



# Seasonal prey switching in non-breeding gentoo penguins related to a wintertime environmental anomaly around South Georgia

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## Abstract

Information is needed on how anomalous environmental conditions affect important Antarctic ecological sentinels during the winter. Using a non-invasive method (scats), the diet of non-breeding gentoo penguins *Pygoscelis papua* at Bird Island, South Georgia, was examined during the winter of 2009 when local environmental conditions were abnormal (e.g. warmer sea surface waters). Scats were collected every 2 weeks from May until October 2009 ( $N=168$ ); the diet was dominated by the amphipod *Themisto gaudichaudii* by frequency of occurrence (77.5% of the samples) and by number (70.5% of the total individuals). By mass, different species of crustaceans (*T. gaudichaudii* and Antarctic krill *Euphausia superba*) and fish (*Champscephalus gunnari*, *Lepidonotothen larseni* and *Pseudochaenichthys georgianus*) were the most important in different periods. Numerically, prey switching occurred at the end of winter, when *E. superba* became more abundant in the penguins' diets in late September and early October (austral spring), when sea surface temperatures became colder. *T. gaudichaudii* is sub-optimal prey for gentoo penguins and its consumption most likely reflects a lack of *E. superba* in local waters. The consumption of *T. gaudichaudii* and fish, in place of *E. superba*, was probably insufficient for the penguins to maintain a body condition suitable for reproduction, contributing to the observed late commencement of breeding (i.e. 2–3 weeks) that year. Our results highlight the sensitivity of gentoo penguin populations to variations in environmental conditions, particularly in terms of how these conditions affect the availability of preferred dietary items and potential follow-on effects in the subsequent breeding season.

**Keywords** *Pygoscelis papua* · Southern Ocean · Diet · Antarctic winter · Abnormal environmental conditions

## Introduction

In the Southern Ocean, penguins represent 80% of the avian biomass, which makes them important components of the Antarctic food web, both as predators and prey (Williams 1995; Lescroël et al. 2004). Gentoo penguins, *Pygoscelis papua*, have a circumpolar distribution and breed on the sub-Antarctic islands and the Antarctic Peninsula (46–65°S); approx. one-third (26–28%) of the breeding population occurs at South Georgia (Williams 1995; BirdLife International 2016). At South Georgia, gentoo penguins are present year-round (Tanton et al. 2004; Ratcliffe et al. 2014), and variation in their diet, and the timing and success of breeding, is a product of local prey availability (Williams 1990, 1991; Tanton et al. 2004). Therefore, predators, such as gentoo penguins, can be important ecological sentinels of local environmental variability and change (Bost et al. 1994; Constable et al. 2014).

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In terms of feeding ecology, gentoo penguins are typically opportunistic inshore feeders, know to dive, at least, up to 140 metres deep (Croxall et al. 1988; Mori and Boyd 2004; Tanton et al. 2004; Thiebot et al. 2011). Their preferred prey may alter between localities (e.g. Antarctic krill *Euphausia superba* and fish at South Georgia, *Euphausia vallentini* and *Themisto gaudichaudii* in Kerguelen; *Loligo gahi* in the Falkland Islands, *E. superba* in Antarctic Peninsula), foraging during daylight to depths that vary according to prey type (Croxall et al. 1988; Bost et al. 1994; Clausen and Pütz 2003; Cimino et al. 2016). Increasing Southern Ocean temperatures are likely to alter the distribution and availability of prey species (Trivelpiece et al. 2011; Constable et al. 2014; Gutt et al. 2015; Reiss et al. 2017) which could have negative impacts on how and where gentoo penguins forage, and consequently their capacity to survive and breed (Forcada et al. 2006; Forcada and Trathan 2009; Waluda et al. 2017; Xavier et al. 2017). No information is known about how gentoo penguins respond to anomalous environmental conditions intra-annually during winter that affect the abundance and availability of preferred prey, such as *E. superba* or fish south of the Polar Front. This is especially relevant during the end part of the winter, when the penguins increase foraging effort to build up energy reserves, during September and October, to fuel subsequent reproduction cycle (Hinke and Trivelpiece 2011; Xavier et al. 2017; Takahashi et al. 2018).

