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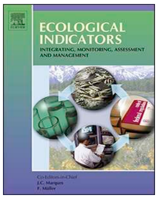

Gentoo penguins as sentinels of climate change at the sub-Antarctic Prince Edward Archipelago, Southern Ocean

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ABSTRACT

Some upper trophic level predators, such as marine mammals, seabirds and large predatory fish have been shown to be useful sentinels for marine ecosystems. Through their demography, diet and foraging behaviour, ecosystem changes associated with climate change can be monitored. The local marine ecosystem at the Prince Edward Archipelago in the Southern Indian Ocean is heavily influenced by the position of the dynamic sub-Antarctic front (SAF) that varies inter-annually in terms of its influence on the local environment. If the SAF migrates southwards, as climate change models have predicted, the abundance of autochthonous and allochthonous prey found within the vicinity of the archipelago will decrease and increase, respectively. We investigated the diet of an inshore forager at the archipelago, the gentoo penguin *Pygoscelis papua*, as a possible sentinel to the expected changes in the prey assemblages in local waters, due to the southward migration of the SAF. We collected stomach content samples from gentoo penguins, using the water off-loading technique, monthly over three years (1994–1996) and then annually during 2012, 2014 and 2015. Prey assemblages within the diet was found to coincide with the proximity of the SAF to the Prince Edward Archipelago as well as the annual life cycles of prey. Due to the plasticity these penguins exhibit in their diet and foraging behaviour, we suggest that they are important sentinel species for the local marine ecosystem of the Prince Edward Archipelago. Regular sample collection from these birds, albeit stomach content samples and/or tissues for stable isotope analysis, should be collected so that variability in the ecosystem can be easily monitored.

1. Introduction

Given that marine ecosystems are highly complex with numerous dimensions, monitoring changes is a daunting task (Hughes et al., 2005). Using upper trophic level (UTL) predators, such as marine mammals, seabirds and large predatory fish, as sentinels of change reduces the challenge of accounting for the multidimensional complexity of marine ecosystems (Boyd and Murray, 2001; Boersma, 2008; Sergio et al., 2008; Gulka et al., 2017). Their demography (e.g. Eerkes-Medrano et al., 2017), diets (e.g. Gulka et al., 2017) or else at-sea distribution (Miller et al., 2009) are influenced by, and therefore often indicative of, the quantity, quality and distribution of available prey. Consequently, UTL predators have been used to study habitats and food webs in relation to the dynamics of prey populations (Soldatini et al., 2016) and oceanographic conditions (Costa et al., 2008).

In the Southern Ocean, the Antarctic Circumpolar Current (ACC) is a key and primary factor for shaping marine habitats (Tynan, 1998). Conflicting models predicted that, in response to climate change, the westerly wind belt will intensify and shift poleward, which may (Thompson and Solomon, 2002; Downes et al., 2011; Kim and Orsi, 2014), or may not (Graham et al., 2012; Chapman, 2017), cause the ACC and its associated frontal systems to shift southwards. If the ACC and its associated fronts shift, lower trophic level species are expected to move south as the oceanographic conditions in which they are

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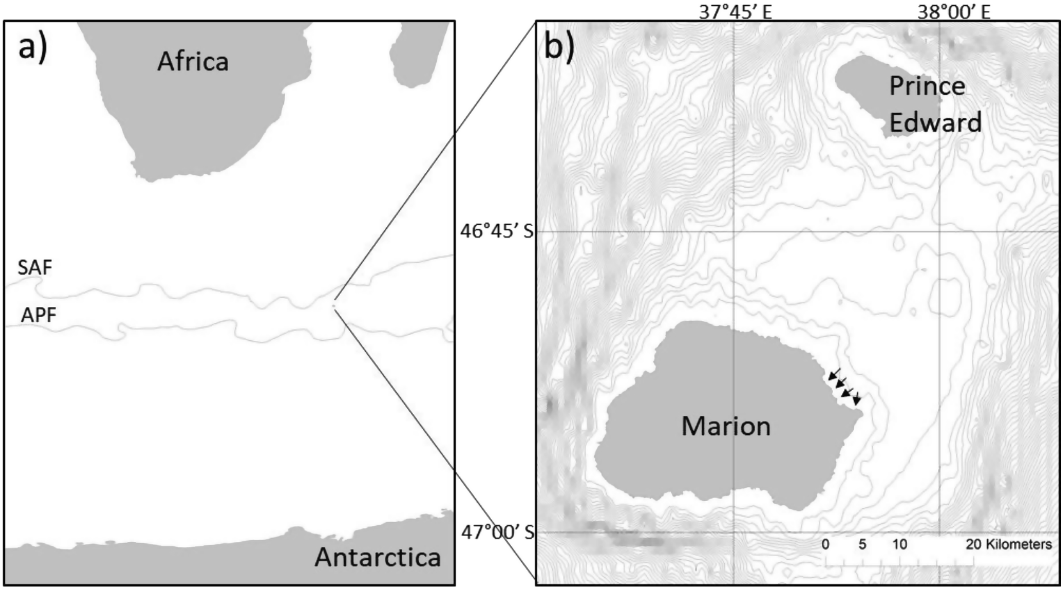

Fig. 1. a) Schematic map of the position of the sub-Antarctic front (SAF) and the Antarctic Polar Front (APF) between Africa and Antarctica. b) The Prince Edward Archipelago, consisting of Prince Edward (top) and Marion (bottom) islands. Arrows indicate locations of colonies where gentoo penguins were sampled for stomach contents. Lines indicate isobaths at 50 m intervals.

currently found move poleward (Constable et al., 2014). The effects this will have on UTL predators will primarily depend on their flexibility to exploit alternative prey or ability to follow changes in prey distributions (e.g. Péron et al., 2012).

