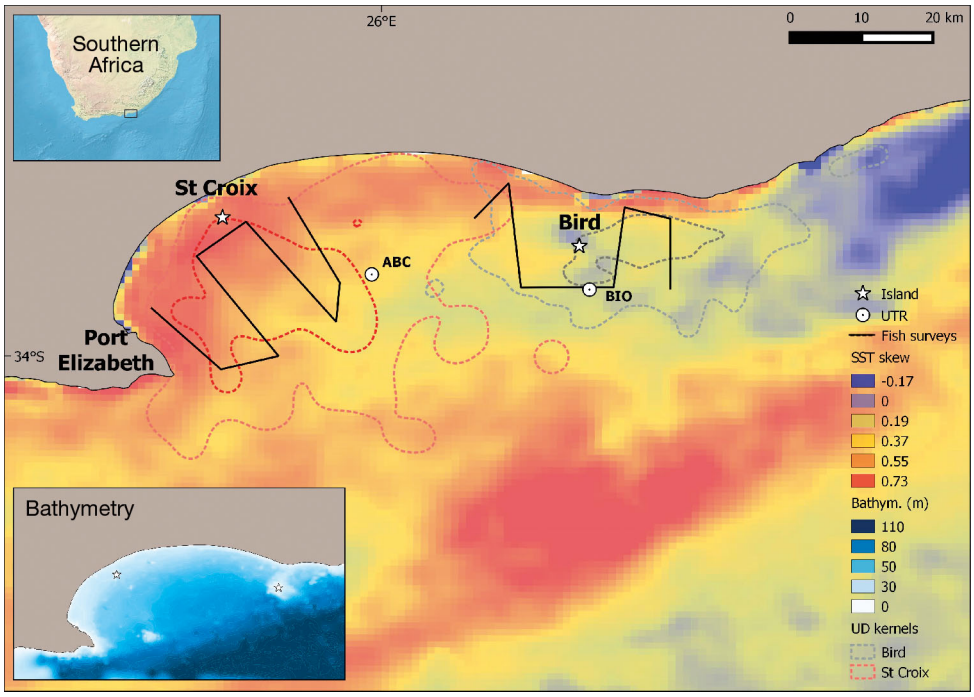

Fig. 1. Study area in Algoa Bay showing locations of fish survey transects around St Croix and Bird islands, and underwater temperature recorders (UTRs) (ABC, Algoa Bay Central; BIO, Bird Island Offshore). Colours show sea surface temperature skewness (SST skew) (3 yr composite: 2011–2013) with prominent upwelling regions appearing in blue. Dotted lines: 50% (dark shades) and 95% (light shades) utilisation distribution kernels of African penguins from St Croix Island (red) and Bird Island (blue) extracted from data used in Pichegru et al. (2012)

ated with trophic exchanges from upwelling to zooplankton production have been estimated at 10–15 d based on modelled simulations for the BUR (Moloney 1992). As refined estimates of these lag times have not been determined for the Algoa Bay region, it is possible that the selected composite span of 30 d may have incorporated more than one productivity event and, for the purposes of this study, is therefore regarded as a cumulative index of productivity.

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 2 UTR moorings maintained by the South African Environmental Observation Network (SAEON): Algoa Bay Central (ABC, maximum depth = 55 m, 5 × 10 m intervals, 1 × 5 m interval) and Bird Island Offshore (BIO, maximum depth = 70 m, 10 m intervals) (Fig. 1), selected because of their proximity to our fish survey routes. Two metrics were calculated from the UTR data: mean temperature (depth averaged temperature at 12:00 h) and thermal stratification (calculated as the standard deviation of temperature in the upper 30 m following Boyd et al. (1992), also at 12:00 h), which is an effective index of thermocline strength (Fiedler 2010). Mean temperature was included to account for thermal tolerance levels of forage fish (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 chl *a* and associated primary and secondary trophic processes 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.

Wind direction and speed data were provided at 14:00 h daily for 2 South African Weather Service (SAWS) recording stations located at Bird Island and Port Elizabeth Harbour. Wind direction was classified into 2 bearing ranges based on the predominant directions: northeasterly winds (bearing range: 11–79°) are responsible for upwelling, and southwesterly winds (bearing range: 191–259°) for mixing in the bay. For the comparative time-series plots, a 14 d running mean was calculated on wind speeds for both directional bins.

To facilitate a visual assessment of the distribution of potential upwelling areas around the 2 penguin breeding colonies during the study period, SST skewness was calculated over the greater regional expanse of Algoa Bay for 3 yr, commencing in 2011. This was done by, first, calculating a 2 wk running mean for each 1 × 1 km grid cell, and, second, 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 Bird and St Croix islands between October 2011 and July 2013. We used a Furuno DFF3 recreational fish-finder with a transom-mounted 200 kHz transducer operating at a variable ping rate between 4 and 10 s^{-1} and using a 3 dB beam angle of 11°. Surveys were conducted on a 7.6 m catamaran ski boat at 7 knots along transects traversing the known foraging ranges of African penguins (Pichegru et al. 2010, 2012, Fig. 1), at seabed 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 07:00 and 16:00 h.

Echo returns were processed using Fish-finder Image Segmentation Helper (FISH) software (McInnes et al. 2015). Aggregation rules and the minimum size classification for pelagic fish schools followed Coetzee (2000) and Lawson et al. (2001): a minimum linking ellipse of 10 × 2 m (length × height) was chosen as the aggregator and an aggregated school area of 10 × 5 m (length × height) was chosen as the minimum school size. A correction factor was applied to the density estimates of each school, the mean backscattering coefficients ($\overline{s_v}$), to correct for oversaturation following the methods described in McInnes et al. (2015) using the scenario 2 regression equation:

$$y = 10^{-5.59+102300x} \quad (1)$$

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

Relative pelagic fish abundance was determined using 2 metrics. First, 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:

$$s_A = 4\pi(1852)^2 s_a \quad (2)$$

where $4\pi(1852)^2$ is the nautical mile-derived scaling factor and s_a is the integral of the mean backscattering coefficients ($\overline{s_v}$) 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. Second, for assessing the influence of individual school biomass, total volumetric abundance (TVA, kg) was calculated as:

$$\mathrm{TVA} = 10^{\frac{S_v - \mathrm{TS_a}}{10}} \times V \quad (3)$$

where S_v is the mean volume backscattering strength, $\mathrm{TS_a}$ 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 target strength 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 was the most common size class measured from penguin diet samples collected in 2012 and 2013 (A. M. McInnes & L. Pichegru unpubl. data).

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 survey routes; higher values indicate more aggregated spatial patterns whereas lower values indicate more dispersed 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 1 approaching the sea surface and values close to 0 indicating fish near the seabed. The selection of this relative index of vertical distribution was motivated by its potential to distinguish between the 3 dominant small pelagic fish species in Algoa Bay and, in particular, to distinguish the more benthic redeye from the more pelagic species, anchovy and sardine (Lawson et al. 2001); anchovy and sardine are targeted the most by African penguins in this region (Randall & Randall 1986, Pichegru et al. 2012). For survey-level models, this metric was aggregated over all schools using the mean altitude index (MAI). Data associated with survey locations that had broken or absent seabeds in the echo returns were removed from analyses that used AI as a response variable.

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: (1) MAI, (2) S_v as a measure of school density, and (3) school cross-sectional area from the DAFF spawner biomass surveys conducted during November of each year between 2010 and 2014 (DAFF unpubl 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 3 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 08:00 and 16:00 h.