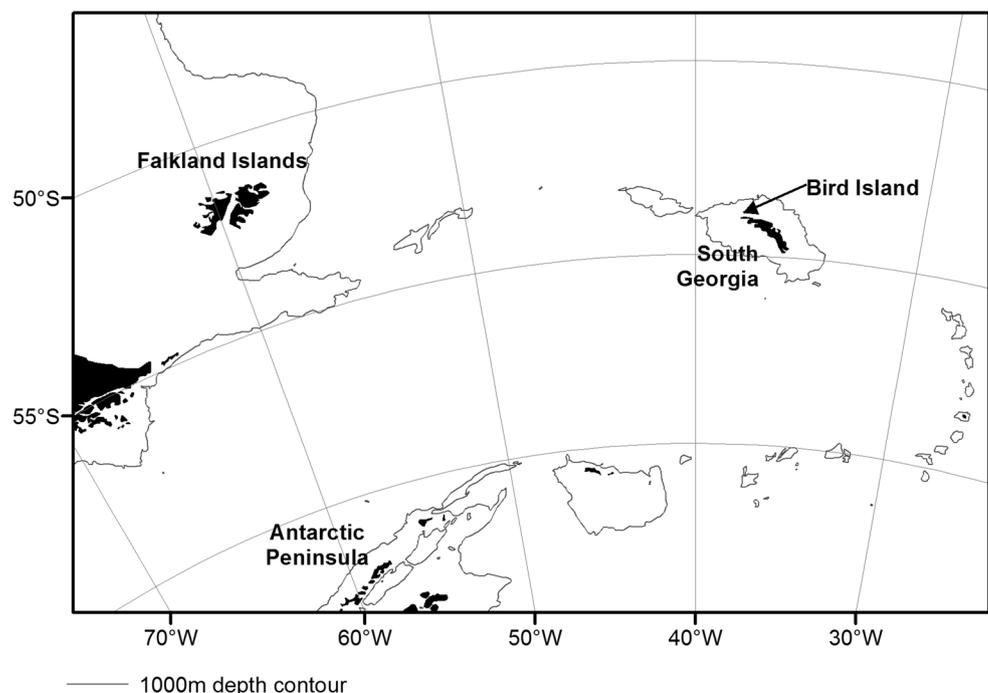
We analysed fresh faecal samples (scats), a non-invasive technique that allows the collection of a large number of samples for dietary studies with relative little effort and no

disturbance to the animals (Libertelli et al. 2004; Trathan et al. 2012; Bowen and Iverson 2013). The disadvantage of this technique is the possible greater prey degradation as a result of longer exposure to digestive enzymes when compared to invasive techniques (Barrett et al. 2007; Williams et al. 2012). Nevertheless, scats have been used with relative success to characterize the diets of a number of land-based marine predators, as their main prey (crustaceans, fish and cephalopods) still have some level of resistance to digestion (e.g. crustaceans, fish and cephalopods have different digestion speeds that can lead to under-representation of these components) (Reid and Croxall 2001; Barrett et al. 2007) and even sex of some crustaceans can be carried out (e.g. on *T. gaudichaudii*; Xavier, unpubl. data).

In 2009, a strong ecosystem anomaly occurred around South Georgia which resulted in warmer surface waters in consecutive months [i.e. Sea surface temperature were higher than the mean temperature between February and September 2009 Xavier et al. (2017) and a low standing stock of *E. superba* (Hill et al. 2009; Xavier et al. 2017). Although such conditions are not unprecedented in this region, the impact they have on the ability of gentoo penguins to find suitable and sufficient prey has yet to be fully ascertained. This study focusses on winter and early spring, when these penguins are building up energy reserves in advance of the reproductive effort.

In this study, we collected fresh faecal samples (scats) from gentoo penguins during the winter and early spring (May to October of 2009) at Bird Island, South Georgia (Fig. 1), and analysed them to (i) describe in detail the

**Fig. 1** Location of the study: Bird Island, South Georgia (with a 1000 m depth contour) (after Xavier et al. 2017)



impact of anomalous environmental conditions on gentoo penguins' diet, (ii) determine what part of the prey populations, in terms of sizes, were consumed (and what insights this may give on prey population dynamics), and (iii) evaluate the implications of environmental variability on a penguin species' resilience in this region.