Lying in the direct path of the ACC, between the sub-Antarctic (SAF) and Antarctic Polar (APF) Fronts, the Prince Edward Archipelago (Fig. 1) seasonally provides a critical breeding and moulting habitat for up to five million UTL predators, including flying seabirds, penguins and seals (Ryan and Bester, 2008). Ascending from a depth of approximately 3000 m, the archipelago comprises two islands, Marion and Prince Edward islands, which are located 19 km apart and separated by a shallow inter-island shelf that ranges from 40 to 400 m in depth (Pakhomov and Froneman, 1999). The local oceanographic conditions are important in governing food availability to the UTL predators, particularly inshore foragers, at the Prince Edward Archipelago. These conditions are strongly influenced by the latitudinal position of the SAF relative to the islands (Perissinotto and Duncombe Rae, 1990; Perissinotto et al., 2000; Ansorge and Lutjeharms, 2002). In general, when the SAF lies far to the north of the islands, the flow rate of the ACC in the proximity of the islands is reduced, which contributes to the formation and entrapment of anti-cyclonic eddies in the inter-island shelf and downstream region of the islands (Perissinotto et al., 1990, 2000; Ansorge and Lutjeharms, 2002). Freshwater runoff from the islands which adds macronutrients from faeces and moulted remains of land-based predators together with increased water stability promotes the development of phytoplankton blooms (Perissinotto et al., 1990). This phenomenon, known as the “island mass effect”, provides an important autochthonous food source in the vicinity of the islands, particularly for the benthic-rich community of the inter-island shelf (Perissinotto, 1992; Pakhomov and Froneman, 1999). By contrast, when the SAF lies in close proximity to the islands there is an intensification of the flow rate of the ACC at the Prince Edward Archipelago, resulting in a flow-through system that prevents the formation of eddies (Perissinotto et al., 2000). During these conditions, allochthonous food sources are dominant in the vicinity of the islands, being transported there from the upstream region of the easterly flowing ACC (Perissinotto, 1992; McQuaid and Froneman, 2008).

In response to a south-ward migration of the ACC and its associated fronts (Thompson and Solomon, 2002; Downes et al., 2011; Kim and Orsi, 2014), it is anticipated that the permanent flow through system will predominate, culminating in the decreased frequency of occurrence of the island mass effect (Pakhomov et al., 2004; Ansorge et al., 2009; Allan et al., 2013). This will most likely result in a decrease of autochthonous prey items available for inshore UTL foragers at the islands (Pakhomov et al., 2004; Allan et al., 2013; Crawford et al., 2014). In agreement with this hypothesis, this possible change seems to be reflected by some UTL predators that breed at the islands. Over the past two decades, the populations and breeding success of two inshore foraging UTL predators, the Crozet shags *Leucocarbo melanogenis* and the gentoo penguins *Pygoscelis papua,* have demonstrated significant and congruent declines (Crawford et al., 2014). By contrast, the breeding populations of some UTL predators that predominantly forage offshore have remained stable or increased, including the sooty *Phoebetria fusca* and wandering *Diomedea exulans* albatrosses, southern *Macronectes giganteus* and northern *M. halli* giant petrels, and the Antarctic fur seal *Arctocephalus gazella*. Notable exceptions are the sub-Antarctic fur seal *A. tropicalis* and light-mantled albatross *P. palpebrata*, which breeding populations on the island have shown a declining trend (Hofmeyr et al., 2006; Ryan et al., 2009; Schoombie et al., 2016; Wege et al., 2016).

The gentoo penguins at Marion Island are good potential candidates as sentinel species of the response of the island ecosystem to global climate change as they predominantly feed within 20 km of the islands, with the inter-island shelf forming an important foraging area (Adams and Wilson, 1987; Carpenter-Kling et al., 2017). In addition, the gentoo penguins display a large degree of foraging plasticity (Lescroël and Bost, 2005), feeding on what is spatially and temporally available (Adams and Klages, 1989; Lescroël et al., 2004; Handley et al., 2016; Waluda et al., 2017; Xavier et al., 2018). The breeding population of gentoo penguins at Marion Island is relatively small, consisting of approximately 700 breeding pairs (Crawford et al., 2014). Since the mid 1990′s, the population of gentoo penguins at the island declined by over 50%, suggesting that there may have been a change in prey availability in the shallow waters around the Prince Edward Archipelago (Crawford et al., 2014).

The aim of this study was to investigate the diet of gentoo penguins at Marion Island over the past two decades and identify possible influences of the position of the SAF on the prey assemblages in the diet. We predicted that there would be a prey composition change in the diet of these birds since the 1980s (Adams and Klages, 1989) brought about by a southward shifting SAF, likely as a result of global climate change. We predicted that as the flow rate of the ACC around the archipelago increases with the southward migration of the SAF, allochthonous prey items, such as *Euphausia vallentini*, will become more dominant within the diet of the birds and autochthonous prey, such as *Nauticaris marionis*, less so (Allan et al., 2013).

2. Materials and methods

2.1. Sample collection

Our study was conducted at four colonies along the north-east coast of Marion Island (46°55′S, 37°40′E, Fig. 1). These colonies are within 7 km of one another and account for approximately 37% of the island's gentoo penguin population (Crawford et al., 2003a). Stomach content samples were collected monthly between March 1994 to December 1995 and July to December 1996, July to August 2012, January and August 2014 and August 2015.

The Convention for the Conservation of Antarctic Marine living Resources Ecosystem Monitoring Programme's (CCAMLR – CEMP) water-offloading technique described in SC-CAMLR (2003) for obtaining stomach content samples was applied. After collection, they were either kept in 70% ethanol or frozen at −20 °C until further processing.

Ethics clearance for the study was obtained through the Nelson Mandela University Research Ethics Committee A14-SCI-ZOO-012 and supported by the Prince Edward Islands Management Committee.

2.2. Stomach content analysis

All samples were sorted according to CEMP procedures (SC-CAMLR, 2003). Where possible, prey species were identified to the lowest possible taxonomical level. Fish were identified mostly from otoliths using available identification guides (Fisher and Hureau, 1985; Hecht, 1987; Gon and Heemstra, 1990; Williams, 1990a; Smale et al., 1995; Reid, 1996) and the number of individuals consumed was recorded as the highest number of right or left otoliths present for that species. To allow for temporal comparisons with previously published (Adams and Klages, 1989) or archived data (Department of Environmental Affairs unpub. data), all Notothenid otoliths measuring < 1 mm were classified as juvenile Nototheniids, bearing in mind that strictly speaking otoliths up to 3.0 mm should be considered as juveniles (Curio et al., 2014). Cephalopods were identified from their beaks (Clarke, 1986; Smale et al., 1993; Xavier and Cherel, 2009) and the number of individuals taken as the highest number of upper or lower beaks of that species. Crustaceans were identified by their morphology (Baker et al., 1990; Branch et al., 1991). The number of crustaceans in a sample was calculated by dividing the cumulative mass of a species by the average mass of one individual of that species (Adams and Klages, 1989). Presence of stones or plant material in the sample was excluded from further analyses (Adams and Klages, 1989).