Aggregated (survey level) biophysical models

The purpose of these models was to gauge the influence of oceanographic variables on aggregated fish parameters at the approximate scale of African penguin foraging ranges around each site. We considered the influence of mean temperature, stratification, SST30 and CHL30 on 3 fish variables: relative fish abundance (s_A), FDI and MAI for surveys around each penguin breeding island modelled separately. The response variables in each of these models comprised 1 aggregated metric per survey with lagged explanatory variables being aggregated in the 30 d period before each survey date. We initially used generalised additive models (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 as a generalised linear model (GLM). Depending on the nature of the response variable and the model diagnostic outputs, 1 of 2 error distributions was used: a gamma distribution with a log link function was used for continuous, positive-value responses that were skewed to the right, and a Gaussian distribution with an identity link function was used for symmetrically distributed responses (either on the original or log-transformed scale). For models including satellite-derived data (SST30 and CHL30) where the explanatory variable was a composite of 30 d, we weighted the observations in the regression model by the frequency of data points for each satellite-derived sample. Periods with better coverage (i.e. less cloud cover) therefore had a stronger influence on the relationship between these variables and the response. All computations were carried out in R (R Core Team 2015). The 'mgcv' package (Wood 2006) was used to fit the GAMs. Penalised regression splines were employed as smoothing functions and generalised cross-validation was used to determine the degree of smoothness. Goodness-of-fit statistics for GLM models were calculated using maximum likelihood pseudo R^2 values with the 'pscl' package (Jackman

2015). To explore potential density-dependent influences on fish dispersal, we applied the same modelling protocol to assess the relationship between s_A and FDI for data from each island.

Disaggregated (school level) biophysical models

Disaggregated models were fitted to examine the response of individual fish school characteristics to oceanographic variables to explore the variation underlying these associations. Mixed-effects models were used to assess the relative significance of oceanographic and temporal variables on 2 responses using pelagic fish school data, specifically TVA, as an indication of school biomass, and AI. The following oceanographic covariates were used: CHL30, SST30, stratification and mean temperature. Temporal covariates included year and season (summer: October–April; winter: May–September) to control for possible annual and seasonal variation, and survey date was included as a random effect. All models were run for each island separately. As with the modelling protocol adopted for the aggregated models, we initially explored the potential for non-linear relationships using generalised additive mixed-effects models (GAMM) and, if linear relationships were evident, resorted to either generalised linear mixed effects (GLMM) or linear mixed effects (LMM) models. For the GLMMs and GAMMS, a gamma error distribution with a log link function was employed when the response was skewed, otherwise a Gaussian distribution with an identity link was specified (after applying a log transformation to the response where necessary). Akaike's information criterion (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 the 'mgcv' package for the GAMMs and the 'lme4' package (Bates et al. 2015) for the GLMMs and LMMs.

Mechanistic drivers of primary production

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

Upwelling events associated with Natal pulses were identified by a decrease in average bottom temperatures over 7 d or more (Goschen et al. 2015). The UTR data from Algoa Bay Central at the 50 and 55 m depth gauges were used to signal the initial stages of these events. Visual inspection of daily SST satellite images (MODIS) over these flagged periods was used to confirm these events.

RESULTS

Fish surveys and school characteristics

A total of 36 acoustic fish surveys were conducted in Algoa Bay between October 2011 and July 2013: 18 surveys each around Bird (mean ± SD survey length: 64.4 ± 6.6 km) and St Croix islands (85.5 ± 15.2 km) (Table S1 in the Supplement at www.int-res.com/articles/suppl/m569p187_supp.pdf). Relative fish abundance (s_A) was consistently greater around Bird Island (median ± interquartile 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 (MAI ± 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 significant difference in FDI 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 Fig. 2. Most (68%) fish aggregations comprised more than 1 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).

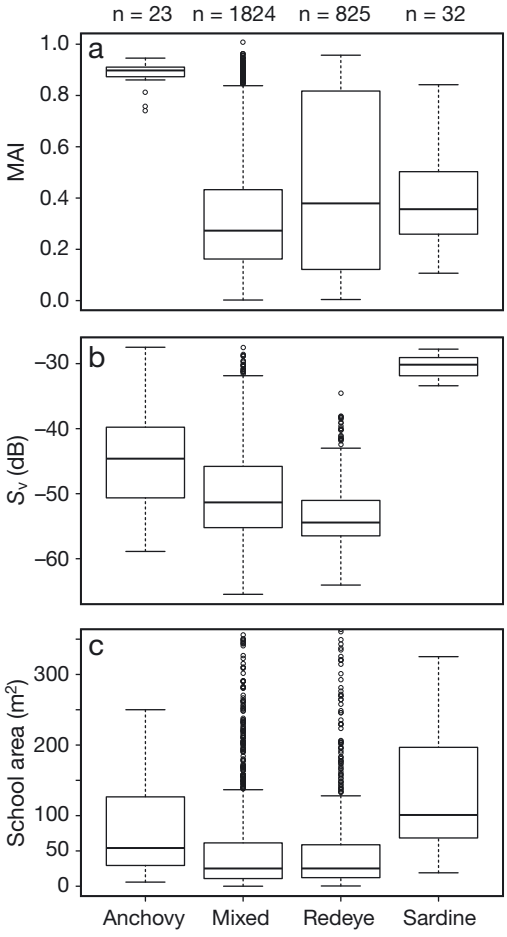

Fig. 2. Boxplots showing medians and interquartile ranges of 3 forage fish school parameters. (a) Mean school altitude index (MAI), (b) mean school density using volume backscattering strength (S_v) and (c) school cross-sectional area for 4 fish school categories: anchovy only, mixed species schools, redeye only and sardine only. Results are from the Department of Agriculture, Forestry and Fisheries (DAFF) spawner biomass survey data collected between 2010 and 2014 in Algoa Bay

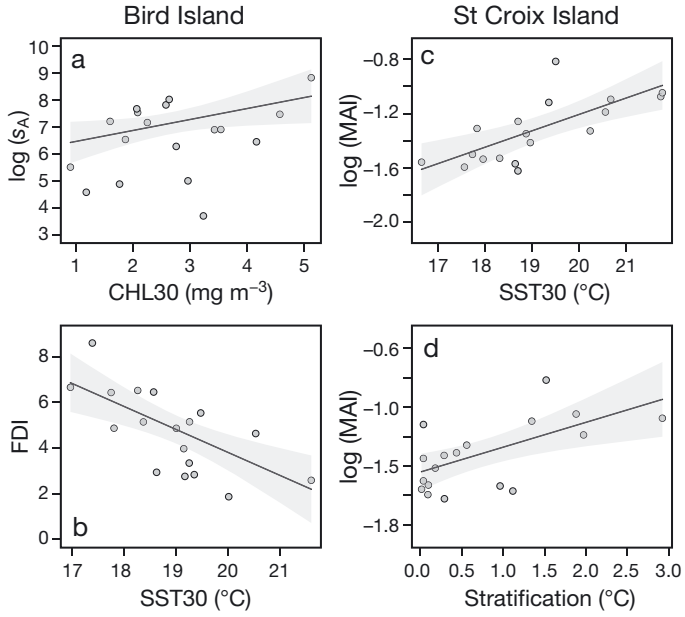

Fig. 3. Model outputs comparing relationships between aggregated fish data (by survey) and oceanographic variables for surveys conducted around Bird and St Croix islands. (a) Relative fish abundance using the nautical area scattering coefficient (s_A) versus chlorophyll *a* concentration composite over a 30 d lag period (CHL30). (b) Fish dispersal index (FDI) versus sea surface temperature composite over a 30 d lag period (SST30). (c) Log-transformed mean altitude index (MAI) versus SST30. (d) Log(MAI) versus thermal stratification (SD of temperature within the upper 30 m). Shaded areas denote 95% confidence intervals

Aggregated (survey level) biophysical models

All smoothing terms in the initial GAM outputs for the biophysical models approximated linear relationships and these models were therefore refitted as GLMs. There was a significant positive correlation between CHL30 and s_A around Bird Island (Fig. 3a), explaining 18% of the variation in fish abundance at this site (Table 1). However, CHL30 did not have a strong influence on s_A around St Croix Island. Neither SST30, water stratification nor mean temperature had much effect on s_A around either island (Table 1).

While there was little influence of oceanographic variables on fish dispersal around St Croix Island, there was a strong negative correlation between FDI and SST30 around Bird Island, with cooler SSTs coinciding with increased fish aggregation (high FDI values; SST explained 46% of variation in FDI at this site; Fig. 3b). There was a strong positive correlation between FDI and relative fish abundance up to ca. 1000 m^2 nmi^{-2} around both sites, with fish generally being more dispersed when fish were less abundant (Fig. 4a,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} (Fig. 4b). These disparities between sites are likely due to the relatively low s_A values recorded around St Croix Island, with the highest s_A estimated at 1142 m^2 nmi^{-2} during April 2013 at this site, compared with Bird Island, which had a maximum of 6803 m^2 nmi^{-2} recorded during May 2012 (Table S1 in the Supplement).