## Materials and methods

### Sampling

Fresh scats were collected from May to October 2009 every 2 weeks at Landing Beach at Bird Island, South Georgia. Sampling periods were given an alphanumeric code indicating month and sequence of sampling (e.g. June 1 = first sampling period in June). Fifteen to 18 fresh scats (i.e. <2 days old, aged according to the colour of the scat: usually fresh scats have a brighter colour than older ones) were collected during each visit to the colony following the protocols and guidelines of the Commission for the Conservation of Antarctic Marine Living Resources (CCAMLR) and the Scientific Committee on Antarctic Research (SCAR) (Laws 2009; CCAMLR 2014). Material was taken to the laboratory within 2 h of collection and analysed the same day. After melting the snow/ice by mixing it with 25–40 ml of warm water (~20 °C), floating material was repeatedly drained through a 1-mm sieve and specimens or cuticles of crustaceans isolated. Sinking material was also examined for the presence of sagittal otoliths and cephalopod beaks. All recovered material was later identified and measured.

### Characterization of the diet

When possible, crustaceans were identified to species level when possible, using a reference collection at Bird Island and identification guides (Kirkwood 1982; Boltovskoy 1999). Availability was estimated as relative frequency of occurrence. Up to 50 randomly selected specimens were measured per scat and per species. Total length was calculated from integument length by using allometric equations (Reid and Measures 1998; Bocher et al. 2001). Specimens of *T. gaudichaudii* were also sexed; antennae are segmented and filamentous in mature males and short in the females (Kane 1966). Sagittal otoliths were used to identify fish species (Hecht 1987; Williams and McEldowney 1990; Smale et al. 1995; Reid 1996), and subsequently measured. Fish length was estimated by using otolith-total size relationships established by previous studies (Adams and Klages 1987; Hecht 1987; Williams and McEldowney 1990; Smale et al. 1995; Reid 1996). Cephalopods were identified by their lower beaks and length and mass estimated (Xavier and Cherel 2009).

To study temporal variation, the diversity of the penguins' diet was spatially clustered using principal component analysis (PCA), by using absolute frequencies for each component in the diet grouped by sampling date. Unidentifiable fish represented only a small part of the fish prey and were excluded from this analysis. Ordination was used to summarize all the variation in the study area, accommodating time as a study unit. PCA analyses were performed using the "ade4" (Chessel et al. 2004) and "BiodiversityR" (Kindt and Coe 2005) packages from R statistical software.

### Inferences on the population dynamics of crustaceans present in the diet

Sex ratio, differences between sexes, and prey size estimations were carried out for the most dominant prey species (species that occurred in >20 samples), *T. gaudichaudii*. Descriptive statistics were performed by month for this prey species. Comparisons between groups were made using a Chi-square ( $\chi^2$ ) statistical test, for which  $p < 0.05$  was considered significant,  $p < 0.01$ , highly significant and  $p \geq 0.05$ , non-significant.

## Results

### Overall diet

During the winter, a total of 168 fresh scats samples were obtained from gentoo penguins, and a total of 2766 specimens of crustaceans, fish and cephalopods identified and measured (Tables 1, 2). Crustaceans occurred in 161 samples (95.3%), fish in 131 samples (77.5%) and cephalopods in only four samples (2.4%). The most frequent species of crustaceans were *T. gaudichaudii* (present in 77.5% of samples) and *E. superba* (26.6%), followed by *Byblis securiger* (14.2%) and *Gondogeneia georgiana* (10.7%) (Table 1). The most representative fish were *Gymnoscopelus braueri* (in 48.5% of the samples; whose identification was not fully confirmed, therefore the query prior to the species name), *Muraenolepis microps* (20.7%), *C. gunnari* (20.1%) and *L. larseni* (11.8%). Cephalopods occurred less frequently than fish and crustaceans, and were represented by only three species: *Kondakovia longimana* (in 1.2% of samples), *Slosarczykovia circumantarctica* (1.2%) and *Psychroteuthis glacialis* (0.6%). The differences in the frequency of occurrence among all species of crustaceans, fish and cephalopods were significant ( $\chi^2 = 1400.46$ ,  $df = 27$ ,  $p < 0.0001$ ).