2.3. Composition of samples

Prey items were initially described by the following terms:

Percentage frequency of occurrence (%FO): the proportion of diet samples containing the prey taxon compared to all diet samples examined per sampling session.
Percentage numerical abundance (%N): the proportion of the total number of individuals of one prey taxon compared to total number of all prey items per sampling session.

Samples were then described by an integrative value, the Simpson's dominance index (λ"), which is used to estimate a prey type's dominance and commonness in the diet (Formula 1, where p_i^2 is the number of prey item, *i,* for a particular prey taxa in any one stomach content sample divided by the total number of items in that stomach content sample). Previously, the dominance of a prey item within a diet has been described using both the index of relative importance (e.g. Handley et al., 2016) and Simpson's dominance index (e.g. Molinero and Flos, 1992). Simpson's dominance index was chosen here as the mass of prey items which is required by the index of relative importance, was not recorded. By dividing λ by the number of stomach content samples (z), the index was rendered independent of sample size as well as incorporated the frequency of occurrence of the prey items (Formula 2). Dominance values for each taxon were expressed as a percentage using Formula 3. This index takes into account the %FO and %N of each taxon (Molinero and Flos, 1992). However, if a taxon has a low %N but a high %FO it will receive a higher dominance value than a prey item that has a high %N but a low %FO.

$$\lambda = \sum p_i^2 \tag{1}$$

$$\lambda' = (\lambda/z) \tag{2}$$

$$\lambda'' = (\lambda'/\sum \lambda') \times 100 \tag{3}$$

2.4. Grouping of samples

Gentoo penguins initiate breeding at Marion Island during the austral winter and have an extended and relatively asynchronous breeding season as opposed to gentoo penguins breeding further south (Bost and Jouventin, 1990; Lynch, 2013). In general, adults start returning to breeding colonies from the beginning of June. Incubation begins in mid-June and is completed by mid-July, with hatching occurring 35–40 days after laying. Crèches start forming from beginning to mid-September and fledging occurs approximately two months later (Williams, 1990b; Crawford et al., 2003a).

To assess dietary variation within and among years, stomach content samples were grouped into six different stages of the annual cycle (Table 1). Stomach content samples were collected from birds returning from the sea, and so the breeding status of the sampled birds was unknown. Therefore, timing of the various stages was inferred from the breeding chronology of gentoo penguins on the island for the

Table 1
Number of stomach content samples collected from gentoo penguins at sub-Antarctic Marion Island during the different stages of the annual cycles of 1994–1996, 2012, 2014, 2015. The start date of each stage in brackets (Crawford et al., 2003a; Departmental of Environmental Affairs, unpub. data).

Year	1994	1995	1996	2012	2014	2015
Breeding stage						
Pre-laying	4 (31-May)	5 (26-Jun)				
Incubation	11 (27-Jun)	10 (02-Jul)	10 (11-Jul)	5 (05-Jul)		
Brooding	7 (01-Aug)	4 (21-Aug)	6 (15-Aug)		10 (01-Aug)	10 (01-Aug)
Crèche	16 (30-Aug)	16 (12-Sep)	11 (15-Sep)			
Post-breeding	11 (10-Oct)	16 (11-Nov)	5 (05-Nov)			
Late post breeding		9 (01-Jan)			12 (01-Jan)	

corresponding annual cycle (Table 1; Crawford et al., 2003a; Department of Environmental Affairs unpub. data).

The different stages were defined as follows:

1. Pre-laying: When adults start returning to the breeding colony, approximately 2–4 weeks before eggs are laid.
2. Incubation: When partners alternate incubating the egg(s).
3. Brooding: When partners alternate feeding and brooding the chick (s).
4. Crèche: When the chick(s) is no longer brooded but both partners are feeding it. As dates for end of the crèche period were not recorded, the crèche period was taken to be approximately 50 days (Williams, 1990b).
5. Post-breeding: The gentoo penguins at Marion Island begin to moult in January (Crawford et al., 2003a). Therefore, this period was defined from the end of the crèche period to 31 December.
6. Late post-breeding: Actively foraging before moult phase (Crawford et al., 2003a).

2.5. Oceanography

To assess the relationship between the prevailing oceanographic conditions and the observed variations in diet, delayed-time daily multi-mission Absolute Dynamic Topography (ADT) was obtained from the Copernicus Marine Environment Monitoring Service (CMEMS, http://marine.copernicus.eu/) and used to identify the geographic locations of the main fronts around the Prince Edward Archipelago during the 1994–1996 and 2012–2015 periods. In accordance with Sokolov and Rintoul (2009) and Swart et al. (2010), optimised values of the Sea Surface Height (SSH) were used to identify the positions of the middle (M-SAF) and southern (S-SAF) branches of the sub-Antarctic Front (SAF), and the northern (N-APF) and middle (M-APF) branches of the Antarctic Polar Front (APF).

2.6. Data analysis

To test for differences in species assemblages within and among annual cycles, an ADONIS test (analogous with a permutational multivariate analysis of variance test (perMANOVA); Anderson, 2001) was employed (package: vegan; Oksanen et al., 2018). A Bray-Curtis resemblance matrix of %N of the species assemblages in the diet was used as the response variable, and stages, years and their interaction were the predictor variables. The ADONIS test followed by post-hoc pairwise ADONIS (package: pairwiseAdonis; Arbizu, 2017) were run with Benjamini and Hochberg correction for multiple comparisons (Benjamini & Hochberg, 1995) to investigate for differences of prey assemblages between years and stages. Results were visualized using a non-Metric Multidimensional Scaling (nMDS) ordination (package: vegan; Oksanen et al., 2018). The fit of each ordination was assessed with a stress value > 0.2 being seen as undesirable (Anderson, 2001).

Variation in the composition of major prey taxa in the diet was investigated by grouping the prey species into four major categories: fish, crustaceans, cephalopods and other. Following this, variation of prey species that were identified as dominant prey items was investigated. To identify dominant taxa in the diet, the dominance indices (i.e. λ” values) of each taxon were ranked, and a cumulative contribution curve was plotted. The dominant taxa were identified as those for which the slope of the cumulative curve was at least 10% of that at the origin; taxa after this point were excluded from analyses as they contributed relatively little to the diet (Landman et al., 2013). The motivation for investigation of only the most dominant taxa was based on the observation that 90% of the taxa in the diet during the breeding stages had a dominance value of less than 1%. Furthermore, these taxa only accounted for 3.5% of the total number of prey items recovered (i.e., 855 of 24 402 prey items recovered from all stomach samples within the study). Therefore, these taxa were presumed to have been of

Table 2
Number of prey items and percentage numerical abundance in brackets found within stomach content samples collected from gentoo penguins during 1982 (LaCock et al., 1984), 1984/85 (Adams and Klages 1989) and 1994–2015 (this study).

