Environmental correlates of temporal variation in the diet of Australian fur seals

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- Dr Roger Kirkwood and Dr Rebecca McIntosh conducted fieldwork supported by Dr Peter Dann from Phillip Island Nature Parks, Victoria.
- Fiona Hume from Tasmania was contracted by Phillip Island Nature Parks to process samples and identify specimens, conducting the laboratory work over the past ten years.

Dr Jason Everett from University of New South Wales assisted with obtaining the sea surface temperature data used in the final analysis.

All other research described in this thesis is my own original work.

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Australian fur seals at Seal Rocks, in Bass Strait, Victoria. Photograph: K Kliska, 2015.

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Abstract

Long term systematic monitoring of the diet of large marine predators can be an effective approach to detect and understand changes in ecosystems vulnerable to environmental change. This study quantified seasonal and annual changes in the frequency of occurrence (%FO) of prey items in the diet of Australian fur seals (*Arctocephalus pusillus doriferus*) in Bass Strait from 1998 to 2014. Using hard part analysis, 71 prey species were identified, with combinations of 8 main species found in more than 70% of the samples. Otolith measurements suggest Australian fur seals consumed predominantly juvenile fishes. I investigated correlations between environmental variables and %FO using generalised additive models. Southern Oscillation Index (SOI) correlated with the %FO of red cod *Pseudophycis bachus*, pilchard *Sardinops sagax* and jack mackerel *Trachurus declivis*. Positive correlations relating to El Niño conditions were found for both red cod and pilchard and correlation with neutral SOI was found for jack mackerel. Correlations identified between long-term environmental change and prey of marine predators suggests large-scale processes can influence prey assemblages at various trophic levels in Bass Strait.

Introduction

The marine coastal environment is experiencing accelerating change (IPCC, 2014). Environmental change is altering species assemblages within ecosystems and ecosystem function (Last, et al., 2011). To understand the effects of these changes on ecosystem function, we need to understand how species will respond to changes in their environment (Otto, et al., 2014, Schmidt, et al., 2015). One approach to detecting changes in the prey species is to systematically monitor the diet of high trophic level predators over time (Boyd and Murray, 2001, Hindell, et al., 2003). Marine predators are ecologically important and as high trophic level consumers, they can be indicators of changes in prey availability and ecosystem health (Boyd and Murray, 2001, Hindell, et al., 2003, Trathan, et al., 2007, Hobday, et al., 2015). Prey presence and prey size are likely to vary over time and this variation can be linked to environmental and oceanographic processes (Croxall, et al., 1992). Monitoring diet provides an indication of the availability of certain prey cohorts within the foraging range of marine predators moderated by animal preference (Lea, et al., 2006). Therefore, by monitoring the diet of a known generalist predator, for example, the Australian fur seal, we may gain an indication of prey available to that predator within an ecosystem.

There are many approaches to the quantification of the diet of marine predators (Bowen and Iverson, 2013). One of the most cost-effective, relatively non-invasive methods that can be used in long term monitoring programs is hard part analysis (Bowen and Iverson, 2013, Tollit, et al., 2015). This method involves the collection of fresh scat and regurgitate and the recovery and identification of undigested prey remains within the collected samples (Kirkwood and Goldsworthy, 2013). Hard part analysis is particularly applicable to marine predators, such as fur seals, that forage in the marine environment but return to terrestrial areas to breed and rest (Renouf, 1991, Bowen and Iverson, 2013).

Australian fur seals are generalist feeders that forage benthically, i.e. on species on or near the sea floor (Arnould and Hindell, 2001, Arnould and Kirkwood, 2008). The largest breeding colony of Australian fur seals is located at Seal Rocks in northern Bass Strait (McIntosh, et al., 2014). This population was exploited during the 1800s and early 1900s (Kirkwood and Goldsworthy, 2013). However, since the cessation of commercial harvesting and government protection of the species in 1975, population numbers have recovered and are now considered

secure (Kirkwood and Goldsworthy, 2013, McIntosh, et al., 2014). Ongoing research efforts at Seal Rocks has provided an opportunity to collect scats and regurgitates for diet analysis since 1997. The aim has been to provide an indication of fish and cephalopod assemblages in the Bass Strait marine ecosystem available to the seals over this period.

The marine environment in South-eastern Australia is one of the fastest changing marine regions in the world (Last, et al., 2011, Hobday and Pecl, 2014, Chambers, et al., 2015). In the south-east of Australia sea temperature is warming four times faster than the global average (IPCC, 2014). Large-scale environmental processes such as El Niño-Southern Oscillation (ENSO) and the Southern Annular Mode (SAM) are intensifying (Marshall, 2003). This intensification of large-scale processes is driving local increases in SST (Berlincourt and Arnould, 2015, Descamps, et al., 2015) However, little is known about the effect of such large-scale environmental processes or the effects of wind strength and direction on prey of high trophic marine predators in Bass Strait.

The diet of Australian fur seals has historically shown temporal and spatial variation (Gales and Pemberton, 1994, Hume, et al., 2004, Littnan, et al., 2007, Kirkwood, et al., 2008, Arnould, et al., 2011). Previous studies have recorded a range of species in the diet including barracouta *Thyrsites atun*, cephalopods and Southern rock lobster *Jasus edwardsii* (McNally and Lynch, 1954); redbait *Emmelichthys nitidus*, jack mackerel, leatherjacket species from the family Monocanthidae, arrow squid *Nototodarus gouldi*, red cod and gurnard species from the family Trigilidae (Kirkwood, et al., 2008); as well as cartilaginous species (Deagle, et al., 2009). The present study aims to improve our understanding of seasonal and annual variability in the diet of Australian fur seals by correlating presence and absence of prey with environmental variables in the Bass Strait marine ecosystem. Specifically, this study aims to: 1) quantify any temporal and seasonal variation in the diet of Australian fur seals; 2) determine prey size class(es) for Australian fur seals; and 3) determine if environmental variables are correlated with any observed changes in the diet of Australian fur seals from Seal Rocks in Victoria, Australia.

Methods

Fieldwork

Fresh scat and regurgitate samples were collected, roughly every two months, between December 1997 and December 2014 from Seal Rocks in Victoria, Australia (38°30'S, 145°10'E). Staff of Phillip Island Nature Parks and trained volunteers performed sample collection. As per methods in Kirkwood, et al. (2008), the individual scats and regurgitates were collected and stored in separate plastic bags and either processed within the next 48 hours or stored frozen until processing at Phillip Island Nature Parks research laboratory. Each year, an experienced contractor (Fiona Hume) processed the samples and identified prey items from otoliths, cephalopod beaks and other identifiable hard parts. The following laboratory methods are summarised from Kirkwood, et al. (2008).