Over time, variability in the frequency of occurrence of the main prey species was mainly driven by a temporal gradient between *T. gaudichaudii* (most abundant from May to the first half of September, with the exception of early June), *G. braueri* (abundant in early June but declining

**Table 1** Summary of all prey from scats in the diet of gentoo penguins *Pygoscelis papua* at Bird Island (South Georgia) from May to October 2009: Frequency of occurrence (FO), corresponding percentage of overall occurrence, mean length (Mean, in mm), minimum and maximum length (Min and Max respectively, in mm) and standard deviation (SD)

	% FO	Mean	Min	Max	SD
CRUSTACEA	95.3				
Amphipoda					
<i>Byblis securiger</i>	14.2	37.1	31.0	43.0	2.94
<i>Gondogeneia georgiana</i>	10.7	13.6	9.0	19.0	1.87
<i>Gondogeneia</i> sp.	0.6				
<i>Orchomenella (Orchomenopsis) acanthura</i>	1.2				
<i>Themisto gaudichaudii</i>	77.5	22.8	15.0	35.0	1.78
<i>Vibilia antarctica</i>	0.6				
Decapoda					
<i>Chorismus antarcticus</i>	3.0				
Decapoda sp.	1.8				
<i>Notocrangon antarcticus</i>	2.4				
Euphausiacea					
<i>Euphausia superba</i>	26.6	38.3	31.7	47.2	2.16
<i>Euphausia triacantha</i>	1.2				
Euphausiacea sp.	4.7				
<i>Thysanoessa</i> sp.	4.1				
Isopoda					
<i>Anthuridae</i> sp.	0.6				
Lophogastrida					
<i>Gnathophausia</i> sp.	1.2				
Mysida					
<i>Antarctomysis maxima</i>	4.7				
FISH	77.5				
Channichthyidae					
<i>Champscephalus gunnari</i>	20.1	107.0	49.7	323.8	44.39
Channichthyidae sp.	1.2				
<i>Pseudochaenichthys georgianus</i>	1.2	240.2	166.3	314.2	104.57
Muraenolepididae					
<i>Muraenolepis microps</i>	20.7	44.2	24.0	112.8	16.24
Myctophidae					
? <i>Gymnoscopelus braueri</i>	48.5	22.4	5.6	87.0	11.17
<i>Protomyctophum bolini</i>	1.2	36.8	30.7	42.9	8.67
<i>Protomyctophum choriodon</i>	0.6	71.0	71.0	71.0	
Nototheniidae					
<i>Lepidonotothen larseni</i>	11.8	89.7	41.5	171.7	34.03
CEPHALOPODA	2.4				
Brachioteuthidae					
<i>Slosarczykovia circumantarctica</i>	1.2	32.5	32.5	32.5	
Onychoteuthidae					
<i>Kondakovia longimana</i>	1.2				
Psychroteuthidae					
<i>Psychroteuthis glacialis</i>	0.6	17.0	17.0	17.0	

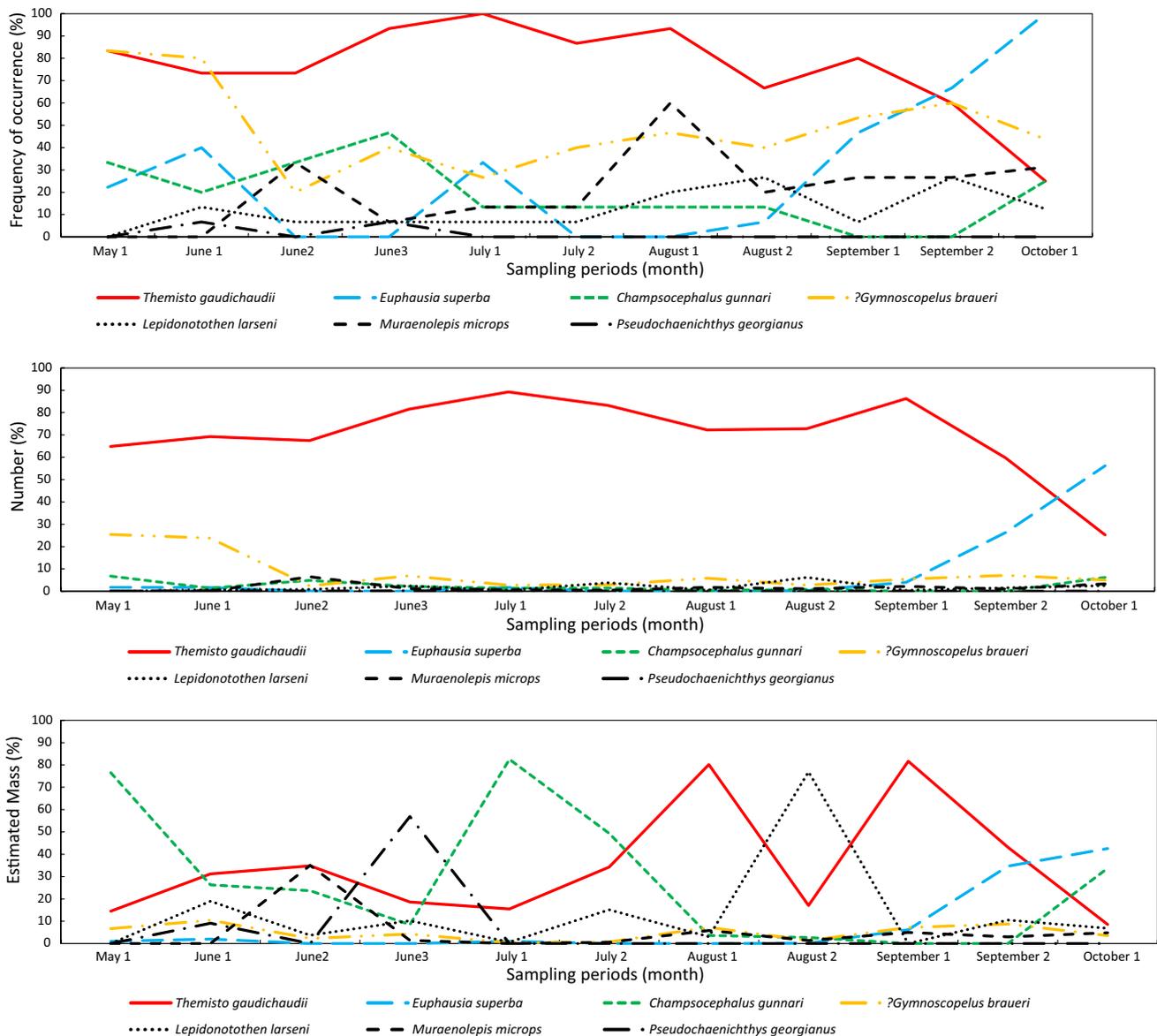
Lengths and corresponding standard deviation only applies to some species