Year	1982	1984/85	1994–2015
No. of stomach content samples	64	144	178
Sample mass (g)	147.0 ± 101.0	139.2 ± 130.5	104.6 ± 94.5
FISH			
Bathylagidae			
Bathylagus antarcticus	–	–	2 (< 0.01)
Bathylagus sp.	–	–	1 (< 0.01)
Channichthyidae			
Channichthys rhinoceratus	–	132 (0.20)	
Harpagiferidae			
Harpagifer georgianus	–	–	1 (< 0.01)
Muraenolepididae			
Muraenolepis sp.	–	4 (< 0.01)	–
Myctophidae			
Electrona carlsbergi	–	4 (< 0.01)	13 (0.05)
Electrona subaspera	–	–	16 (0.07)
Electrona sp.	–	–	1 (< 0.01)
Gymnoscopelus braueri	–	–	21 (0.09)
Gymnoscopelus fraseri	–	–	24 (0.10)
Gymnoscopelus nicholsi	–	32 (0.05)	15 (0.06)
Gymnoscopelus opisthopterus	–	–	11 (0.05)
Gymnoscopelus piabilis	–	–	14 (0.06)
Gymnoscopelus sp.	–	1 (< 0.01)	1 (< 0.01)
Krefftichthys anderssoni	–	24 (0.04)	12 (0.05)
Lampichthys procerus	–	–	12 (0.05)
Metelectrona ventralis	–	–	2 (< 0.01)
Protomyctophum bolini	–	21 (0.03)	12 (0.05)
Protomyctophum choriodon	–	–	14 (0.06)
Protomyctophum normani	–	122 (0.18)	–
Protomyctophum tenisoni	–	30 (0.04)	246 (1.01)
Unidentified Myctophid	7 (0.63)	15 (0.02)	1 (< 0.01)
Nototheniidae			
Dissostichus eleginoides	–	11 (0.02)	13 (0.05)
Gobionotothen acuta	–	27 (0.04)	1 (< 0.01)
Gobionotothen angustifrons	–	–	1 (< 0.01)
Gobionotothen gibberifrons	–	–	2 (< 0.01)
Gobionotothen marionensis	–	–	44 (0.18)
Lepidonotothen larseni	–	–	2764 (11.33)
Lepidonotothen squamifrons	618 (55.38)	1231 (1.83)	6 (0.02)
Notothenia coriiceps	21 (1.88)	–	–
Notothenia cyanobrancha	–	–	1 (< 0.01)
Paranotothenia magellanica	21 (1.88)	–	1 (< 0.01)
Trematomus sp.	–	–	1 (< 0.01)
Unidentified Juvenile Nototheniid	–	442 (0.66)	2369 (9.71)
Unidentified Nototheniid	–	–	1 (< 0.01)
Paralepididae			
Arctozenus risso	–	–	1 (< 0.01)
Unidentified Fish	–	3 (< 0.01)	7 (0.03)
CRUSTACEANS			
Amphipoda			
Paramoera fissicauda	–	–	1 (< 0.01)
Themisto gaudichaudii	–	77 (0.11)	84 (0.34)
Hyperiella sp.	–	13 (0.02)	–
Vibilia sp.	–	2 (< 0.01)	1 (< 0.01)
Nematocarcinus longirostris	–	3 (< 0.01)	–
Primno macropa	–	–	2 (< 0.01)
Primno sp.	–	2 (< 0.01)	–
Unidentified Gammarid	–	–	1 (< 0.01)
Unidentified Amphipod	–	12 (0.02)	1 (< 0.01)
Euphausiacea			
Euphausia longirostris	–	–	2 (< 0.01)
Euphausia vallentini	–	55,496 (82.52)	13,536 (55.47)
Thysanoessa vicina	–	–	10 (0.04)
Unidentified Euphausiid	–	–	3121 (12.79)
Decapoda			
Nauticaris marionis	439 (39.34)	8685 (12.92)	1305 (5.35)
Unidentified Crab	–	–	1 (< 0.01)
Unidentified Decapod	7 (0.63)	–	14 (0.06)
Isopoda			
Cymodocella sp.	–	–	1 (< 0.01)

(*continued on next page*)

Table 2 (*continued*)

Unidentified Isopod	–	–	3 (0.01)
Copepoda			
Unidentified Copepod	–	–	4 (0.02)
Unidentified Crustacean	–	–	3 (0.01)
CEPHALOPODS			
Octopodidae			
Octopus sp.	–	810 (1.2)	366 (1.50)
Ommastrephidae			
Martialia hyadesi	–	–	1 (< 0.01)
Onycoteuthidae	3 (0.27)	10 (0.02)	
Moroteuthis ingens	–	–	79 (0.32)
Kondakovia longimana	1 (0.09)	9 (0.01)	5 (0.02)
Unidentified Squid	–	25 (0.04)	163 (0.67)
Other			
GASTROPODS			
Calliostomatidae			
Margarella expansa	–	4 (< 0.01)	61 (0.25)
Borsoniidae			
Typhlodaphne platamodes	–	–	1 (< 0.01)
Muricidae			
Nodulotrophon septus	–	–	1 (< 0.01)
BIVALVIA			
Limidae			
Limatula pygmaea	–	–	2 (< 0.01)
Unidentified Bivalve	–	–	1 (< 0.01)
ECHINODERMATA			
Echinoidea			
Sterechinus agassizii	–	–	1 (< 0.01)
Ophiuroidea		1 (< 0.01)	–
Total N	1116	67,248	24,402

minor significance.

Permutational two-way analysis of variance (5000 permutations; Manly, 2007) tests were used to determine whether %N of major prey taxa and dominant prey items significantly differed across stages and years. If any significance was found, these were followed by Dunn's post-hoc tests with Bonferroni corrections for multiple comparisons (package: dunn.test; Dinno, 2017).

All data analyses were performed using R version 3.4.2. (R Core and Team, 2017). All values are reported as mean ± standard deviation and significance is specified as $p < 0.05$, unless otherwise stated.

3. Results

In total, 178 stomach content samples were collected during the study (Table 1). Of the 178 samples analysed, stones and seaweed occurred in a total of 46 and 21 samples, respectively.