Laboratory methods

Individual scats were soaked in warm water with 2ml of biodegradable detergent for at least two hours before processing. After soaking, each scat was sieved through three tiers of nested sieves 600µm, 500µm and 212µm where all diagnostic fish parts (otoliths, mouth parts, body plates and spines) cephalopod beaks and crustacean remains were collected using small tweezers. These hard parts were then placed onto a petri dish to dry. Once dry, all hard parts were stored in individually labelled plastic containers for analyses.

Hard parts were identified to species level, assigned to a family group or recorded as unidentified (see Kirkwood et al. 2008). Sagittal otoliths were identified to species level where possible, using a stereo microscope (Olympus SZ61), and comparison to reference collections and the atlas *Otoliths of Common Australian Temperate Fish: A photographic guide*, by Furlani, et al. (2007). Counts of left and right otoliths provided estimates of the minimum number of fish present in each sample. The presence of teeth, mouthparts, spines and distinctive vertebrae of leatherjacket species were recorded as one individual per sample, except where multiple leatherjacket spines were present, in which case each spine was counted as one fish. Cephalopod species were counted by the presence of upper and lower beaks and identified by comparing lower beaks with reference collections and the atlas *Cephalopod beak identification and biomass estimation techniques: tools for dietary studies of Southern Australian finfishes,*

by Lu and Ickeringill (2002). As per Hume, et al. (2004), *Octopus berrima* and *O. pallidus* could not be distinguished and so were recorded as *O. berrima/O. pallidus*.

Prey species Monocanthidae (leatherjackets), Neosebastidae (gurnard perches), Sebastidae (sea perches), Triglidae (gurnards), Macrouridae (whiptail), Ostracontidae (cowfish), Myctophidae (myctophids) and Bothidae (flounder) were identified to family level. All otoliths identified as *Pseudophycis* species were identified as red cod to remain consistent with previous studies (Kirkwood, et al., 2008). Gempylidae otoliths were identified as the abundant barracouta species *Thyrsites atun*; all eroded gempylid otoliths were assumed to be this species, rather than the less common gemfish *Rexea solandri*. Otoliths that were unable to be identified were recorded as unidentified.

Prey species size classes

For prey size class estimates, only otoliths from fish species were measured, as cephalopod beaks were preserved by drying and may have shrunk providing a false estimation of prey size. To obtain prey size, the diameter of 2084 otoliths from the posterior to anterior margin was measured using stereomicroscopy at either 1x (larger otoliths) or 2x (smaller otoliths) magnification. Individual otoliths were placed under a microscope camera. Each otolith was photographed (Olympus DP22-CU, DP2-SAL) and then measured using the MOTIC software program, calibrated to 1000mm scale. Measurements of otolith length were taken of pristine (class 4) and almost pristine (class 3) otoliths as previously defined by Kirkwood et al. (2008) to obtain species-specific fish lengths. For class 3 otoliths, fish length was tested for realistic variation, i.e. would they accord with an unrealistic size estimate on back calculation, therefore prey size classes could be estimated with confidence. Fish length was then calculated using equations from Furlani, et al. (2007). Juvenile fish were defined as sexually immature fish, with maturity size estimates for red cod from Kemp, et al. (2012); jack mackerel from Marshall, et al. (1993); redbait and pilchard Ward, et al. (2012). A precision estimate was obtained to quantify the precision of observer otolith length measurements. This was calculated by taking measurements of otoliths from each of the four main prey species. The measurements were repeated twenty times in the same order and recorded on different sheets to avoid observer bias. The standard error of the mean otolith measurement values for all samples was 0.05mm. For individual fish species the precision estimate for redbait was 0.2mm (n=7 x 20 repeat measurements); red cod 0.3mm (n=3 x 20 repeat measurements); jack mackerel 0.3mm (n=7 x 20 repeat measurements); and pilchard 0.1mm (n=3 x 20 repeat measurements). The precision estimates for fish length overall were low <0.3mm, resulting in small error that would not influence size class estimates of fish.

Environmental data

Environmental data was obtained to explore potential correlates of variation in the seal diet. All datasets were subsetted to match the time series of the study beginning on the 1st of January 1998 and ending on the 30th of December 2014. Environmental data was standardised by taking the value of a covariate and subtracting the mean of the dataset for that covariate. To ensure independence between the environmental data each covariate was checked for collinearity prior to analysis (Zuur, et al., 2010). Daily L3S gridded Advanced Very High Resolution Radiometer (AVHRR) skin (surface) sea surface temperature (SST) was obtained from the Integrated Marine Observing System (IMOS) Data Portal (http://imos.aodn.org.au/imos/) at 0.02-degree resolution for the region of Bass Strait (39-41°S, 144-148°E). Annual SST values were calculated by averaging the monthly values from each year. Average monthly values of SST were calculated as the arithmetic mean of the daily SST across the whole region for a calendar month. Seasonal SST values were calculated by averaging the monthly averaging the monthly mean values in each season.

Local wind speed and direction were obtained from the coastal weather station located at the Laverton Royal Australian Air force (RAAF) base (GPS coordinates: S37.860, E144.761) monitored by the Bureau of Meteorology, Australia. The RAAF base is located approximately 100km northwest of Seal Rocks. A long-term time series was obtained with 8 daily measurements at 3-hour intervals. Due to gaps in sampling effort, a subset of the daily measurements that were consistently sampled throughout the time series was taken from 0:00; 09:00 and 15:00 hours. From this subset, mean seasonal values on an annual basis were calculated. Direction values were derived based on circular mean values from cardinal compass bearings. Preliminary analysis showed that wind speed varied depending on direction of the cardinal compass defined as: north, south, east and west. Both wind speed and the interaction between speed and direction were then included in the analysis.

To determine if broad scale oceanographic processes are linked to variation in prey presence or absence, datasets for both Southern Annular Mode (SAM) and Southern Oscillation Index (SOI) were obtained. The SAM index indicates the variation in westerly winds oscillating around Antarctica. Where the SAM index is negative, the band increases around Antarctica and

results in low-pressure weather systems over Australia and stronger westerly winds. SAM anomaly data were obtained from the British Antarctic Service (BAS) in two different datasets. Annual records were obtained from the BAS website (http://www.antarctica.ac.uk/bas research/data) and monthly records were obtained from the BAS Natural Environment Research Council website (http://www.nercbas.ac.uk/icd/gjma/sam.html). The monthly dataset was pre-standardised as outlined in Marshall (2003), therefore the data was not standardised again. SOI data were obtained from the NOAA Climate Prediction Centre as monthly anomaly values. These data are based on centred 30-year periods of Oceanic Niño Index and provide a measure of the El Niño-Southern Oscillation (ENSO). In this index El Niño conditions are defined as five consecutive months above the set threshold of 0.5 and La Niña conditions are defined as five consecutive months below the set threshold of -0.5. The SOI data were provided as anomalies, therefore the dataset was not further standardised.