The MAI did not vary with oceanographic conditions around Bird Island, although both SST30 and stratification had positive influences on MAI around St Croix Island (Fig. 3c,d) explaining 51 and 38% of variation, respectively (Table 1). SST30 and stratifi-

Table 1. Model outputs for aggregated pelagic fish school data (by survey) and the influence of oceanographic explanatory variables using generalised linear models (GLM) and linear regression models (LM). Coefficients (β) and standard errors (SE) are given for the following variables: CHL30, chlorophyll *a* composite over 30 d lag; SST30, sea surface temperature composite over 30 d lag; strat, stratification (SD of temperature within the upper 30 m); mtemp, mean temperature through the water column. Bold outputs denote significant outcomes at the 5% level. ***p < 0.001, **p < 0.01, *p < 0.05

Explanatory variables	Response variables								
	s_A			FDI			MAI		
	Model	β (SE)	R^2	Model	β (SE)	R^2	Model	β (SE)	R^2
Bird Island									
CHL30	GLM	**0.41** (0.19)*	0.18	LM	0.29 (0.39)	0.03	LM	−0.003 (0.01)	0.01
SST30	GLM	−0.27 (0.21)	0.08	LM	**−1.00** (0.27)**	0.46	LM	0.01 (0.01)	0.08
strat	GLM	−0.39 (0.47)	0.04	LM	−0.44 (0.77)	0.02	LM	−0.004 (0.03)	0.002
mtemp	GLM	0.25 (0.13)	0.17	LM	−0.11 (0.25)	0.01	LM	0.01 (0.01)	0.08
St Croix Island									
CHL30	GLM	0.02 (0.11)	0	GLM	−0.06 (0.05)	0.07	GLM	−0.02 (0.04)	0.02
SST30	GLM	0.10 (0.13)	0.02	GLM	0.09 (0.06)	0.11	GLM	**0.12** (0.03)**	0.51
strat	GLM	−0.18 (0.25)	0.02	GLM	0.07 (0.12)	0.02	GLM	**0.17** (0.06)**	0.38
mtemp	GLM	−0.12 (0.14)	0.05	GLM	−0.08 (0.07)	0.07	GLM	−0.06 (0.04)	0.14

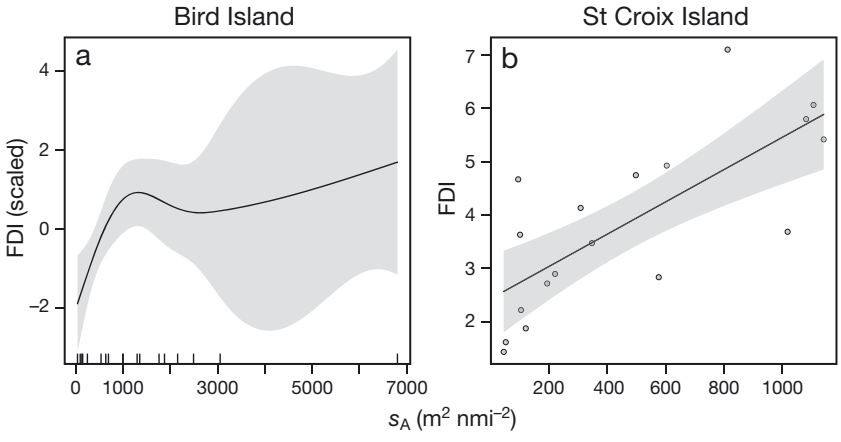

Fig. 4. Influences of relative fish abundance (s_A) on fish dispersal index (FDI) for fish recorded around (a) Bird and (b) St Croix islands. High FDI values indicate school clustering. For Bird Island, a generalised additive model was used with the rug plot denoting the sample effort. For St Croix Island, a linear regression was used. Shaded areas denote 95% confidence intervals

cation 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 SST30 and stratification increased.

Disaggregated (school level) biophysical models

For biophysical models using school biomass (TVA) as a response, we used a total of 2807 and 2591 pelagic fish schools recorded around Bird and St Croix islands, respectively. The best-fitting model for TVA around Bird Island only included CHL30, which positively influenced fish school biomass (Table 2, Fig. 5a). For St Croix Island, only SST30 was included in the best-fitting model, which was positively correlated to fish school biomass (Table 2, Fig. 5b).

The sample of schools recorded off Bird Island was reduced to 2046 schools to eliminate unreliable school altitude measures (see Methods) for the biophysical models that used AI as a response. For the best-fitting models (Table 2), SST30 had a significant positive influence on school altitude and schools were significantly elevated under cooler mean water temperature profiles around both islands (Table 3, Fig. 6a–d). Fish schools were recorded at higher altitudes during winter around both islands and these differences were accentuated around Bird Island (Table 3, Fig. 6). The best-fitting model for Bird Island included a positive influence of thermal stratification on AI values (Table 3, Fig. 6e) and a strong year effect with schools significantly lower in the water column during 2012 and 2013 (Table 3). The best-fitting model for St Croix Island included CHL30, which had a significant positive influence on school altitude (Table 3, Fig. 6f).

Mechanistic drivers of primary production

As expected, northeasterly winds had a positive association and southwesterly winds had a negative association with chl *a* around both islands (Table 4).

Table 2. Linear mixed-effects models used to determine the influence of oceanographic and temporal covariates on fish school data for surveys conducted around Bird and St Croix islands. Akaike's information criterion (AIC) and the difference in AIC of each model from the lowest AIC for each nested model set (ΔAIC) are given. Abbreviations: TVA, total volumetric abundance of fish (kg); AI, school altitude index; CHL30, chlorophyll *a* concentration composite over 30 d lag period; SST30, sea surface temperature composite over 30 d lag period; strat, stratification (SD of temperature within the upper 30 m); mtemp, mean temperature through the water column. For all models, survey date was included as a random effect. Shaded rows represent best-fitting models for each nested set

Model no.	Model	AIC	ΔAIC
Bird Island			
BT1	log(TVA)~CHL30+SST30+strat+mtemp+year+season	11936.84	17.36
IBT2	log(TVA)~CHL30+SST30+strat+year+season	11932.02	12.54
BT3	log(TVA)~CHL30+SST30+year+season	11929.82	10.34
BT4	log(TVA)~CHL30 +year+ season	11925.24	5.76
BT5	log(TVA)~CHL30 + season	11921.6	2.12
BT6	log(TVA)~CHL30	11919.48	0
BA1	AI~CHL30+SST30+strat+mtemp+year+season	−2587.81	0.6
BA2	AI~SST30+strat+mtemp+year+season	−2588.41	0
St Croix Island			
ST1	log(TVA)~CHL30+sst30+strat+mtemp+year+season	10006.48	10.2
ST2	log(TVA)~CHL30+sst30+strat+mtemp+year	10004.14	7.86
ST3	log(TVA)~CHL30+sst30+strat+year	10001.64	5.36
ST4	log(TVA)~CHL30+sst30+year	10001.05	4.77
ST5	log(TVA)~CHL30+SST30	9998.75	2.47
ST6	log(TVA)~SST30	9996.28	0
SA1	AI~CHL30+SST30+strat+mtemp+year+season	−2632.9	4.3
SA2	AI~CHL30+SST30+strat+mtemp+season	−2635.99	1.21
SA3	AI~CHL30+SST30+mtemp+season	−2637.2	0

These relationships were stronger around St Croix Island, especially for the influence of northeasterly winds, although none of these results were significant. To ascertain the potential influence of wind on the differences in chl *a* levels between the summers of 2011–2012 and 2012–2013, we compared average wind speeds for northeasterly and southwesterly winds between these 2 periods (Table 5). There were no significant differences between these summers for northeasterly winds around both islands, but southwesterly winds were significantly stronger around Bird Island during the summer of 2011–2012 compared with 2012–2013 (Table 5, Fig. 7a). Five potential Natal pulse events were identified during the study period, of which 2 events were confirmed through visual inspection of SST images, each lasting ca. 2 wk from 11 April 2012 and from 19 May 2013 (Fig. 8). The 2012 event coincided with the highest levels of monthly chl *a* around both islands for 2012 (Fig. 7b).