sharply afterwards) and *E. superba* (abundant only in the second half of September and October, Table 2, Figs. 2, 3). By number, *T. gaudichaudii* was the most numerous species all through the study period except in early October, when it was overtaken by *E. superba* (Fig. 2). By mass,

there was no consistently dominant species; the balance shifted among fish from *C. gunnari* in late May and July, to *P. georgianus* in late June and *L. larseni* in late August; among crustaceans *T. gaudichaudii* dominated in early and mid-June, early August and September, and *E. superba* in

**Table 2** Descriptive Frequency of occurrence (% FO) in samples of all the obtained species in the diet of gentoo penguins *Pygoscelis papua*, by each of the sampling dates (named by order as the 1st, 2nd or 3rd sampling date of the month)

	May 1 <i>n</i> = 18	Jun 1 <i>n</i> = 15	Jun 2 <i>n</i> = 15	Jun 3 <i>n</i> = 15	Jul 1 <i>n</i> = 15	Jul 2 <i>n</i> = 15	Aug 1 <i>n</i> = 15	Aug 2 <i>n</i> = 15	Sep 1 <i>n</i> = 15	Sep 2 <i>n</i> = 15	Oct 1 <i>n</i> = 16
<b>CRUSTACEA</b>											
Amphipoda											
<i>Byblis securiger</i>	0	0	33	33	40	33	20	0	0	0	0
<i>Gondogeneia georgiana</i>	0	0	20	0	7	40	27	27	0	0	0
<i>Gondogeneia</i> sp.	0	0	0	0	7	0	0	0	0	0	0
<i>Orchomenopsis acanthura</i>	0	0	7	0	7	0	0	0	0	0	0
<i>Themisto gaudichaudii</i>	83	73	73	93	100	87	93	67	80	60	25
<i>Vibilia antarctica</i>	0	0	0	0	0	0	7	0	0	0	0
Decapoda											
<i>Chorismus antarcticus</i>	0	0	0	0	0	0	0	0	0	20	13
Decapoda sp.	0	0	0	0	0	7	0	7	0	0	6
<i>Notocrangon antarcticus</i>	6	0	0	0	0	0	0	0	0	20	0
Euphausiacea											
<i>Euphausia superba</i>	22	40	0	0	33	0	0	7	47	67	100
<i>Euphausia triacantha</i>	0	0	0	0	0	0	0	0	13	0	0
Euphausiacea sp.	0	0	0	7	0	20	13	0	13	0	0
<i>Thysanoessa</i> sp.	0	0	0	0	0	0	0	0	7	40	0
Isopoda											
<i>Anthuridae</i> sp.	0	0	0	0	0	7	0	0	0	0	0
Lophogastrida											
<i>Gnathophausia</i> sp.	0	0	0	13	0	0	0	0	0	0	0
Mysida											
<i>Antarctomysis maxima</i>	0	0	13	20	7	0	0	0	0	13	0
<b>FISH</b>											
Channichthyidae											
<i>Champocephalus gunnari</i>	33	20	33	47	13	13	13	13	0	0	25
Channichthyidae sp.	0	0	0	7	0	0	0	7	0	0	0
<i>Pseudochaenichthys georgianus</i>	0	7	0	7	0	0	0	0	0	0	0
Muraenolepididae											
<i>Muraenolepis microps</i>	0	0	33	7	13	13	60	20	27	27	31
Myctophidae											
? <i>Gymnoscopelus braueri</i>	83	80	20	40	27	40	47	40	53	60	44
<i>Protomyctophum bolini</i>	11	0	0	0	0	0	0	0	0	0	0
<i>Protomyctophum choriodon</i>	0	7	0	0	0	0	0	0	0	0	0
Nototheniidae											
<i>Lepidonotothen larseni</i>	0	13	7	7	7	7	20	27	7	27	13
Osteichthyes sp.	0	0	0	0	7	0	7	27	0	0	6