Data analysis

Frequency of occurrence

The frequency of each prey species, *i*, was calculated as per the equation: $F_i = n_i/(n-e)$ where n_i is the number of samples containing species *i* in a sampling period (month, season or year), n and e are the total number of samples and empty samples collected in a sampling period, respectively. When calculating %FO 'empty' samples were defined as all samples without hard parts or with only unidentifiable remains and unclassifiable remains. The %FO was calculated at seasonal and annual time scales by aggregating all samples within that time period. Seasons were defined as per the austral calendar beginning on the first day of a defined month: December for summer; March for autum; June for winter; and September for spring. Main prey was defined as accounting for >10% %FO in any year or >5% of %FO across all years. For modelling purposes a second dataset was created from %FO, identified as presence (number of scats with species *i* present) and absence (number of scats with species *i* absent) of the main nine prey species at a seasonal timescale. The %FO of a species from this second dataset was the response variable included in all models.

Modelling

I applied both Generalised Additive Models (GAM) and Generalised Additive Mixed Models (GAMM) to determine if environmental variation was correlated with the presence of prey in

the seal diet. GAMs can accommodate multiple complex relationships between the covariates and response variables (Wood, 2006). They can also be applied to data with binomial errors (Hastie, 1990). Model selection by Akaike Information Criterion (AIC) values can be applied to GAMs with a non-gaussian distribution (Burnham and Anderson, 2004). However, GAMs cannot account for serial dependence in time series data and can overfit the data (Phillips, 2011). GAMMs build on the GAM structure by allowing the specification of both random effects and correlation structures. The latter can be used to account for serial dependence typically present in time-series data (Wood, 2006). GAMMS with non-gaussian errors cannot rely on AIC or likelihood ratio tests because they are fit using penalised quasi-likelihood (Venables and Ripley, 2002). Therefore GAMs were fit first to identify the model best supported by the data via AIC and GAMMs were then used to fit this best supported model, accounting for serial dependence in the response variable.

In this study, preliminary analyses suggested the degree of serial dependence was relatively low for most species (-0.007 to 0.058). GAMMs with binomial errors and a logit link were fitted to the data to investigate if the presence of prey was correlated with time on a seasonal timescale.

All combinations of covariates (single, double, triple and all) were fitted as GAMs (binomial distribution, logit link function) resulting in 16 candidate models. To investigate the effect of wind direction it was modelled as an interaction with wind speed. The model with the lowest AIC value was then fitted as a GAMM (binomial distribution, logit link function) with a AR(1) correlation structure applied to a combined season/year variable to account for serial dependence (Zuur, et al., 2009). Dropping non-significant terms then reduced the model further. The adjusted R-Squared value from the GAMM summary was used as an indication of variance explained by the final model. All analyses were completed using the R statistical framework version 3.1.2 (R Core Development team, 2015) with models fitted to the data with the "mgcv" package in R - statistical program (Wood, 2006).

Results

Variation in seal diet

Over 17 years and 105 sampling days, 3028 samples (scats and regurgitate) were collected. Fish otoliths from 63 species were identified accounting for \sim 90% of the items in the diet (n=10934) and cephalopods beaks from 8 species were identified accounting for just under 10% of the items in the diet (n=1115). To calculate the importance of each species in the diet, the frequency of occurrence (%FO) of each species within a sample was calculated at seasonal and annual timescales.

The %FO of species in the seal diet varied over time annually (Figure 1; Figure 2) with 8 species found in more than 70% of the samples (mean %FO >10% per year). There were notable shifts in the main species during the earlier part of the study: red cod in 1998 and 1999, leatherjackets in 2000 and 2001, and redbait from 2002 to 2005 (Figure 1). From 2006 jack mackerel and leatherjacket both dominated the diet. The prevalence of pilchard increased from 2012 to 2014 with a maximum %FO of 14% in 2012. The %FO of barracouta %FO was highest in 1999 and 2000 at 22% and 23% respectively and gurnard %FO highest from 2012-2014 at 16%, 25% and 23% respectively. The most dominant cephalopod species was arrow squid contributing 5% %FO. Other squids, predominantly the cuttlefish *Sepia apama* contributed 4.7% of %FO.

The %FO of species also varied seasonally (Figure 2). Leatherjacket was consistent with %FO above 10% in all sampled winter and summer seasons and 80% of all autumn seasons. In the beginning of the time series barracouta %FO was higher in summer and spring with a maximum %FO of 37% in the summer of 1998, and at 31% and 34% in the following summers of 1999 and 2000 respectively. In the four years redbait dominated the diet from 2002 to 2005 the %FO was above 20% in autumn and winter and peaked at 55% in autumn of 2005, however %FO was still above 10% in both spring and summer except in 2004 where %FO was at 9% in spring and no sampling was done in summer. From 2006 when jack mackerel dominated the diet %FO was high in both summer and autumn seasons at 36% and 15% respectively and continued in this pattern through to 2014 where the %FO was at 19% in summer and 14% in autumn. Pilchard was more prevalent in summer and autumn with %FO highest at 25% and 14% in 2014 respectively. In the years 2012-14 when gurnard %FO was highest in the diet, it was most prevalent in winter with a maximum %FO of 36% in winter 2014, and at 31% and 23% in the

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winters of 2013 and 2012 respectively. Cephalopod presence was seasonal with %FO highest during autumn 2007 at 25% and above 10% in autumns from 2006-08.

Prey size classes

Of the 2084 otoliths in pristine condition, 1319 were from main prey species. From this selection prey size classes were determined for red cod, pilchard, jack mackerel and redbait species (Table 3). Measurements are presented here as the mean value plus or minus the standard deviation. All pilchard were <84mm indicating that only juveniles of these this species were found in the diet. The size of red cod ranged from 14-347mm (mean=152±8mm, n=127) with 3% of red cod found to be of adult size >315mm (n=4). The size of jack mackerel ranged from 84-352mm (mean=196±4mm, n=500), with 0.6% of jack mackerel of adult size >315mm (n=3). The size of redbait ranged from 91-268mm (mean=141±3, n=564) with 5% of adult size >157 mm (n=30).

Environmental variation over time

Five environmental covariates were investigated as predictors for the diet of the Australian fur seal over time. Mean annual sea surface temperature (SST) ranged from 14.8-16°C (mean 15.5± 0.1°C) and showed a gradual increase throughout the time series (Figure 3a.). In 1999 SSTs were notably low on average with a mean value of 14.8°C compared to the overall mean of 15.5°C (range=14.8-16°C). SST was highest in 2012 with a mean value of 15.9°C (range=12.6-19.3°C) and remained above the overall mean in 2013 and 2014. SOI varied with both El Niño and La Niña events occurring during the time series (Figure 3b). El Niño events occurred in 1998, 2002/2003, 2006, and in 2009/2010 (Bureau of Meteorology, 2015). La Niña events occurred in 1998 until 2001; 2007/2008; and in 2010, 2011 and 2012 (Bureau of Meteorology, 2015). The SAM index was highly variable with the strongest positive index (3) recorded in 2000 (Figure 3c). The strongest negative SAM index was recorded in 2002 at -2. In 2010 the SAM index was strongly positive with two seasons (winter and spring) above the mean at 2.35. The mean overall wind strength was 17 kmh⁻¹ (range: 14-20 kilometres/hour (kmh⁻¹)). Wind strength was most variable in year 2002 with strong winds from a southerly direction (Figure 3d). Wind strength varied upon direction, with stronger wind on average from the south (Figure 4).