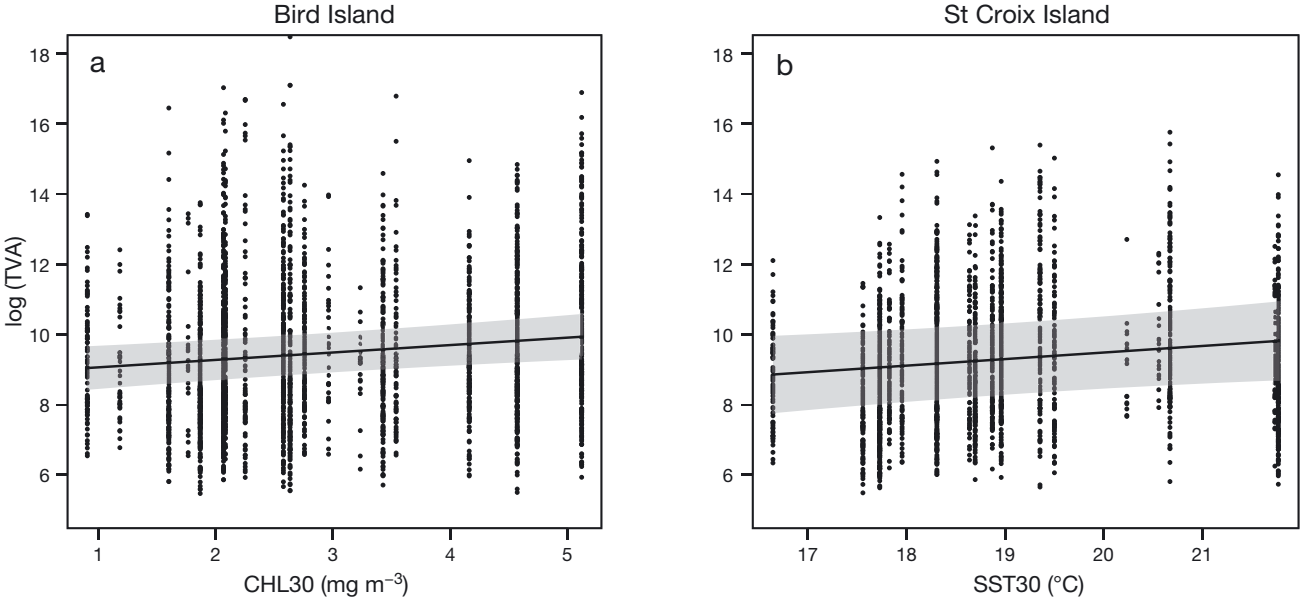

Fig. 5. Linear mixed-effects model predictions for the influences of 30 d composite lags of (a) chlorophyll *a* concentration (CHL30) and (b) sea-surface temperature (SST30) on normalised total volumetric fish abundance (TVA) for Bird and St Croix islands, respectively. Grey shaded areas represent 95% confidence intervals

Table 3. Best-fitting 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 and St Croix islands. Variable abbreviations: TVA, total volumetric abundance of fish (kg); AI, school altitude index; CHL30, chlorophyll *a* concentration composite over 30 d lag period; SST30, sea surface temperature composite over 30 d lag period; strat, stratification (SD of temperature within the upper 30 m); mtemp, mean temperature through the water column; season, winter (W). $^{***}p < 0.001$, $^{**}p < 0.01$, $^{*}p < 0.05$

Explanatory variables	Model no. (response)			
	Bird Island		St Croix Island	
	BT6 (TVA)	BA2 (AI)	ST6 (TVA)	SA3 (AI)
CHL30	0.21 (0.07)**	–	–	0.09 (0.03)**
SST30	–	0.19 (0.04)***	0.19 (0.09)*	0.23 (0.03)***
strat	–	0.19 (0.07)**	–	–
mtemp	–	–0.23 (0.08)**	–	–0.10 (0.04)**
year (2012)	–	–0.83 (0.22)***	–	–
year (2013)	–	–0.88 (0.27)**	–	–
season (W)	–	1.01 (0.23)***	–	0.25 (0.07)***

Table 4. Generalised least square regression coefficients (β) and standard errors (SE) for correlations between mean monthly wind speed (NE, northeasterly; SW, southwesterly) and chlorophyll *a* concentrations (chl *a*) for Bird and St Croix islands between 2011 and 2013

Explanatory variables	Response (chl *a*)	
	Bird Island	St Croix Island
NE wind	0.05 (0.26)	0.35 (0.25)
SW wind	–0.08 (0.11)	–0.17 (0.10)

Table 5. Wind speed comparisons between the summers of 2011–2012 and 2012–2013 at Bird Island and Port Elizabeth Harbour weather stations, given as medians (interquartile range, IQR). Mann-Whitney test statistics (w) and corresponding p-values are provided for statistical comparisons between years for northeasterly and southwesterly winds at each site. $^{*}p < 0.05$. Bold outputs denote significant outcomes at the 5% level

Station	2011–2012	2012–2013	w	p
Northeasterly				
Bird Island	6.5 (4.4)	7.6 (4.7)	246	0.31
PE Harbour	7.5 (4.8)	5.9 (3.3)	615	0.16
Southwesterly				
Bird Island	6.1 (4.2)	5.2 (3.2)	3278	**0.03***
PE Harbour	9.8 (5.1)	8.8 (4.9)	4760	0.14

DISCUSSION

Influence of oceanographic factors on fish abundance

The 3 dominant species of forage fish in Algoa Bay, which are the main prey of adult African penguins in the area (Randall & Randall 1986, Crawford et al. 2011), obtain most of their energy from zooplankton, although anchovy and redeye tend to consume larger zooplankton than filter-feeding sardine (James 1987, 1988, Van Der Lingen 2002). In the BUR, temporal lapses associated with trophic exchanges between upwelling, plankton and small pelagic fish are probably >10 d (*sensu* Moloney 1992) and will vary according to the different feeding preferences of the dominant small pelagic fish species present and site specific biophysical conditions. Given the limitations imposed on this study in obtaining finer assessments of detailed trophic relationships, the results presented here must be interpreted as cumulative or cruder forms of the actual processes prevalent during the study period. Nevertheless, the biophysical associations determined from this research provide interesting hitherto undocumented relationships between relative indices of trophic coupling that have an important bearing on marine top predators in Algoa Bay.

CHL30 had the greatest influence on relative fish abundance around Bird Island for both aggregated fish abundance and for school biomass, and was the only oceanographic variable remaining in the best-fitting model explaining fish school biomass (Table 3). In contrast to these findings around Bird Island, CHL30 had little influence on relative fish abundance around St Croix Island (Tables 1 & 3). Levels of chl *a* were consistently greater around Bird Island than St Croix Island (Fig. 7b), which corresponds to the greater propensity for upwelling near Bird Island over the study period (Fig. 1). Despite the differences in productivity between sites, mean monthly chl *a* exhibited similar temporal concentration trends around both islands (Fig. 7b), which fails to explain the lack of a response by fish to CHL30 around St Croix Island. This inter-site discrepancy could be better explained by the differences in fish abundance between sites, due to greater and more variable fish abundance around Bird Island (Fig. 7e). 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 Island being open to fishing during this period. This was part of an island-closure feasibility study implemented by DAFF to gauge the effects of purse-seine fishing on survival indices of African penguins