<b>CEPHALOPODA</b>											
Brachioteuthidae											
<i>Slosarczykovia circumantarctica</i>	0	0	0	0	0	0	0	13	0	0	0
Onychoteuthidae											
<i>Kondakovia longimana</i>	0	7	0	7	0	0	0	0	0	0	0
Psychroteuthidae											
<i>Psychroteuthis glacialis</i>	0	0	7	0	0	0	0	0	0	0	0



**Fig. 2** Frequency of occurrence, by number and by mass of the top prey taxa (>5% by number and/or mass) in the diet of gentoo penguins *Pygoscelis papua* at Bird Island, during Winter 2009

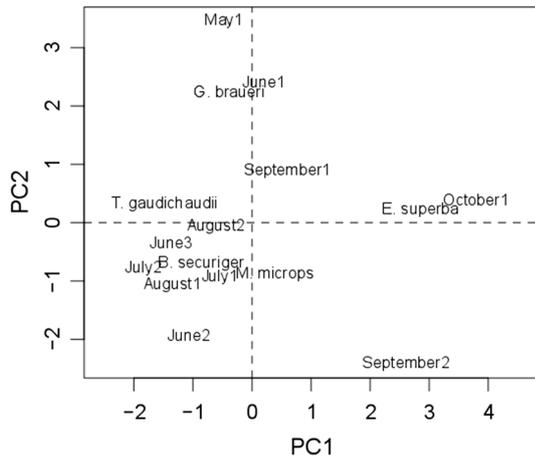
early October) (Fig. 2). Other species were less abundant in the diet and made lower dietary contributions in terms of frequency of occurrence, number or mass (Tables 1, 2).

Based on the PCA analyses, a temporal gradient was noted for *?G. braueri* near the first sampling periods in May and June, *E. superba* (located close to the first sampling period of October), *T. gaudichaudii* (located close to the second sampling period in August) and both *B. securiger* and *M. microps* (close to the second sampling date of June to the end of August, and in the second sampling date of September) (Fig. 3).

## Crustaceans

### Sex ratio of *T. gaudichaudii* in scats

As *T. gaudichaudii* was the most dominant prey item, scat samples analyses allowed a detailed examination of their sex ratios and size differences (between sexes) by month. At all sampling times, female *T. gaudichaudii* significantly outnumbered males in all sampling periods except in period June 2 ( $\chi^2_1 = 3.75$ ,  $p = 0.053$ ). However, sex ratios were significantly different between months (in total, females = 85%,



**Fig. 3** Principal component analysis on the diet of gentoo penguins *Pygoscelis papua*. Ordination diagram for the first two components of the principal component analysis, which explain 66.31% of the variance. Sampling dates are represented in black. Crustacean species have high contribution to Component I, while fish species have high contribution to component II

males = 15%) ( $\chi^2_{10} = 506.7, p < 0.0001$ ) (Table 3). In the first

sampling period (May 1), females represented 91% in the samples. This value continuously decreased until the first sampling period of July (July 2; 58% females), from which point onwards, the ratio of females increased reaching highest proportions in the last four sampling periods (from 95 to 100% females). Body lengths were not statistically different between male and female *T. gaudichaudii* (Fig. 4; *t* test,  $t_{12} = 0.727, p = 0.249$ ). Detailed statistics of size frequency distributions by sex are given in Table 3.