3.1. General diet composition

During the study, a total of 62 prey taxa were identified from the stomach content samples (Table 2; Supplementary material Table S1). Of the 24 402 individual prey items recovered, 23.1% were fish, 74.1% were crustaceans, 2.5% were cephalopods and 0.3% comprised of gastropods, bivalves and a single sea urchin. Fish, crustaceans and cephalopods were present in the diet during every stage. The fish *Lepidonotothen larseni* was the only species found in the diet during every stage (Supplementary Table S1). The crustacean *Nauticaris marionis* and an unidentified cephalopod *Octopus* sp. were the next most commonly occurring species within stomach content samples as they were found in almost every stage (Supplementary Table S1). Only four prey items were identified as dominant in the diet. These included: *L. larseni* (λ“ = 40.5), juvenile nototheniids (λ“ = 11.1) and the crustaceans *Euphausia vallentini* (λ“ = 14.3) and *N. marionis* (λ“ = 12.2).

An ADONIS test revealed that interaction between year and stage was significant ($F_5 = 2.4$, $R^2 = 0.05$, $p < 0.01$). However, these significant differences were difficult to discern from the nMDS ordination (Fig. 2), as no clear pattern could be observed. Post hoc pairwise Adonis tests showed that of the 171 comparisons made, 76 were significantly different (See Supplementary material Table S1 for details).

3.2. Dietary variation according to stages

During the post-breeding stage in 1995 and 1996 there was significantly lower abundance of fish than during the incubation, brooding, crèche and late post-breeding stage of 1995 ($p_{year} = 0.01$; $p_{stage} < 0.01$; $p_{year*stage} = 0.01$, Fig. 3). Significantly greater abundances of crustaceans occurred during the post-breeding stage than during pre-laying, incubation, brooding and late post-breeding stages ($p_{year} = 0.03$; $p_{stage} < 0.01$; $p_{year*stage} = 0.27$; Fig. 3). In addition, there were greater abundances of crustaceans within the stomach content samples during 1996 compared to 1995. Furthermore, there was significantly more cephalopods found with stomach contents samples collected during the pre-laying stage than during incubation ($p_{year} = 0.16$; $p_{stage} = 0.04$; $p_{year*stage} = 0.14$).

There was a significantly greater proportion of *L. larseni* in stomach content samples collected in incubation, brooding and crèche stages than in the ones collected in post-breeding and late post breeding stage ($p_{year} = 0.38$; $p_{stage} < 0.01$; $p_{year*stage} = 0.16$; Fig. 4.). Significantly more juvenile nototheniids were identified in late post breeding samples than in any other breeding stage ($p_{year} < 0.01$; $p_{stage} < 0.01$; $_{pyear*stage} = 0.87$; Fig. 4), and this prey taxa was particularly recovered in the 2014 and 2015 samples. *Nauticaris marionis* was significantly more abundant in samples collected during the brooding stage of 1996 than during brooding stage of 2015, crèche stages of 1995 and 1996, and late post breeding stage of 2014 ($p_{year} = 0.09$; $p_{stage} < 0.01$; $p_{year*stage} = 0.02$; Fig. 4). In contrast, there were significantly less *N. marionis* during the brooding stage of 2014 and post breeding stage of 1995 than during brooding stages of 1994 and 1996, and incubation and crèche stages of 1994. During the post-breeding stage of 1996, significantly more *E. vallentini* were recovered from stomach content samples than during incubation, brooding and crèche stages of 1994, incubation and late post breeding stages of 1995, incubation and brooding stages of 1996, incubation stage of 2012 and late post breeding stage of 2014 ($p_{year} = 0.92$; $p_{stage} < 0.01$; $p_{year*stage} < 0.01$).

3.3. Links between diet and oceanographic variability

Throughout the study the positions of the southern branch of the sub-Antarctic Front (S-SAF), as well as cyclonic and anticyclonic eddies relative to the islands varied greatly, being located primarily north of the islands during 1994–1996, while it was recorded south of the islands during 2012–2015 (Fig. 5). An increased frequency of *N. marionis* in samples during the incubation and crèche of 1994, incubation and brooding stages of 1996 and incubation stage of 2012 coincided with the position of the S-SAF being relatively far from Marion Island (Figs. 4 and 5). In constrast, an increased presence of *E. vallentini* in the samples occurred when the position of the S-SAF and eddies were relatively close to the island during the stage considered or in the months prior to that stage (Figs. 4 and 5); specifically during the prelaying, crèche and post-breeding stages of 1994, crèche and post-breeding stages of 1995, incubation, crèche and post-breeding stages of 1996, brooding and moult stages of 2014 and brooding stage of 2015. During 1995 when the diet was dominated by fish, the S-SAF and strong eddies were close to the island throughout the year. Contrastingly, during 1996, when the gentoo penguin stomach samples were dominated by both crustaceans species *N. marionis* and *E. vallentini*, the S-SAF was relatively far from the island for most of the year (Figs. 4 and 5). Interestingly, the stages during which high proportions of juvenile Nototheniids were observed in the stomach samples all occurred when the S-SAF was located primarily south of the islands (Figs. 4 and 5).

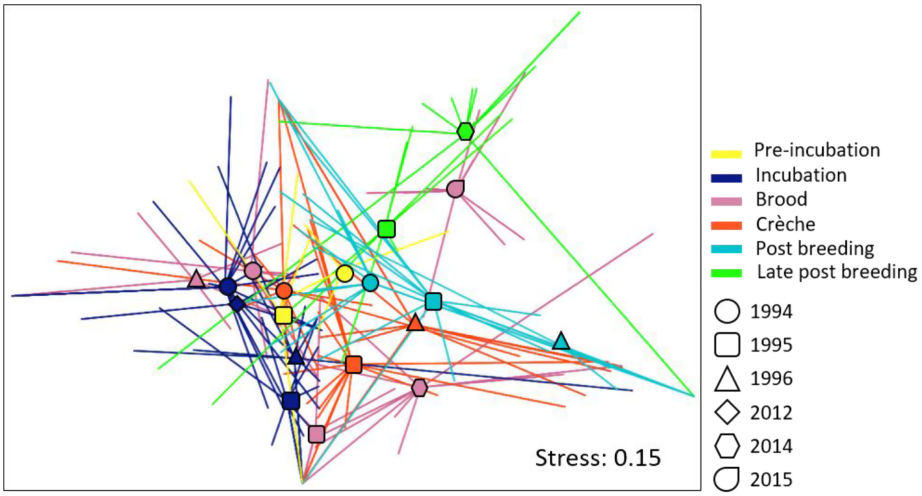

Fig. 2. Two-dimensional nMDS ordination showing the differences in the diet of gentoo penguins at Marion Island during different stages of the annual cycles from 1994 to 1996, 2014, 2012 and 2015.