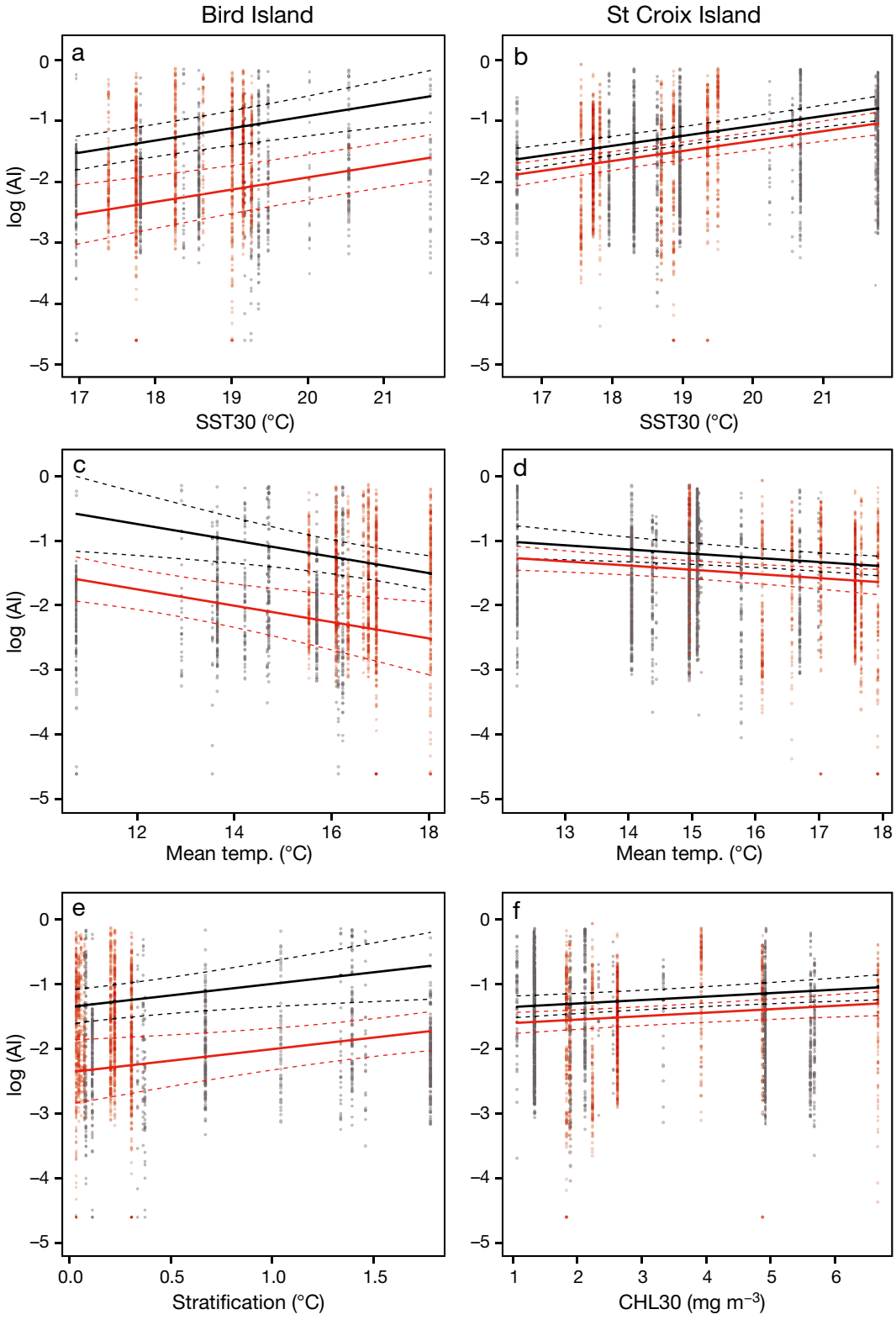

Fig. 6. Generalised linear mixed-effects model predictions for the influences of oceanographic variables. (a,b) 30 d composite lags of sea surface temperature (SST30), (c,d) mean temperature through the water column, (e) stratification (SD of temperature within the upper 30 m) and (f) 30 d composite lags of chlorophyll *a* concentration (CHL30) on normalised school altitude index values (AI) for Bird and St Croix islands. Hatched lines represent 95 % confidence intervals for summer (red) and winter (black)

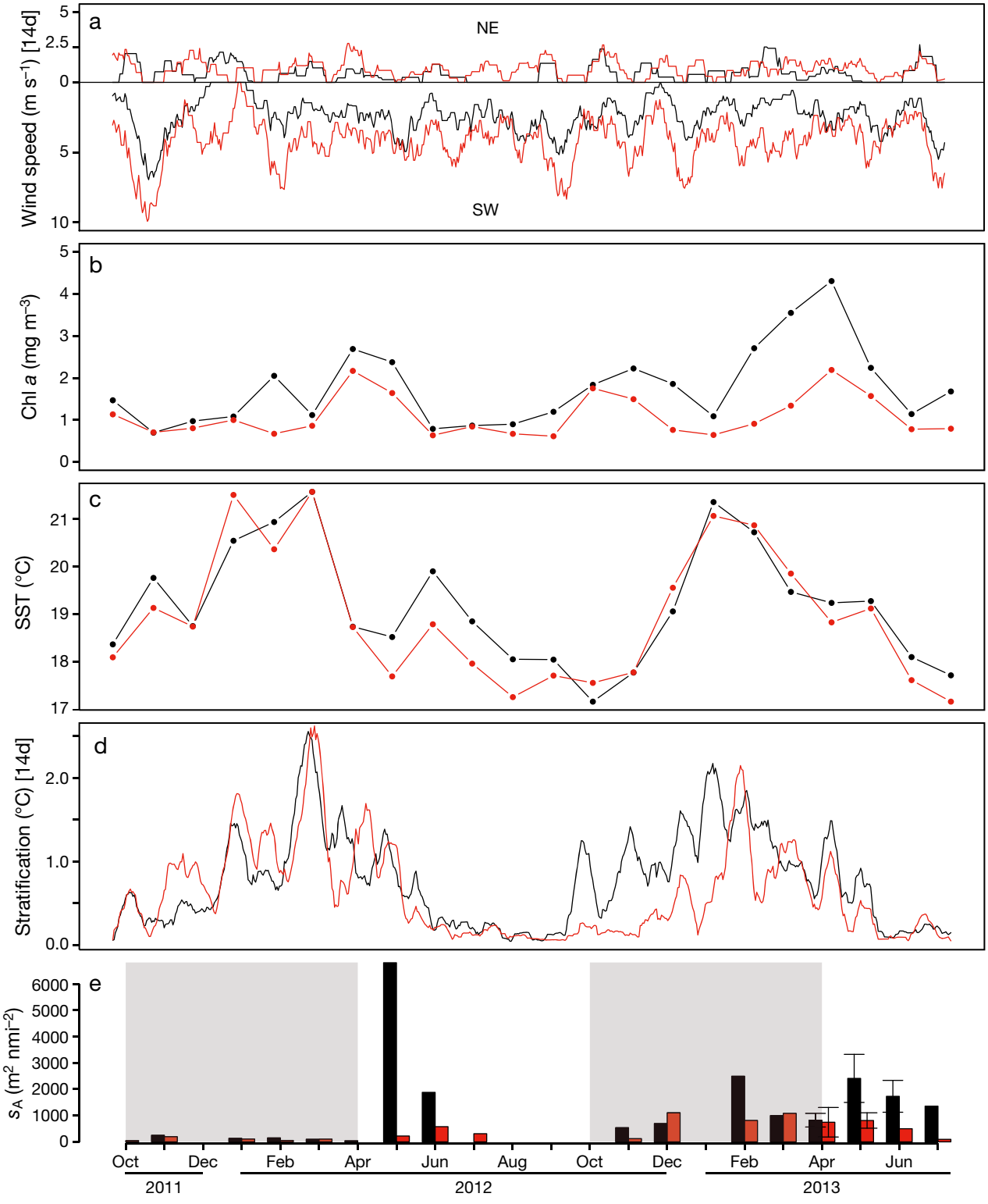

Fig. 7. Time series of oceanographic variables and fish abundance recorded in Algoa Bay between October 2011 and July 2013 for Bird (black) and St Croix (red) islands. (a) Wind speed using a 14 d running mean for 2 bearing bins, northeasterly winds (NE, top) and southwesterly winds (SW). (b) Mean monthly chlorophyll *a* concentration (chl *a*). (c) Mean monthly sea surface temperature data (SST). (d) Temperature stratification through the water column using a 14 d rolling mean. (e) Relative fish abundance (s_A). Error bars are SD for months with 2 surveys and shaded areas denote summer months