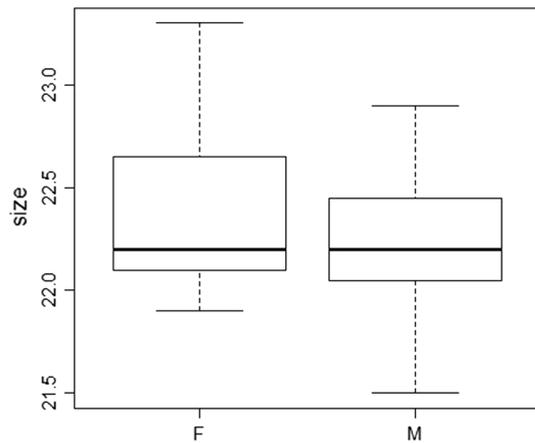
**Importance of *Euphausia superba* in scats**

*Euphausia superba* was the second most abundant crustacean in the diet. From the first sampling date of May to the second sampling date of August, some individuals were present but were too digested to calculate total length. Therefore, descriptive statistics regarding size were only calculated for the months of September and October (Table 4) when *E. superba* became more abundant in the diet; of the 30 samples taken in September, 17 contained *E. superba*, while in October, was present in all the 16 samples. Body lengths of *E. superba* in these two months were not significantly different (*t* test,  $t_{244} = 6.747, p = 0.063$ ), although the

**Table 3** *Themisto gaudichaudii* monthly distribution by sex and sampling date, found in scats from gentoo penguins *Pygoscelis papua* from Bird Island (South Georgia) between May and October 2009

	Samples collected	FO	Sex	N	Sex ratio	Mean	SD	$\chi_2$	P
May	18	15	F	133	0.91	21.9	1.39	98.6	< 0.0001
			M	13	0.09	22.0	1.58		
June 1	15	11	F	206	0.82	22.2	1.51	105.0	< 0.0001
			M	44	0.18	22.1	1.27		
June 2	15	11	F	47	0.61	22.0	1.50	3.8	0.053
			M	30	0.39	21.5	1.33		
June 3	15	14	F	199	0.58	22.5	1.57	8.8	0.003
			M	144	0.42	22.2	1.21		
July 1	15	15	F	166	0.65	22.2	1.64	22.6	< 0.0001
			M	90	0.35	22.2	1.36		
July 2	15	13	F	296	0.97	22.8	1.50	267.3	< 0.0001
			M	10	0.03	22.7	2.45		
August 1	15	13	F	298	0.95	23.3	1.43	250.7	< 0.0001
			M	17	0.05	22.9	1.64		
August 2	15	10	F	244	1.00	23.5	1.93	241.0	< 0.0001
			M	1	0.00	24.0	–		
September 1	15	12	F	205	0.99	23.4	2.14	199.1	< 0.0001
			M	2	0.01	30.0	7.07		
September 2	15	9	F	219	1.00	23.2	1.81	219.0	< 0.0001
			M	0	0.00	–	–		
October	16	4	F	51	1.00	24.0	2.36	51.0	< 0.0001
			M	0	0.00	–	–		

“FO” corresponds to Frequency of Occurrence, with no sex distinction, “N” corresponds to number of individuals, “SR” corresponds to Sex Ratio. “Mean” corresponds to mean length and Standard deviation is “SD”. “ $\chi_2$ ” Chi-square statistic and level of significance (“P”) values refer to test regarding significance in sex ratio



**Fig. 4** Box and whiskers' plot distributions of sampled *Themisto gaudichaudii* found in the diet of gentoo penguins *Pygoscelis papua*, divided by two groups represented in the x-axis: Females (F) and Males (M). The y-axis represents size in millimetres

mean size was smaller in September ( $37.2 \pm 2.2$  mm of total length;  $n = 111$ ) than in October ( $39.0 \pm 2.0$  mm,  $n = 134$ ).