Environmental effects on prey

GAMs were fitted to the %FO of each of the main prey species identified in the seal diet with all possible combinations of covariates (see red cod example: Table 4 and supplementary material). The GAM with the lowest AIC value for redbait, jack mackerel, squid, leatherjacket and pilchard species included all the covariates; for barracouta and red cod the best model included SST, SOI and wind; for gurnard the best model included SOI, SAM and wind; and for arrow squid the best model included SST, SAM and wind (Table 5).

Southern Oscillation Index

The GAMM results showed that SOI correlated to %FO of three main prey species (Table 6). A positive SOI (El Niño conditions) was significantly correlated with the presence of red cod (p=<0.001) (Figure 5a) with the model explaining 14% of the variation (Table 6). The 1997/1998 El Niño was one of the strongest on record at 1.6 SOI compared to the mean for the entire time series at 1.2 and longest at 13 months compared to the mean duration for the entire time series at 11.7 months. The presence of red cod was highest in 1998 with a %FO of 53% (Figure 5b). In autumn 2002 and autumn and winter in 2006 El Niño conditions were present again and red cod %FO was 22% and 24% respectively (Figure 5b). The presence of pilchard was also positively correlated with SOI (p=<0.001) (Figure 5c) however the model was weak, explaining -3% of the variation present, with none of the predictors explaining the variability in %FO (Table 6). Pilchard recently reappeared in the seal diet on average contributing 23% %FO in 2014 (Figure 5d). This coincided with a drawn out transition phase from La Niña to El Niño (Bureau of Meteorology, 2015). The presence of jack mackerel was also correlated with SOI (p=<0.001) (Figure 5e). The GAMM model showed that SOI events explained 16% of the variation of jack mackerel in the diet (Table 6). The %FO of jack mackerel peaked when the SOI was relatively neutral. In 2004 and 2013 the SOI was neutral and the annual %FO of jack mackerel was 27.9% and 49.7% respectively. %FO of jack mackerel in spring was >50% in both these years (Figure 5f). In 2008 a weak La Niña event occurred and jack mackerel %FO was also high at 30.5% (Figure 5f).

Other environmental predictors

Following the model selection process I found no correlation between sea surface temperature, wind speed and direction or SAM in predicting %FO of main prey items of Australian fur seals.

Discussion

Large-scale environmental processes drive biological changes at various temporal scales. This study showed temporal variation in the diet of Australian fur seals at Seal Rocks, Bass Strait, from 1998-2014. Large-scale environmental processes, such as the El Niño Southern Oscillation (ENSO), are known to drive physical and biological processes within marine ecosystems (Fogt and Bromwich, 2006, Dann and Chambers, 2013, Sebille, et al., 2014) and were therefore expected to influence prey assemblages within Bass Strait. The seal diet dataset spanned multiple El Niño Southern Oscillation (ENSO) events, and %FO of three species in the seal diet was correlated with the Southern Oscillation Index (SOI) as a measure of ENSO.

This study confirms variation in the diet of Australian fur seals exists at both annual and seasonal time scales, suggesting temporal variation of prey species exists within the Bass Strait marine ecosystem. The prey species identified in this study were comparable to previous studies on the diet of Australian fur seals (Hume, et al., 2004, Littnan, et al., 2007, Kirkwood, et al., 2008), however they were not over a time series of this length. Similar to previous studies (Hume, et al., 2004, Littnan, et al., 2007, Kirkwood, et al., 2008) a high number of prey species were identified, however only eight of these species were found in more than 70% of the samples. The hard part analysis used in this study is limited to identifying remains of prey species that survive passing through the digestive tract (Tollit, et al., 1997). Other techniques such as pyro-sequencing DNA have found cartilaginous species in the diet of Australian fur seals (Deagle, et al., 2009). A recent review of diet analysis techniques of marine mammals, demonstrated that systematic sampling of diet using hard part analysis provides an indication of diet composition over time and is a valid technique for detecting large scale changes in the diet of pinnipeds (Bowen and Iverson, 2013). By applying this technique, prey identified in this study did not vary from those identified by Kirkwood, et al. (2008), which used the same dataset until 2006, with the exception of pilchard.

The fluctuation of pilchard abundance in South Australian and Bass Strait marine ecosystems has been previously documented in the diet of seabirds and seals (Page, et al., 2005, Kirkwood, et al., 2008, Chiaradia, et al., 2010). However, until now it has not been documented as a main prey item of Australian fur seals. From 2012, pilchard made up >10% of the diet of Australian fur seal each year. The pilchard population within Bass Strait underwent a mass mortality, the largest ever recorded for one species of marine fish, in 1995 and a second smaller mortality

event in 1998 (Whittington, et al., 2008, Chiaradia, et al., 2010). This population decrease altered the trophic structure of the marine ecosystem in Bass Strait (Kirkwood, et al., 2008). Pilchards may have been present in the diet of Australian fur seals pre-1998, however the appearance of pilchard as a main prey item from 2012 onwards suggests the pilchard population has increased, which has also been documented in commercial fisheries. Pilchards are a commercially valuable species, caught in the Small Pelagic Fishery off southern Australia (Ward, et al., 2012). The findings from this present study could be applied in ecosystem based modelling (e.g. Atlantis) for fisheries management within Bass Strait to further develop the sustainable practices of the Small Pelagic Fishery. The appearance of pilchard in the seal diet was also significantly linked to large-scale environmental variation - the SOI.

The present study showed that SOI is significantly correlated with prey-specific variation in Australian fur seal diet. However, the relationship is weak for three of the main prey species identified. These findings are consistent with previous research by Ward and Staunton-Smith (2002), with the presence of pilchards in this study correlated with El Niño events. El Niño events influence the Bonney upwelling system off the coast of South Australia, and therefore the productivity of the area (Middleton, et al., 2007). The correlation identified with La Niña and jack mackerel is consistent with previous research by Jordan, et al. (1995) who identified the spawning of this species occurring in summer during times of high SST and La Niña events. The results of the present study suggest that large-scale environmental processes influence presence of prey in the diet of Australian fur seals in Bass Strait, supporting previous research by Knox, et al. (2014). Knox, et al. (2014) identified positive correlations with SOI and body growth in Australian fur seals, inferring that SOI drives prey availability to seals. Hoskins and Arnould (2014) also determined SOI has an impact on dive effort of female Australian fur seals from Kanowna Island, Bass Strait. However, research by Gibbens and Arnould (2009) at Kanowna Island found no correlation between SOI and biological variables (pup production; timing and synchrony of breeding and female body condition). They therefore hypothesised that prey availability in the Bass Strait continental shelf region is temporally stable. The work by Gibbens and Arnould (2009) was performed over 10 years (1997-2007), whereas the present study identifies correlations with SOI and the %FO of prey over 17 years, covering an additional 2 El Niño events. Other fine scale environmental parameters such as SST may influence prey presence in Bass Strait (Middleton, et al., 2007).