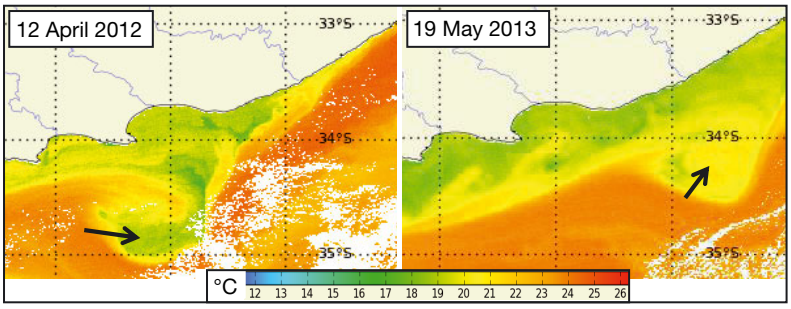

Fig. 8. Satellite-derived sea surface temperature maps showing 2 Agulhas meanders, so-called Natal pulse events, recorded during the study period. Arrows point to the centres of the core meanders with propagating cooler waters shown via plumes inshore in the region of Algoa Bay. White pixels represent cloud cover

(Pichegru et al. 2010). It is possible that removal of fish around St Croix Island may have masked the natural biophysical 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 closer to a more stable source population of pelagic fish that expand their range into the eastern part of the bay during favourable periods more frequently than they reach 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 3 yr of this study (Shabangu et al. 2011, 2012, Mhlongo et al. 2013).

The positive relationship between SST and fish abundance around St Croix Island closely resembles the association of sardines and SST at coarser scales (Agenbag et al. 2003). Agenbag et al. (2003) used the locations of purse-seine catches to establish environmental preferences of small pelagic fish species caught off South Africa. Their results show a strong positive relationship between sardine catches and SSTs up to 22°C, in contrast to anchovy and redeye catches, which decreased significantly at SSTs >15°C and >18°C, respectively. These diverging SST preferences may relate to more sardine schools being present around St Croix Island during warmer SST periods. The largest and most dense schools recorded by DAFF in this region between 2010 and 2014 were sardine schools (Fig. 2b,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.

Influence of oceanographic factors 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 was favoured by lower SST30 values (Fig. 3b) and, to some extent, this can be explained by increasing relative fish abundance under these conditions (Fig. 4a), i.e. 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 relative 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 relative 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.

Influence of oceanographic factors on the vertical distribution of prey

The thermal profile played a significant role in the vertical distribution of pelagic fish schools around both islands. Conditions that favoured the elevation of schools in the water column resembled thermocline conditions that are known to predominate in this region during summer (Schumann et al. 2005), with the mixed surface layer typically occurring down to depths of 20–30 m during this season (Goschen 1991). 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). The positive correlation between CHL30 and school altitude around St Croix Island may be due to differential species-specific preferences, with sardines generally occurring at higher altitudes (Lawson et al. 2001)

(Fig. 2) and potentially favouring recently upwelled areas.

Despite similar SSTs around both islands during the course of this study (Fig. 7c), stratification was generally stronger around Bird Island (Fig. 7d), which probably explains the differential effects of this variable on school altitude between islands (Table 3). The propensity for fish schools to be higher in the water column during winter was biased to some extent by the earlier part of this season (May–June) when fish were found at higher altitudes compared with during July (Table S1 in the Supplement) when strong southwesterly winds were associated with vertical mixing of the water column (Fig. 7a,d). Deep vertical mixing is likely to suppress primary and secondary production, potentially driving pelagic fish into deeper more productive waters and likely making them less accessible to predators such as African penguins (van Eeden et al. 2016). The accentuated seasonal differences in school altitude around Bird Island may relate to a disproportionate influx of redeye into this region during summer. Redeye was the only pelagic fish species recorded in the east of Algoa Bay in all 3 November spawner biomass surveys between 2011 and 2013 (Shabangu et al. 2011, 2012, Mhlongo et al. 2013) and this species tends to be distributed more inshore during summer (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 related to strong southwesterly winds during this season (Table 4, Fig. 7a), which promote mixing of the water column (Lutjeharms et al. 1996) and suppress upwelling activity in areas south of the prominent capes, such as around Bird Island (Goschen & Schumann 1995). In comparison, strong northeasterly winds around Bird Island during 2013 and weaker southwesterly winds would have favoured stronger and more frequent upwelling.

The anomalous spike in chl *a* around both islands during April and May 2012 (Fig. 7b) was linked to a Natal pulse offshore in the Agulhas Current and the associated influx of cool, upwelled waters into the bay (Fig. 8). This event likely played an important role in driving primary and secondary production, leading to the increase in fish abundance 1 mo later, especially around Bird Island (Fig. 7b,e). The Natal pulse event in May 2013 also coincided with relatively high chl *a* values, but this event was preceded by even higher chl *a* values in the month leading up to this event (Fig. 7b), which was probably linked to a combination of wind-induced and shear-edge upwelling events.

Implications of biophysical associations for African penguins and other predators

Our results indicate the complex and highly variable nature of marine habitats in Algoa Bay. This is significant for the African penguin population because 2 of this species' largest colonies are situated at either end of the bay. The St Croix Island population is currently the largest globally (8685 pairs in 2014, South African Dept of Environmental Affairs (DEA) unpubl. data), with more than double the population of Bird Island (2837 pairs, DEA unpubl. data), yet the biophysical associations as determined from this study indicate that conditions for their prey are more favourable around Bird Island. Consequently, the probability of density-dependent effects on the St Croix Island 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.

Oceanographic influences on the horizontal (FDI) and vertical (AI and MAI) distribution of small pelagic fish in Algoa Bay are significant in terms of the access and predictability of prey available to African penguins and other predators. Seabirds are known to associate with 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 and gannets, the vertical distribution of prey is a critical determinant of the types of assemblages they target (Zamon et al. 1996, Boyd et al. 2015). Our results demonstrate how these prey parameters vary both in space and time with marked seasonal and site-specific differences in prey availability. To refine and identify specific aspects of the biophysical associations emerging from this study that have a more direct bearing on the foraging performance of African penguins, information on the vertical and horizontal distributions of prey targeted by this species in Algoa Bay will need to be assessed.

Seabird species endemic to the BUR have shown marked eastward shifts in their distributions since

the mid 1990s (Crawford et al. 2015) due to environmental and fisheries-related influences on the distribution of their prey species, mostly small pelagic fish (Roy et al. 2007, Coetzee et al. 2008). The largest populations of 2 of these endemics, African penguins and Cape gannets, are now situated at the eastern edge of the BUR in Algoa Bay and the survival of these species is closely linked to the future ecological status of this region. The propensity of upwelling and the thermal properties of water in the eastern BUR are likely to change under recent warming of the Agulhas Current (Rouault et al. 2010) and a predicted increase in Agulhas-derived episodic meander events, e.g. Natal pulses (Lutjeharms & de Ruijter 1996). These mechanisms, coupled with localised changes in wind-induced upwelling events (Roy et al. 2007), are likely to play an increasingly more prominent role in the ecology of pelagic fish and associated predators in Algoa Bay. Furthermore, these environmental changes will have an important bearing on the competitive influence of commercial fishing operations on pelagic predators in Algoa Bay. The biophysical processes as identified in this study have the potential to be integrated into ecosystem models, which could elucidate forecasted habitat suitability for marine predators under different climate change and resource depletion scenarios in the BUR. Models of this nature are indispensible for motivating resource management policies that can be implemented at appropriate spatiotemporal scales.

Acknowledgements. We thank the South African Department of Agriculture, Forestry and Fisheries (DAFF), the South African Environmental Observation Network (SAEON) and the South African Weather Services (SAWS) for providing data used in the analyses. Funds for this research were provided by the Percy FitzPatrick Institute of African Ornithology, the Department of Science and Technology–National Research Foundation (DST-NRF) Centre of Excellence, the African Species Champion Project of the Charl van der Merwe Trust and the Responsible Fisheries Alliance. Carl van der Lingen is thanked for useful insights into the ecology of small pelagic fish. The anonymous reviewers of the original manuscript are thanked for their valuable recommendations.