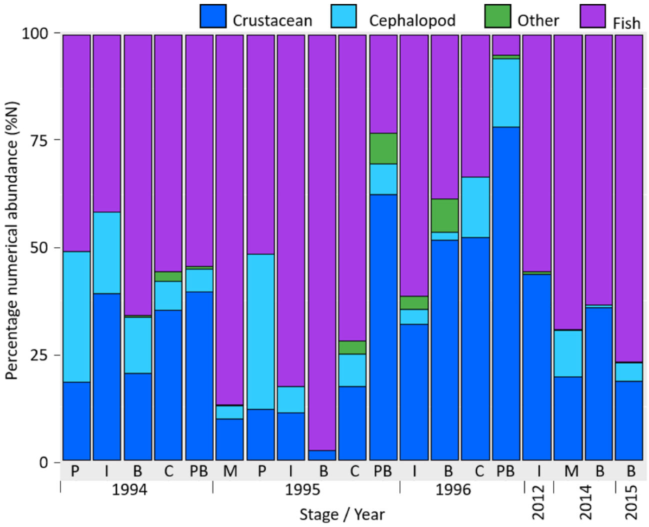

Fig. 3. Relative contributions, in terms of percentage numerical abundance, of major prey taxa to the diet of the gentoo penguins at Marion Island during different stages; pre-laying (P), incubation (I), brooding (B), crèche (C), post breeding (PB)and late post breeding (M)) within different years (1994–1996; 2012; 2014 and 2015).

4. Discussion

This study investigated the temporal variability in the diet of gentoo penguins at Marion Island over three consecutive years in the 1990′s and then more recently, during 2012, 2014 and 2015. Significant differences in diet composition were evident among years and among stages within the annual cycle. The latter variation was, however, not consistent across years. A surprising amount of variability, both intra and inter-annually, in the diet of gentoo penguins over the past three decades were observed. The dynamic nature of their prey composition appeared to be closely linked to the position of the SAF which influences the local oceanographic context, with greater abundance of pelagic prey being present in stomach content samples when the SAF was relatively close to the archipelago. In agreement with our predictions, over the long term component of this study (1994–2015), there seemed to be a gradual increase in abundance of the pelagic krill *Euphausia vallentini* and juvenile nototheniid fish and a decrease in the benthic krill *Nauticaris marionis* in the stomach samples of the gentoo penguins breeding at Marion Island.

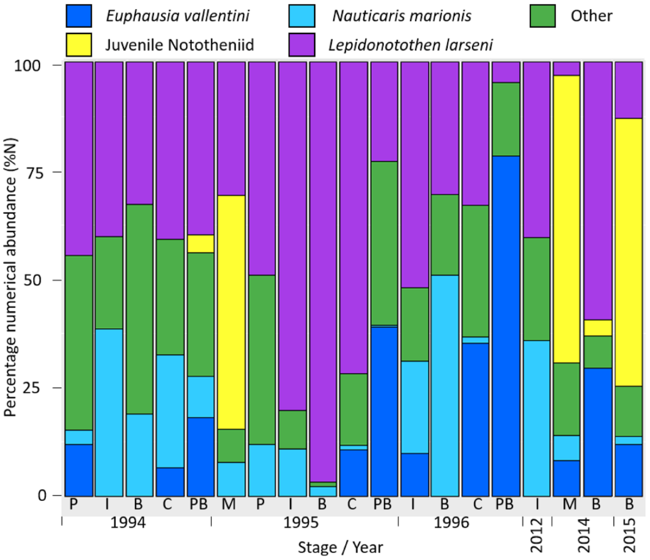

Fig. 4. Relative contributions, in terms of percentage numerical abundance, of dominant prey items in the diet of the gentoo penguins at Marion Island during different stages (pre-laying (P), incubation (I), brooding (B), crèche (C), post-breeding (PB) and late post-breeding (M)) within different years (1994–1996; 2012; 2014 and 2015).

4.1. General diet description

The diet of the gentoo penguin at Marion Island comprised mainly of crustaceans, fish and cephalopods, the relative proportions of which varied throughout the study period. All gastropods and bivalves found in the stomach samples occurred in low numbers ($< 0.3\%$ of individual prey items found) and were most likely consumed opportunistically rather than selected for by the gentoo penguins. The proportions of fish, crustaceans and cephalopods in the diet of the gentoo penguins at Marion Island was similar to their diet in other northern breeding localities where, typically, the diet is more heterogeneous than at southern localities, comprising of fish, crustaceans and cephalopods with the fish component ranging from partial to complete dominance (Adams and Klages, 1989; Robinson and Hindell, 1996; Clausen and Pütz, 2002; Lescroël et al., 2004; Handley et al., 2016; Waluda et al., 2017; Xavier et al., 2018). By contrast, at Antarctic breeding localities the diet tends to be dominated by crustaceans (Volkman et al., 1980; Williams, 1991; Polito et al., 2015).