Increases in SST are already driving changes in the coastal marine environment in south-eastern Australia (Last, et al., 2011, Lough and Hobday, 2011). SST has been previously observed to alter prey of high trophic level predators within the Bass Strait marine ecosystem (Gibbs, 1992, Kirkwood, et al., 2008). Increases in SST have also been predicted to affect availability and distribution of prey for marine mammals (Schumann, et al., 2012) The present study did not identify a correlation between SST and %FO of prey in the seal diet. In a previous analysis performed by Kirkwood, et al. (2008), using the same dataset up until 2006, a trend between SST and redbait was apparent. This difference between the present study and that by Kirkwood et al. (2008) is presumably due to the increase in the length of the time series in this study and the application of contemporary modelling techniques. The coarse scale of the data may explain the lack of correlation, or that SST only provides surface values and not temperature changes occurring in the water column. In addition to SST, other fine scale environmental parameters such as wind, driven by larger scale processes of SAM may also influence prey movement in Bass Strait and the diet of Australian fur seals.

The SAM influences westerly winds in southern Australia (Lovenduski and Gruber, 2005). Westerly winds drive nutrient rich upwelling water from the Bonney upwelling system into western Bass Strait and influence the flow of currents through Bass Strait (Middleton, et al., 2007, Sandery and Kämpf, 2007). Upwelling changes primary productivity within entire ecosystems, influencing the prey available to higher trophic level predators (Armbrecht, et al., 2014). The Bonney upwelling has been previously linked to foraging and breeding success of top predators, including the Australian fur seal in Bass Strait (Gibbens and Arnould, 2009, Berlincourt and Arnould, 2015). Zonal wind strength has been correlated with foraging effort in Australian fur seals at other breeding colonies in Bass Strait (Hoskins and Arnould, 2014). Modelling predicts that SAM will influence the strengthening of the East Australian Current occurring between latitudes 44S & 55S, including Bass Strait (Cai, et al., 2005). In the present study no correlation was found between prey presence in the Australian fur seal diet and the SAM index or wind speed and direction. This may be due to the large scale on which SAM operates or that other large scale processes, as shown in this study (ENSO), influence prey presence. However, Fogt and Bromwich (2006) showed that SAM and ENSO are coupled, thereby the influences of SAM and wind on the ecology of prey within Bass Strait requires further investigation. It is not only the presence of and the driving forces of prey in the diet of the Australian fur seal that is interesting, but also the size of the prey.

Very little variation was found with prey size in this study, with predominantly juvenile fish of redbait, red cod, jack mackerel and all pilchard fish of juvenile size observed in the diet. As pilchards, as previously motioned, mass mortality in southeast Australia in both 1995 and 1998 (Chiaradia, et al., 2010) and juveniles of this species may be highly abundant, however, it is interesting that they may be targeting juvenile fish of multiple main preys. Perhaps juveniles are easier to catch and manipulate or are higher in abundance than larger fish. Due to this lack of variation, I did not model the results, and further information is required before pursuing further research into the size of prey the seals are eating. Firstly, the estimation of prey size in this study was limited as no regression equations or correction factors are available to calibrate for the otolith erosion caused by digestion. To account for this we only measured otoliths considered in pristine condition, with limited erosion. Secondly, larger sized fish may be broken up prior to ingestion, by shaking at the surface, as shown in captive feeding trials by Hocking, et al. (2014), biasing the measuring of otoliths to smaller individuals who could be swallowed whole. Therefore, interpretation of the prey size classes in this study requires validation through application of regression equations or experimentally derived correction factors (Tollit, et al., 2003). With neither available for these fish species more research is needed to better understand the biology and behaviour of the prey species. Perhaps fisheries data could provide some insight into the availability of these species and their relative size classes in Bass Strait.

Other factors such as physiology, foraging behaviour and individual specialisation may also influence the selection of prey by different cohorts of Australian fur seals, and therefore prey the observed diet (Arnould, et al., 2011). Physiology of seals varies between age, gender and life cycle of seals affecting their ability to dive and obtain certain prey items (Renouf, 1991). Australian fur seals also use various prey capture techniques (Hocking et al. 2014) that may result in individual variation within diet. This study is limited as the sex, age and breeding status of the samples collected for hard part analysis was unknown, therefore the study is limited to investigating the diet of the general population from Seal Rocks.

The study was also limited in some seasons by sampling effort. To obtain faecal samples that will accurately provide data on the diet of a marine mammal >60 samples per time period is recommended (Trites and Joy, 2005). On an annual timescale this study exceeds the recommendations (Table 1.), however not all seasons have been sampled adequately, with two summer seasons and five spring seasons lower than recommended and six summer seasons and one spring season lacking data altogether (Table 2.). Therefore, interpretation of the seasonal

variation in the diet requires some consideration. For example, redbait does not appear in the diet in summer 2004, however no sampling was completed in that season.

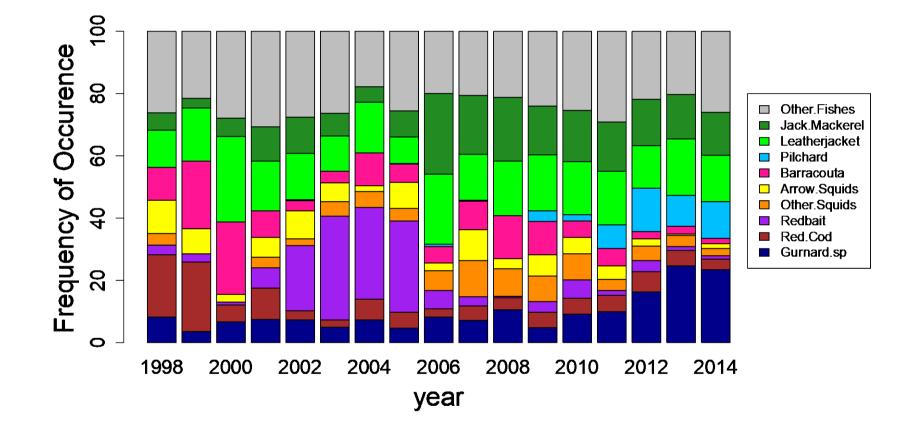
In addition to the correlations identified, the lack of correlations for the other five main species is also of interest. Other main fish species such as gurnard and redbait did not appear to be influenced by the environmental predictors investigated in this study. However, previous work by Kirkwood, et al. (2008), identified SST influences redbait presence in the seal diet. SST influences the reproduction of Cephalopod species, such as squid species identified in the diet, however no correlation was identified in this study. Previous studies identified that arrow squid demonstrate extreme plasticity to environmental conditions (Jackson, et al., 2003). The lack of correlation found in this study may be due to either high adaptability of these prey species in Bass Strait or the environmental predictors investigated. As previously discussed environmental predictors can vary geographically; therefore the findings of this study are also restricted to Australian fur seals in central Bass Strait.