LITERATURE CITED

Agenbag JJ, Richardson AJ, Demarcq H, Fréon P, Weeks S, Shillington FA (2003) Estimating environmental preferences of South African pelagic fish species using catch size- and remote sensing data. Prog Oceanogr 59: 275–300

Akaike H (1973) Information theory and an extension of the maximum liklihood principle. In: Petrov BN, Csaki F (eds) Proc 2nd Int Symp Information Theory, Akademiai Kiado, Budapest, p 267–281

Bakun A (2006) Wasp-waist populations and marine ecosystem dynamics: navigating the 'predator pit' topographies. Prog Oceanogr 68:271–288

Barange M, Hampton I, Soule M (1996) Empirical determination of *in situ* target strengths of three loosely aggregated pelagic fish species. ICES J Mar Sci 53:225–232

Bates D, Maechler M, Bolker BM, Walker S (2015) Fitting linear mixed-effects models using lme4. J Stat Softw 67: 1–48

Benoit-Bird KJ, McManus MA (2012) Bottom-up regulation of a pelagic community through spatial aggregations. Biol Lett 8:813–816

Bertrand A, Segura M, Gutiérrez M, Vásquez L (2004) From small-scale habitat loopholes to decadal cycles: a habitat-based hypothesis explaining fluctuation in pelagic fish populations off Peru. Fish Fish 5:296–316

Bertrand A, Gerlotto F, Bertrand S, Gutiérrez M and others (2008) Schooling behaviour and environmental forcing in relation to anchoveta distribution: an analysis across multiple spatial scales. Prog Oceanogr 79:264–277

Bertrand A, Grados D, Colas F, Bertrand S and others (2014) Broad impacts of fine-scale dynamics on seascape structure from zooplankton to seabirds. Nat Commun 5:5239

BirdLife International (2016) IUCN Red List for birds. Downloaded from www.birdlife.org on 17 October 2016

Blamey LK, Shannon LJ, Bolton JJ, Crawford RJM and others (2015) Ecosystem change in the southern Benguela and the underlying processes. J Mar Syst 144:9–29

Bon C, Della Penna A, Ovidio F, Arnould JYP, Poupart T (2015) Influence of oceanographic structures on foraging strategies: Macaroni penguins at Crozet Islands. Mov Ecol 3:32

Boyd AJ, Taunton-Clark J, Oberholster GPJ (1992) Spatial features of the near-surface and midwater circulation patterns off western and southern South Africa and their role in the life histories of various commercially fished species. S Afr J Mar Sci 12:189–206

Boyd C, Castillo R, Hunt GL, Punt AE, VanBlaricom GR, Weimerskirch H, Bertrand S (2015) Predictive modelling of habitat selection by marine predators with respect to the abundance and depth distribution of pelagic prey. J Anim Ecol 84:1575–1588

Cairns D (1987) Seabirds as indicators of marine food supplies. Biol Oceanogr 5:261–271

Chavez FP, Messié M (2009) A comparison of eastern boundary upwelling ecosystems. Prog Oceanogr 83:80–96

Chavez FP, Ryan J, Lluch-Cota SE, Niquen C M (2003) From anchovies to sardines and back: multidecadal change in the Pacific Ocean. Science 299:217–221

Coetzee J (2000) Use of a shoal analysis and patch estimation system (SHAPES). Aquat Living Resour 13:1–10

Coetzee JC, van der Lingen CD, Hutchings L, Fairweather TP (2008) Has the fishery contributed to a major shift in the distribution of South African sardine? ICES J Mar Sci 65:1676–1688

Connan M, Hofmeyr GJG, Pistorius PA (2016) Reappraisal of the trophic ecology of one of the world's most threatened Spheniscids, the African penguin. PLoS ONE 11:e0159402

Cotté C, Park Y, Guinet C, Bost C (2007) Movements of foraging king penguins through marine mesoscale eddies. Proc Biol Sci 274:2385–2391

Cox S, Scott B, Camphuysen C (2013) Combined spatial and tidal processes identify links between pelagic prey species and seabirds. Mar Ecol Prog Ser 479:203–221

Crawford RJM, Jahncke J (1999) Comparison of trends in abundance of guano-producing seabirds in Peru and southern Africa. S Afr J Mar Sci 21:145–156

Crawford RJM, Shannon LJ, Whittington PA, Murison G (2000) Factors influencing growth of the African penguin colony at Boulders, South Africa, 1985–1999. S Afr J Mar Sci 22:111–119

Crawford RJM, Dundee BL, Dyer BM, Klages NTW, Meÿer MA, Upfold L (2007) Trends in numbers of Cape gannets (*Morus capensis*), 1956/1957–2005/2006, with a consideration of the influence of food and other factors. ICES J Mar Sci 64:169–177

Crawford RJM, Underhill LG, Coetzee JC, Fairweather T, Shannon LJ, Wolfaardt AC (2008) Influences of the abundance and distribution of prey on African penguins *Spheniscus demersus* off western South Africa. Afr J Mar Sci 30:167–175

Crawford RJM, Altwegg R, Barham BJ, Barham PJ and others (2011) Collapse of South Africa's penguins in the early 21st century. Afr J Mar Sci 33:139–156

Crawford RJM, Makhado AB, Waller LJ, Whittington PA (2014) Winners and losers — response to recent environmental change by South African seabirds that compete with purse-seine fisheries for food. Ostrich 85:111–117

Crawford RJM, Makhado AB, Whittington PA, Randall RM, Oosthuizen WH, Waller LJ (2015) A changing distribution of seabirds in South Africa — the possible impact of climate and its consequences. Front Ecol Evol 3:1–11

Cury P, Bakun A, Crawford R, Jarre A, Quinones R, Shannon L, Verheye H (2000) Small pelagics in upwelling systems: patterns of interaction and structural changes in 'wasp-waist' ecosystems. ICES J Mar Sci 57:603–618

Cury PM, Boyd IL, Bonhommeau S, Anker-Nilssen T and others (2011) Global seabird response to forage fish depletion — one-third for the birds. Science 334:1703–1706

Daskalov G (2003) Long-term changes in fish abundance and environmental indices in the Black Sea. Mar Ecol Prog Ser 255:259–270

FAO (Food and Agriculture Organization) (2014) FAO yearbook: fishery and aquaculture statistics 2012 (S and IB of the F and A Department, Ed.). FAO, Rome

Fauchald P (2009) Spatial interaction between seabirds and prey: review and synthesis. Mar Ecol Prog Ser 391: 139–151

Fiedler PC (2010) Comparison of objective descriptions of the thermocline. Limnol Oceanogr Methods 8:313–325

Goschen WS (1991) Ocean dynamics associated with prominent capes and bays off the south coast of South Africa. PhD thesis, University of Port Elizabeth

Goschen WS, Schumann EH (1988) Ocean current and temperature structures in Algoa Bay and beyond in November 1986. S Afr J Mar Sci 7:101–116

Goschen WS, Schumann EH (1995) Upwelling and the occurrence of cold water around Cape Recife, Algoa Bay, South Africa. S Afr J Mar Sci 16:57–67

Goschen WS, Schumann EH (2011) The physical oceanographic processes of Algoa Bay, with emphasis on the western coastal region. South African Environmental Observation Network internal publication no. P0106-110000-730002:1–84

Goschen WS, Schumann ES, Bernard KS, Bailey SE, Deyzel SH (2012) Upwelling and ocean structures off Algoa Bay and the south-east coast of South Africa. Afr J Mar Sci 34: 525–536

Goschen WS, Bornman TG, Deyzel SHP, Schumann EH (2015) Coastal upwelling on the far eastern Agulhas Bank associated with large meanders in the Agulhas Current. Cont Shelf Res 101:34–46

Harding CT (2013) Tracking African penguins (*Spheniscus demersus*) outside of the breeding season: regional effects and fishing pressure during the pre-moult period. MSc thesis, University of Cape Town

Heath RGM, Randall RM (1989) Foraging ranges and movements of jackass penguins (*Spheniscus demersus*) established through radio telemetry. J Zool (Lond) 217:367–379

Hyrenbach KD, Veit RR, Weimerskirch H, Hunt GL (2006) Seabird associations with mesoscale eddies: the subtropical Indian Ocean. Mar Ecol Prog Ser 324:271–279

Jackman S (2015) pscl: classes and methods for R developed in the Political Science Computational Laboratory, Stanford University