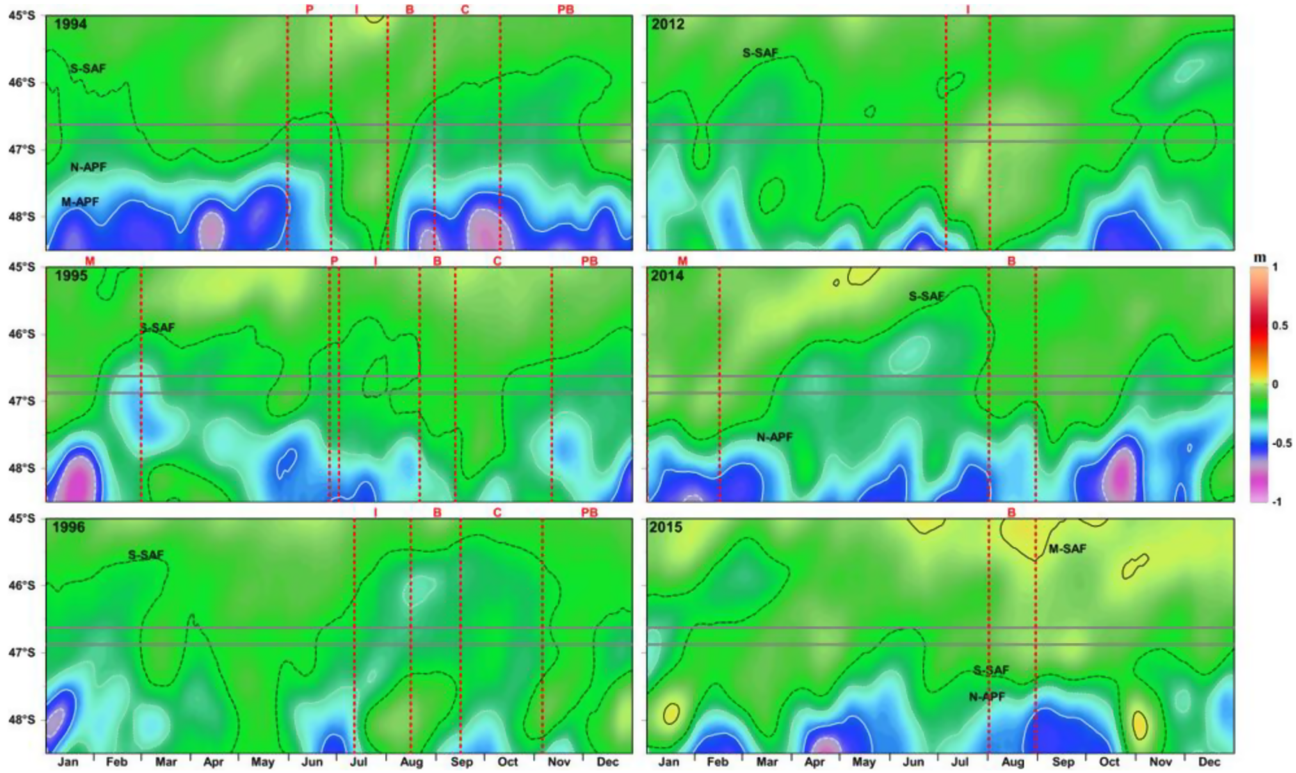

Fig. 5. Daily Sea Surface Height along 37°52′E during 1994, 1995, 1996, 2012, 2014 and 2015. The locations of the middle (M-SAF) and southern (S-SAF) branches of the sub-Antarctic Front (SAF) and the middle (M-APF) and northern (N-APF) branches of the Antarctic Polar Front (APF) are indicated. Horizontal grey lines indicate the locations of Marion and Prince Edward islands. Vertical dashed red lines indicate the sampled annual breeding stages of gentoo penguins at Marion Island (pre-laying (P), incubation (I), brooding (B), crèche (C), post-breeding (PB) and late post-breeding (M)). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

The high frequency of occurrence of Nototheniid fish, *N. marionis* and *E. vallentini,* in the diet of gentoo penguins at Marion Island appears largely to reflect the available habitat and prevailing oceanography in the region of the islands. Nototheniid fish are widely distributed across the Southern Ocean, occurring most commonly in neritic waters where they form important components of both benthic and pelagic ichthyofauna (Dewitt et al., 1990). The caridean shrimp, *N. marionis,* is restricted to the shelf regions of sub-Antarctic islands and forms the second largest component of the benthic biomass on the inter-island shelf at the Prince Edward Archipelago (Perissinotto and McQuaid, 1990; Branch et al., 1993; Haley et al., 2017). In addition, the pelagic euphausiids, *E. vallentini* and *Thysanoessa vicina*, are the numerically dominant components of the macrozooplankton within Polar Frontal Zone waters (Hunt and Pakhomov, 2003). The shallow inter-island shelf between Prince Edward Island and Marion Island provides ideal habitat for the birds to forage on demersal and benthic prey at accessible depths, as well as to encounter pelagic species which are advected into the shallow shelf waters between the islands by the easterly flowing ACC.

4.2. Temporal variation

4.2.1. Within year variation

Fish became increasingly important in the gentoo penguin diet during their breeding season, peaking during the brooding stage. This finding complements that of Adams and Klages (1989), who studied intra-annual variation in the diet of the gentoo penguin at Marion Island during 1984/85. A notable exception during this study was during brooding in 1996, when crustaceans were the dominant prey type consumed. Interestingly, this was the only brooding stage for the years studied, where the S-SAF was located far north of the islands (Fig. 5). Seabirds often select prey with higher energetic value during an energetically demanding time such as the brooding period (e.g. Browne et al., 2011). However, rather than selecting prey of high energy value, gentoo penguins at Marion Island and elsewhere may choose the most available prey. The most dominant fish species within the gentoo penguins' diet, *L. larseni,* has a pelagic phase, which at Marion Island lasts throughout spring and summer until the larvae adopt a benthic life during autumn or winter (Dewitt et al., 1990). Their shift to a benthic habitat accords with an increase in their contribution to the diet of gentoo penguins during brooding. In addition, greater numbers of juvenile Nototheniids were present within the gentoo penguins' diet during the late post-breeding stage which coincides with summer months. Dietary switch could also happen as a consequence of interspecific competition (Williams, 1981; Ridoux, 1994), as the increase of importance coincides with the mass arrival of the largely, euphausiid consuming macaroni *Eudyptes chrysolophus* and rockhopper penguins *E. chrysocome* at Marion Island (Brown and Klages, 1987).

4.2.2. Among year variation: 1994–1996

The proportions of fish and crustaceans in the diet of the gentoo penguin at Marion Island were variable between years. During 1994, fish and crustaceans were present in the diet in relatively equal proportions; this then progressed to a fish dominated diet for the majority of 1995 and a crustaceans dominated diet in 1996. Elsewhere, the proportions of major taxa in the diet also varied between years: South Georgia (Waluda et al., 2017); Antarctica (Coria et al., 2000) and the Falkland Islands (Clausen and Pütz, 2002; Handley et al., 2016).

From 1994 to 1996, the crustacean component in the diet of the gentoo penguins changed from predominantly *N. marionis* during 1994 to *E. vallentini* during 1995 and 1996. In none of these years did these crustacean species occur in similar quantities in the diet; rather when one was dominant, the other was absent, or found only in small quantities. A similar switch of these crustacean species was observed in the diet of the gentoo penguins at Marion Island during 1984/85 (Adams and Klages, 1989).