Diet can vary at different colonies across the range of Australian fur seals. The samples from this study are from Seal Rocks located in northern Bass Strait. Seal Rocks is approximately 200kms from the edge of the continental shelf. Other Australian fur seal colonies to the west and east in Bass Strait are closer to the continental shelf slope and diet can vary with proximity to the shelf slope (Littnan, et al., 2007). Additionally tracking studies have identified that there is small overlap in foraging areas between larger breeding colonies (Arnould and Kirkwood, 2008, Kirkwood and Arnould, 2012), that may influence the diet of seals at those sites. Geographical location changes the extent to which environmental parameters influence productivity in an area, for example: areas closer to upwelling are generally more productive than those in northern Bass Strait. Therefore environmental parameters may correlate differently to seal diet in other areas, due to differences in local ocean oceanography and biological production. Other environmental parameters (e.g. chlorophyll A) that were not explored in this study, because they are not available for this time series, may influence the diet of Australian fur seals in those areas. Extending the regular collection of long-term data to several Australian fur seal colonies across their range and considering other environmental variables (e.g. chlorophyll A) could further develop our understanding of how environmental factors influence the diet of Australian fur seals. However, this is difficult due to the remote location of sites, expense of work, and the weather-dependent nature of boat work. In addition to geographical location of the study site the impact of fisheries on prey assemblages should be considered.

The impact of commercial fisheries on prey species for top predators can range from direct harvest to indirect cascade effects and the removal of species at various trophic levels (Daskalov, et al., 2007). Historically, commercial fishing in the form of trawling was more active in this region. However, due to a buyback scheme in 2005/2006, trawling activity has reduced (Minnegal and Dwyer, 2008). Fishing pressure in this area has decreased with quota restrictions based on ecosystem-based modelling and there is a low level of spatial overlap between the Australian fur seals and three of the Bass Strait fisheries: gillnet; Danish seine and otter trawl (Arnould and Kirkwood, 2008). The impact on fisheries catch on the diet of Australian fur seals has not been investigated during this study, and previous work by Kirkwood, et al. (2008) did not find any correlations between prey assemblages and catch per unit effort. However the reduction in trawling activity coincided with notable shifts in the main species in the Australian fur seal's diet during 2006 (this study). Therefore, further investigation is recommended.

In summary, this study has demonstrated that the diet of Australian fur seals changes temporally and is influenced by large-scale processes. The results from this study further develop our understanding of how large-scale environmental processes influence ecological changes in the Bass Strait marine ecosystem. I applied contemporary modelling techniques to long-term diet data to identify correlations between prey assemblages and identify the influence of long-term environmental change on prey assemblages. This approach has potential to be applied into the future to monitor the ecological changes occurring in marine coastal environments.

Figures and tables:



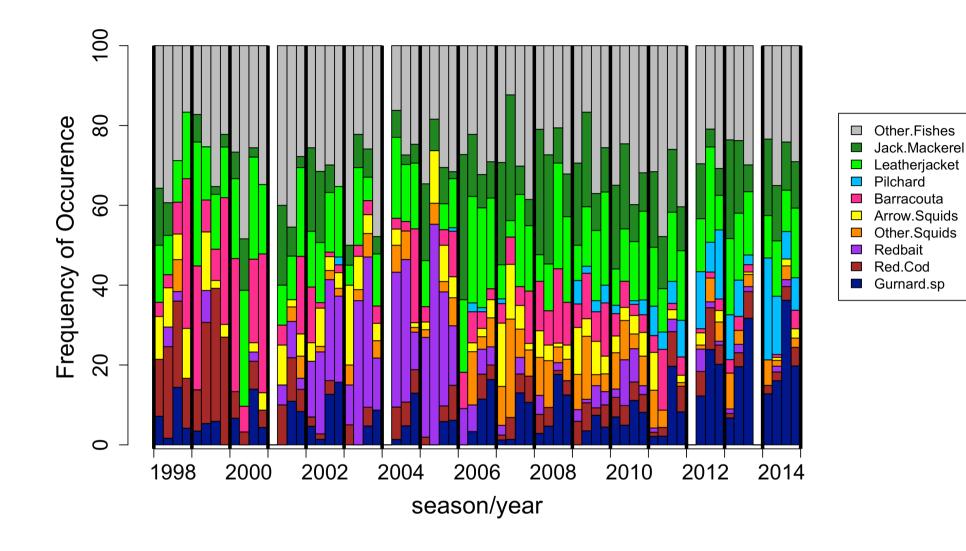


Table 1. Annual sample sizes of scat and regurgitate collected for hard part analysis.

| | | | | | | | | | Year | | | | | | | | |
|-------------|------|------|------|------|------|------|------|------|------|------|------|------|------|------|------|------|------|
| | 1998 | 1999 | 2000 | 2001 | 2002 | 2003 | 2004 | 2005 | 2006 | 2007 | 2008 | 2009 | 2010 | 2011 | 2012 | 2013 | 2014 |
| Sample size | 347 | 323 | 145 | 153 | 358 | 193 | 301 | 442 | 366 | 588 | 421 | 441 | 530 | 482 | 496 | 546 | 349 |

Table 2. Seasonal sample sizes of scat and regurgitate collected for hard part analysis.

| | | | | | | | | | Year | | | | | | | | |
|----------------------|------|------|------|------|------|------|------|------|------|------|------|------|------|------|------|------|------|
| Seasonal sample size | 1998 | 1999 | 2000 | 2001 | 2002 | 2003 | 2004 | 2005 | 2006 | 2007 | 2008 | 2009 | 2010 | 2011 | 2012 | 2013 | 2014 |
| Summer | 101 | 46 | 0 | 0 | 61 | 0 | 0 | 70 | 17 | 110 | 78 | 50 | 174 | 122 | 0 | 70 | 0 |
| Autumn | 88 | 109 | 43 | 29 | 101 | 45 | 99 | 47 | 108 | 81 | 163 | 145 | 72 | 57 | 241 | 178 | 176 |
| Winter | 180 | 61 | 63 | 73 | 115 | 109 | 105 | 180 | 115 | 198 | 118 | 125 | 131 | 160 | 82 | 236 | 70 |
| Spring | 29 | 81 | 39 | 51 | 58 | 39 | 97 | 145 | 126 | 148 | 62 | 121 | 153 | 143 | 130 | 0 | 103 |

Table 3: Prey size classes for prey consumed by Australian fur seals at Seal Rocks from 1998-2014. All equations are from Furlani, et al. (2007). Class JUV refers to juveniles; remaining percentage represents adults i.e. a fish of sexually mature size class.