Jahncke J, Checkley DMJ, Hunt GL (2004) Trends in carbon flux to seabirds in the Peruvian upwelling system: effects of wind and fisheries on population regulation. Fish Oceanogr 13:208–223

James A (1987) Feeding ecology, diet and field-based studies on feeding selectivity of the Cape anchovy *Engraulis capensis* Gilchrist. S Afr J Mar Sci 5:673–692

James AG (1988) Are clupeid microphagists herbivorous or omnivorous? A review of the diets of some commercially important clupeids. S Afr J Mar Sci 7:161–177

Katara I, Pierce GJ, Illian J, Scott BE (2011) Environmental drivers of the anchovy/sardine complex in the Eastern Mediterranean. Hydrobiologia 670:49–65

Lawson G, Barange M, Freon P (2001) Species identification of pelagic fish schools on the South African continental shelf using acoustic descriptors and ancillary information. ICES J Mar Sci 58:275–287

Lutjeharms JRE, Roberts HR (1988) The Natal pulse: an extreme transient on the Agulhas Current. J Geophys Res 93:631–645

Lutjeharms JRE, de Ruijter WPM (1996) The influence of the Agulhas Current on the adjacent coastal ocean: possible impacts of climate change. J Mar Syst 7:321–336

Lutjeharms JRE, Meyer AA, Ansorge IJ, Eagle GA, Orren MJ (1996) The nutrient characteristics of the Agulhas Bank. S Afr J Mar Sci 17:253–274

Lutjeharms J, Cooper J, Roberts M (2000) Upwelling at the inshore edge of the Agulhas Current. Cont Shelf Res 20: 737–761

McInnes AM, Khoosal A, Murrell B, Merkle D and others (2015) Recreational fish-finders — an inexpensive alternative to scientific echo-sounders for unravelling the links between marine top predators and their prey. PLoS ONE 10:e0140936

Mhlongo N, Coetzee J, Shabangu F, Merkle D, Hendricks M, Geja Y (2013) Results of the 2013 spawner biomass survey. Dep Agric For Fish Branch Fish Manag Internal Report SWG-PEL/45, Cape Town, p 1–12

Mhlongo N, Yemane D, Hendricks M, van der Lingen CD (2015) Have the spawning habitat preferences of anchovy (*Engraulis encrasicolus*) and sardine (*Sardinops sagax*) in the southern Benguela changed in recent years? Fish Oceanogr 24:1–14

Moloney CL (1992) Simulation studies of trophic flows and nutrient cycles in Benguela upwelling foodwebs. South African J Mar Sci 12:457–476

Nel DC, Lutjeharms JRE, Pakhomov EA, Ansorge IJ, Ryan PG, Klages NTW (2001) Exploitation of mesoscale oceanographic features by grey-headed albatross *Thalassarche*

chrysostoma in the southern Indian Ocean. Mar Ecol Prog Ser 217:15–26
Paleczny M, Hammill E, Karpouzi V, Pauly D (2015) Population trend of the world's monitored seabirds, 1950–2010. PLoS ONE 10:e0129342
Palomera I, Olivar MP, Salat J, Sabatés A, Coll M, García A, Morales-Nin B (2007) Small pelagic fish in the NW Mediterranean Sea: an ecological review. Prog Oceanogr 74: 377–396
Petersen SL, Ryan PG, Gremillet D (2006) Is food availability limiting African penguins *Spheniscus demersus* at Boulders? A comparison of foraging effort at mainland and island colonies. Ibis 148:14–26
Piatt JF (1990) The aggregative response of common murres and Atlantic puffins to schools of capelin. Stud Avian Biol 14:36–51
Pichegru L, Grémillet D, Crawford RJM, Ryan PG (2010) Marine no-take zone rapidly benefits endangered penguin. Biol Lett 6:498–501
Pichegru L, Ryan PG, van Eeden R, Reid T, Grémillet D, Wanless R (2012) Industrial fishing, no-take zones and endangered penguins. Biol Conserv 156:117–125
Pichegru L, Cook T, Handley J, Voogt N, Watermeyer J, Nupen L, McQuaid C (2013) Sex-specific foraging behaviour and a field sexing technique for Endangered African penguins. Endang Species Res 19:255–264
Pinheiro J, Bates D, DebRoy S, Sarkar D (2015) nlme: linear and nonlinear mixed effects models. R Core Team, R Package version 3
R Core Team (2015) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna
Randall RM, Randall BM (1986) The diet of jackass penguins *Spheniscus demersus* in Algoa Bay, South Africa, and its bearing on population declines elsewhere. Biol Conserv 37:119–134
Reisinger RR, Karczmarski L (2010) Population size estimate of Indo-Pacific bottlenose dolphins in the Algoa Bay region, South Africa. Mar Mammal Sci 26:86–97
Roel BA, Armstrong MJ (1991) The round herring *Etrumeus whiteheadi*, an abundant, underexploited clupeoid species off the coast of southern Africa. S Afr J Mar Sci 11: 267–287
Rouault M, Pohl B, Penven P (2010) Coastal oceanic climate change and variability from 1982 to 2009 around South Africa. African J Mar Sci 32:237–246
Roy C, van der Lingen CD, Coetzee JC, Lutjeharms JRE (2007) Abrupt environmental shift associated with changes in the distribution of Cape anchovy *Engraulis encrasicolus* spawners in the southern Benguela. African J Mar Sci 29:309–319
Schumann E, Perrins L, Hunter I (1982) Upwelling along the south coast of the Cape Province, South Africa. S Afr J Sci 78:238–242
Schumann E, Churchill J, Zaayman H (2005) Oceanic variability in the western sector of Algoa Bay, South Africa. Afr J Mar Sci 27:65–80
Shabangu F, Coetzee J, Dagmar M, Kanakana M (2011) Results of the 2011 spawner biomass survey. Dep Agric For Fish Branch Fish Manag Internal Report SWG-PEL/91, Cape Town, p 1–11
Shabangu F, Coetzee J, Merkle D, Mushanganyisi K, Phillips M (2012) Results of the 2012 spawner biomass survey. Dep Agric For Fish Branch Fish Manag Internal Report SWG-PEL/66 p 1–12
Shannon LV, Hutchings L, Bailey GW, Shelton PA (1984) Spatial and temporal distribution of chlorophyll in southern African waters as deduced from ship and satellite measurements and their implications for pelagic fisheries. S Afr J Mar Sci 2:109–130
Shannon LJ, Christensen V, Walters CJ (2004) Modelling stock dynamics in the southern Benguela ecosystem for the period 1978–2002. Afr J Mar Sci 26:179–196
Shannon L, Neira S, Taylor M (2008) Comparing internal and external drivers in the southern Benguela and the southern and northern Humboldt upwelling ecosystems. Afr J Mar Sci 30:63–84
Sherley R, Underhill L, Barham B, Barham P and others (2013) Influence of local and regional prey availability on breeding performance of African penguins *Spheniscus demersus*. Mar Ecol Prog Ser 473:291–301
Van Der Lingen C (2002) Diet of sardine *Sardinops sagax* in the southern Benguela upwelling ecosystem. S Afr J Mar Sci 24:301–316
Van Eeden R, Reid T, Ryan P, Pichegru L (2016) Fine-scale foraging cues for African penguins in a highly variable marine environment. Mar Ecol Prog Ser 543:257–271
Weller F, Cecchini LA, Shannon L, Sherley RB and others (2014) A system dynamics approach to modelling multiple drivers of the African penguin population on Robben Island, South Africa. Ecol Modell 277:38–56
Wilson RP (1985) The Jackass penguin (*Spheniscus demersus*) as a pelagic predator. Mar Ecol 25:219–227
Wilson RP, Nagy KA, Obst BS (1989) Foraging ranges of penguins. Polar Rec (Gr Brit) 25:303–308
Wood S (2006) Generalized additive models: an introduction with R. CRC Press, London
Zamon J, Greene C, Meir E (1996) Acoustic characterization of the three-dimensional prey field of foraging chinstrap penguins. Mar Ecol Prog Ser 131:1–10

Editorial responsibility: Peter Corkeron, Woods Hole, Massachusetts, USA

Submitted: September 23, 2016; Accepted: February 9, 2017
Proofs received from author(s): April 1, 2017