The varying latitudinal position of the SAF has an important influence on the macrozooplankton community structure of the inter-island shelf within the Prince Edward Archipelago (Pakhomov and Froneman, 1999; Hunt and Pakhomov, 2003). When the SAF lay north, relatively far from the islands, macrozooplankton, with special mention of *E. vallentini*, on the inter-island shelf had a smaller size and biomass, compared to years when the SAF lay closer to the islands (Hunt and Pakhomov, 2003). This decrease was attributed to the reduced advection of *E. vallentini* onto the shelf due to increased water stability that resulted from anti-cyclonic eddies (Pakhomov and Froneman, 1999; Hunt and Pakhomov, 2003). Therefore, the latitudinal position of the SAF may drive variation in the composition of crustacean species to the diet of gentoo penguins at Marion Island, with greater proportion of pelagic crustaceans consumed when the SAF is relatively close to the island, increasing their availability. Thus, the within and among season changes in diet composition of gentoo penguins during this study most likely reflect changes in the availability of the different prey items in the inshore and inter-island shelf region at the Prince Edward Archipelago.

4.2.3. *Long term variation*

In samples collected during the more recent part of the study (2012, 2014 and 2015), nine prey species were identified that were absent from samples collected during 1994–1996 (Supplementary material Table S2). These included the fishes *Harpagifer georgianus* and *Gobionotothen acuta*, amphipods from the genus *Vibilia* and from the infraorder Gammarida; the euphausiid *Euphausia longirostris*; and the cephalopod *Martialia hyadesi* (Table 2). However, in stomach content samples collected in 1984/85, *G. acuta* and a *Vibilia* sp. were present. In addition, the following species were present in stomach content samples during 1984/85 and were not present in the current study: the fish species *Channichthys rhinoceratus*, *Muraenolepis* sp. and *Protomyctophum normani* and the crustacean *Nematocarcinus longirostris* (Table 2). The identification of fish during this and previous studies (LaCock et al., 1984; Adams and Klages, 1989) was done through the identification of otoliths. This is a difficult process, especially if the otoliths are damaged or eroded, and may lead to misidentification of species. For example, LaCock et al. (1984) misidentified *Lepidonothothen squamifrons* as *Harpagifer georgianus* (Adams and Klages, 1989). Furthermore, otoliths which were identified as *G. acuta* and *G. angustifrons* during this study were likely misidentified *G. marionensis* (Miya et al., 2016). Apart from *G. acuta* specimens collected by Duhamel et al. (1983), this species has not been reported in the vicinity of the Prince Edward Archipelago (Duhamel et al., 2014). Recent genetic analysis showed that *G. angustifrons* and *G. marionensis* are not two distinct species (Miya et al., 2016). Other species which may have been misidentified include *G. gibberifrons* and *G. cyanobranchia*, which have never been recorded at the Prince Edward Archipelago, and *Channichthys rhinoceratus*, which is endemic to the Kerguelen Plateau (Duhamel et al., 2014). Therefore, we did not consider these prey items as indicative of change in the prey available to the gentoo penguins.

There is, however, evidence to support long-term change in the diet of gentoo penguins at Marion Island. In the 1980s, the dominant fish species eaten was *Lepidonotothen squamifrons* (LaCock et al., 1984; Adams and Klages, 1989), whereas after 1994 it was *L. larseni*. A similar change occurred in the diet of the Crozet shag at the islands. The dominant fish in their diet was *L. squamifrons* in 1984/85 (Espitalier-Noel et al., 1988) but *L. larseni* during the late 1990s and early 2000s (Crawford et al., 2003b). The change from near complete dominance of *L. squamifrons* to its near absence in the diet of gentoo penguins and Crozet shags suggests that its availability decreased around the Prince Edward Archipelago.

Limited sampling suggests that there may have been an increase of pelagic prey, particularly *E. vallentini* and juvenile nototheniid fish, in the diet of the gentoo penguin over the past two decades. However, given the large temporal variability in the diet of the gentoo penguin and the few samples collected in more recent years it is difficult to be sure of this. Previously, it was hypothesized that reduced availability of a main prey type, *N. marionis,* may have contributed to the decrease of gentoo penguins at Marion Island (Crawford et al., 2003a; Allan et al., 2013). Although we also found significantly less *N. marionis* in stomach samples collected in more recent years, densities of *N. marionis* on the shelf region of the islands have apparently remained stable over the past three decades (Haley et al., 2017). Hence, the increase of pelagic prey items in the diet of the gentoo penguin may not reflect a decline of *N. marionis* but rather an increase in availability of pelagic prey in the shallow waters surrounding the islands, likely the result of a southward shift of the SAF. As predators try to maximize energy gain per unit effort (optimal foraging theory, Stephan and Krebs, 1986), it may be that as *E. vallentini* (Hunt and Pakhomov, 2003) occurs at shallower depths in the water column than *N. marionis* (Perissinotto and McQuaid, 1990; Branch et al., 1993), it is energetic more cost effective to prey upon *E. vallentini* when they are temporally more available. During 2012–2015, the S-SAF was mostly located south of the islands, whereas from 1994 to 1996 it was mainly to the north. However, it is not yet clear whether this is part of a natural cycle or whether this shift related to climate change. Partial support for a long-term southward shift in the SAF is provided by a depletion in carbon isotopic values of the *N. marionis* over the past three decades, thought most likely due to these organisms feeding on pelagic prey that are advected to the islands rather than produced at the islands (Allan et al., 2013)

4.3. *The gentoo penguin as a sentinel for change in the local environment at the Prince Edward Archipelago*

Here we have shown that the diet of the gentoo penguin at Marion Island demonstrates a high degree of plasticity and likely varies in response to prey availability, which is probably driven by prevailing oceanographic conditions. Other studies similarly found that changes in diet were linked to variability in oceanography, prey life cycles and resulting prey availability (Lescroël et al., 2004; Lescroël and Bost, 2005; Miller et al., 2010; Handley et al., 2016; Xavier et al., 2018). For this reason, we argue that the diet of gentoo penguins may represent a powerful tool to monitor changes in the local environment at the Prince Edward Archipelago. Our results suggest that the main prey of gentoo penguins at the archipelago has shifted from benthic to pelagic organisms, most likely in response to an altered location of the SAF near the islands. Clearly, increased frequency of sampling would strengthen the potential use of the gentoo penguin as a sentinel species of ecosystem change. To limit stress associated with collecting stomach samples, future studies should consider supplementing this approach with DNA-based analyses on fecal samples and stable isotope analyses of gentoo penguin tissue, including moulted feathers, to potentially monitor the proportions of fish, *N. marionis* and *E. vallentini* in the diet (Kowalczyk et al., 2014).

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Competing interest

The authors have no competing interests.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.ecolind.2019.01.008.

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