| Species | Length | n | Mean ± SD (mm) | Sexual maturity (mm) | Range mm | Equation | | | | |
|----------------------|--|-----|----------------------|----------------------------|-------------|-----------------|--|--|--|--|
| Red cod | Total | 127 | 152±8 | 315 | 14-347 | 6.33OL^1.62 | | | | |
| Pilchard Jack | Standard | 99 | 66±3 | 146 | 43-84 | 32.070L^1.35 | | | | |
| Mackerel | Fork | 500 | 196±4 | 315 | 84-352 | 16.796OL^1.3992 | | | | |
| Redbait | Fork | 564 | 141±3 | 157 | 91-268 | 20.125OL^1.2238 | | | | |
| Environmental correl | nvironmental correlates of temporal variation in the | | | | | | | | | |

diet of Australian fur seals

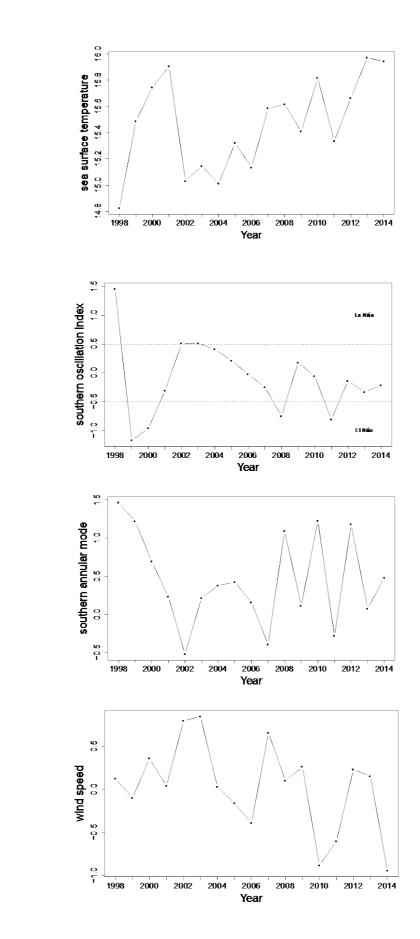


Figure 3. Environmental variation throughout the time series: a) SST; b) SOI; c) SAM and d) Wind speed.

Environmental correlates of temporal variation in the diet of Australian fur seals

Kim Kliska

a)

c)

d)

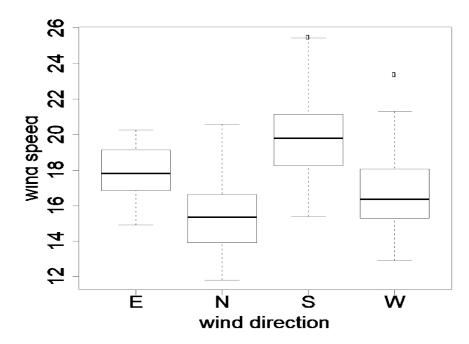


Figure 4. Boxplot showing the mean seasonal wind speed and direction throughout the time series. Direction was measured by the cardinal compass: E=East, N=North, S=South and W=West, outliers are shown for S and W.

Table 4: Generalised additive models results for red cod, an example of the model selection process in descending order. Covariates are the same as those listed in Table 5 (for all other species see Supplementary material).

| Covariates | AIC | ΔAIC | RL | W | rSq | D.exp |
|---------------------------------|--------|--------------|------|------|-------|-------|
| SST+SOI+wind*wind direction | 336.98 | 0.00 | 1.00 | 0.93 | 0.31 | 52.10 |
| SST+SOI+SAM+wind*wind direction | 342.19 | 5.20 | 0.07 | 0.07 | 0.27 | 49.41 |
| SOI+SAM+wind*wind direction | 351.18 | 14.20 | 0.00 | 0.00 | 0.23 | 44.57 |
| SOI+wind*wind direction | 352.82 | 15.84 | 0.00 | 0.00 | 0.21 | 42.96 |
| SST+wind*wind direction | 366.48 | 29.50 | 0.00 | 0.00 | 0.10 | 37.57 |
| SAM+wind*wind direction | 374.54 | 37.56 | 0.00 | 0.00 | 0.17 | 25.11 |
| SST+SAM | 376.33 | 39.35 | 0.00 | 0.00 | 0.16 | 25.17 |
| SST+SOI+SAM | 376.33 | 39.35 | 0.00 | 0.00 | 0.16 | 25.17 |
| SST+SOI | 381.02 | 44.04 | 0.00 | 0.00 | 0.04 | 29.84 |
| wind*wind direction | 381.02 | 44.04 | 0.00 | 0.00 | 0.04 | 29.84 |
| SOI | 381.44 | 44.46 | 0.00 | 0.00 | 0.14 | 20.33 |
| SOI+SAM | 382.27 | 45.28 | 0.00 | 0.00 | 0.14 | 21.06 |
| SST | 387.20 | 50.22 | 0.00 | 0.00 | 0.03 | 26.10 |
| Null model | 424.60 | 87.61 | 0.00 | 0.00 | 0.00 | 0.00 |
| SAM | 425.06 | 88.07 | 0.00 | 0.00 | -0.02 | 1.68 |

AIC= Akaike Information Criterion; Δ AIC = the difference in AIC from that of the best fitting model; RL=Relative likelihood; W=weight; rSq=R Squared; and D.exp=Deviance explained.

Table 5: The best generalised additive models, selected using AIC for all main prey identified in the diet of Australian fur seals. All covariates are seasonal values by year; SST refers to sea surface temperature; SOI refers to Southern Oscillation Index; SAM refers to the Southern annular mode and wind is local wind speed and direction.

| | | | | Deviance |
|---------------|-----------------------------------|--------|-----------|-----------|
| Species | Model | AIC | R Squared | explained |
| Red cod | SST+SOI+ wind*wind direction | 336.98 | 0.31 | 52.10 |
| Redbait | SST+SOI+SAM+wind*wind direction | 343.86 | 0.77 | 80.70 |
| Pilchard | SST+SOI+SAM+wind*wind direction | 177.78 | 0.89 | 91.31 |
| Jack Mackerel | SST+ SOI+SAM+wind* wind direction | 395.45 | 0.27 | 52.56 |
| Barracouta | SST+SOI +wind* wind direction | 335.66 | 0.34 | 59.15 |
| Gurnard sp. | SOI+SAM+wind*wind direction | 398.29 | 0.39 | 55.00 |
| Squid sp. | SST+SOI+SAM+wind*wind direction | 276.06 | 0.41 | 61.88 |
| Arrow Squid | SST+SAM+wind*wind direction | 399.68 | 0.14 | 33.89 |
| Leatherjacket | SST+SAM+SOI+wind*wind direction | 395.45 | 0.27 | 52.56 |

Table 6: Generalised additive mixed model results. The p-values show the significant correlations for Southern Oscillation Index with R-squared adjusted showing the degree of variance explained by the model.

| Species | Covariates | P values (SOI) | R-squared (adj) |
|---------------|------------|-------------------|-----------------|
| Red cod | SOI | <0.00 | 0.14 |
| Pilchard | SOI | < 0.01 | -0.03 |
| Jack Mackerel | SOI | < 0.01 | 0.16 |

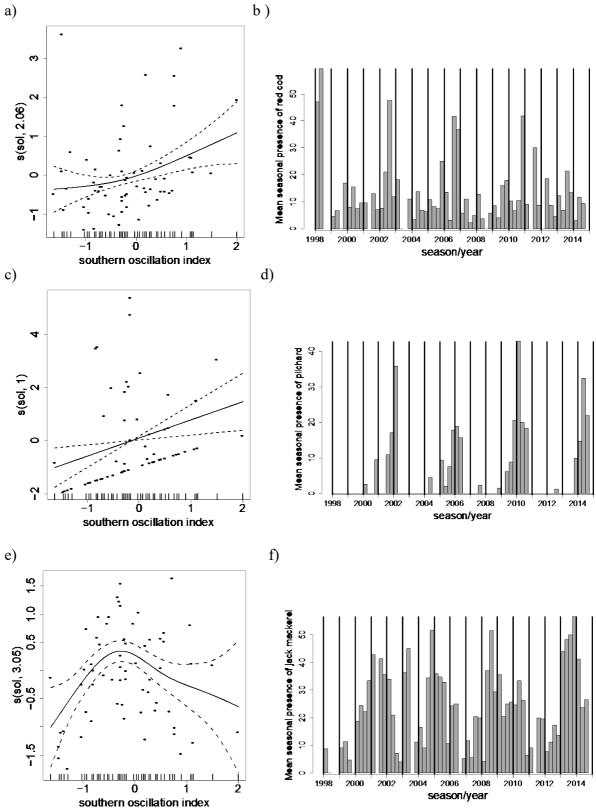


Figure 5: GAM plots from the generalised additive mixed models for significant relationships between frequency of occurrence of prey and the Southern Oscillation Index, the dotted line indicates 95% confidence intervals for model prediction. Mean seasonal %FO of species throughout the time series the black line indicates years, each bar a season. : a and b) red cod; c and d)pilchard; e and f) jack mackerel.

Supplementary information:

Supplementary material is available at the ICESJMS online version of the manuscript.

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Supplementary material

Additional tables:

Table 1: Generalised additive model results for pilchard. The model selection is listed in descending order. All covariates are seasonal values by year; SST refers to sea surface temperature; SOI refers to southern oscillation index; SAM refers to the southern annular mode and wind is local speed and direction.

| Covariates | AIC | Δ AIC | RL | W | rSq | D.exp |
|----------------------------------|---------|--------|------|------|-------|-------|
| SOI+SAM+SST+ wind*wind direction | 177.78 | 0.00 | 1.00 | 0.99 | 0.89 | 91.31 |
| SOI+SAM+ wind*wind direction | 188.12 | 17.57 | 0.01 | 0.01 | 0.84 | 86.68 |
| SOI+wind*wind direction | 208.41 | 41.54 | 0.00 | 0.00 | 0.78 | 79.07 |
| SST+ wind*wind direction | 244.43 | 55.34 | 0.00 | 0.00 | 0.53 | 68.55 |
| SAM+ wind*wind direction | 244.43 | 59.72 | 0.00 | 0.00 | 0.53 | 68.55 |
| SAM+SST+ wind*wind direction | 247.81 | 59.72 | 0.00 | 0.00 | 0.52 | 66.43 |
| Wind*wind direction | 280.22 | 69.17 | 0.00 | 0.00 | 0.56 | 56.93 |
| SOI+SST+ wind*wind direction | 309.87 | 124.13 | 0.00 | 0.00 | 0.50 | 46.84 |
| SAM+SOI+SST | 316.83 | 125.24 | 0.00 | 0.00 | 0.38 | 47.56 |
| SOI+SAM | 323.29 | 154.94 | 0.00 | 0.00 | 0.41 | 43.43 |
| SST+SOI | 366.50 | 168.49 | 0.00 | 0.00 | 0.31 | 29.85 |
| SOI | 380.23 | 211.55 | 0.00 | 0.00 | 0.28 | 28.30 |
| SAM+SST | 416.83 | 238.13 | 0.00 | 0.00 | 0.01 | 16.99 |
| SST | 450.64 | 261.68 | 0.00 | 0.00 | -0.01 | 8.15 |
| SAM | 473.39 | 295.32 | 0.00 | 0.00 | 0.00 | 0.00 |
| Null model | 1120.87 | 317.92 | 0.00 | 0.00 | -1.54 | 70.67 |

Table 2: Generalised additive model results for jack mackerel. The modelselection is listed in descending order. All covariates are the same as Table5.

| Covariates | AIC | ΔΑΙΟ | R L | W | rSq | D.exp |
|----------------------------------|--------|--------|------|------|-------|-------|
| SOI+SAM+SST+ wind*wind direction | 395.45 | 0.00 | 1.00 | 0.50 | 0.27 | 52.56 |
| SOI+SST+ wind*wind direction | 397.21 | 1.76 | 0.42 | 0.21 | 0.27 | 50.34 |
| SOI + wind*wind direction | 397.56 | 2.10 | 0.35 | 0.18 | 0.28 | 50.33 |
| SOI+SAM+ wind*wind direction | 398.50 | 3.05 | 0.22 | 0.11 | 0.28 | 48.40 |
| SOI+SAM+SST | 415.97 | 20.52 | 0.00 | 0.00 | 0.20 | 39.11 |
| SOI+SST | 428.94 | 33.49 | 0.00 | 0.00 | 0.18 | 31.12 |
| SOI+SAM | 429.01 | 33.56 | 0.00 | 0.00 | 0.21 | 31.36 |
| SST+ wind*wind direction | 441.88 | 46.42 | 0.00 | 0.00 | 0.20 | 23.32 |
| SOI | 457.56 | 62.11 | 0.00 | 0.00 | -0.04 | 29.60 |
| SAM+ wind*wind direction | 458.14 | 62.69 | 0.00 | 0.00 | -0.06 | 29.91 |
| SAM+SST+ wind*wind direction | 458.14 | 62.69 | 0.00 | 0.00 | -0.06 | 29.91 |
| Wind*wind direction | 464.76 | 69.30 | 0.00 | 0.00 | -0.04 | 25.12 |
| SAM+SST | 480.95 | 85.50 | 0.00 | 0.00 | 0.03 | 10.20 |
| SAM | 481.78 | 86.32 | 0.00 | 0.00 | 0.00 | 12.00 |
| SST | 500.42 | 104.96 | 0.00 | 0.00 | -0.04 | 3.04 |
| Null model | 500.93 | 105.48 | 0.00 | 0.00 | 0.00 | 0.00 |

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