### Fish

The otoliths recovered from the scats represented 496 identifiable fish in 78% of samples. Unidentifiable otoliths and fish bones occurred in 21 samples (12.4%). *G. braueri* was the most frequent fish species (48.5%), followed by *Mureanolepis microps* (20.7%; Table 1). The estimated total length and mass of ingested fish ranged, respectively, from < 1 mm and 0.04 g (*G. braueri*) to 324 mm and 201 g (*C. gunnari*; Table 5).

### Cephalopods

A total of five cephalopod individuals were identified through their lower beaks: two *K. longimana* (for which size could not be estimated), one *P. glacialis* (LRL = 1.2 mm, ML = 17 mm, M = 2.08 g) and two *S. circumantarctica* (one individual with LRL = 0.8 mm, ML = 32.5 mm, M = 1.27 g; for the other individual could not be estimated).

**Table 4** *Euphausia superba* monthly samples, frequency of occurrence (FO), number (N) and mean total lengths

	Samples collected	FO	N	Mean	Min	Max	SD
May	18	1	4	UN			
June	45	5	6	UN			
July	30	5	5	UN			
August	30	1	1	UN			
September total	30	17	111	37.2	22.7	41.4	2.27
October total	16	16	134	39.0	31.7	43.3	1.99

## Discussion

In 2009, gentoo penguins at South Georgia in 2009 fed mainly, and continuously, on other prey than *E. superba* throughout the winter. Gentoo penguins consumed chiefly female amphipods, likely in gravid condition (see below). Given that the apparent low body condition of gentoo penguins during this time (Xavier et al. 2017), due to occurrence of adults found dead on the beaches (potentially a sea-bird wreck), the nutritional value of these alternative prey appeared to be insufficient and may have delayed the onset of breeding in the following season by 2–3 weeks (Trathan, unpubl. data). Indeed, the timing of return to the colony to breed and the onset of breeding in the following season are likely to reflect the availability/abundance of prey around South Georgia, within 10–30 km (Tanton et al. 2004). Our study provides a valuable case study on the importance in winter, under abnormal conditions, on constraining successful breeding in the following season.

### Characterization of the diet

High variations in diet composition between (not consecutive) years, and within a season, have been reported for gentoo penguins from South Georgia; in previous studies the frequency of occurrence of *E. superba* ranged from 50 to 95%, while *Champocephalus gunnari* was at times the most frequently consumed prey (Kato et al. 1991; Williams 1991; Croxall et al. 1999; Waluda et al. 2017), showing that not only the main prey species changed but also the main components (from crustaceans to fish). Some of these previous diet studies (Kato et al. 1991; Williams 1991; Croxall et al. 1999) were all conducted after fish species (e.g. *C. gunnari*) have been reduced in Scotia Sea waters due to commercial fishing (Kock 1992; Kock and Jones 2005; Kock et al. 2012). Despite no evidence of decline of the abundance of *E. superba* in recent decades (Hill et al. 2016), there have been marked inter-annual variations in its abundance (Fielding et al. 2014), which have been linked to low *C. gunnari* abundance: in seasons of poor *E. superba* availability, the proportion of *E. superba* in the diet of *C. gunnari* was

**Table 5** Fish size estimation (observed otolith length “OL” in mm, estimated total length “TL” in mm and estimated mass “M” in g, for “n” measured individuals) for four different species (*Champocephalus gunnari*, *Gymnoscopelus braueri*, *Lepidonotothen larseni* and *Muraenolepis microps*), by month, in the diet of gentoo penguins *Pygoscelis papua*

	No samples	Freq	n	OL				TL				M			
				Mean	Min	Max	SD	Mean	Min	Max	SD	Mean	Min	Max	SD
<i>Champocephalus gunnari</i>															
May total	18	7	15	1.2	0.9	2.0	0.33	115.6	80.5	208.1	38.07	8.5	1.5	42.9	11.59
June total	45	15	20	0.9	0.6	1.8	0.29	85.0	49.7	183.6	32.15	3.5	0.3	27.7	6.71
July total	30	4	10	1.6	0.8	2.9	0.58	156.9	69.9	323.8	69.66	32.1	0.9	201.2	60.02
August total	30	4	4	1.1	1.0	1.1	0.06	96.7	91.2	102.2	6.32	3.0	2.4	3.6	0.67
September total	30	0	0												
October total	16	4	15	1.1	0.8	1.2	0.13	97.2	69.9	113.3	14.22	3.3	0.9	5.1	1.52
Total	169	34	64	1.1	0.6	2.9	0.38					9.0	0.3	201.2	25.75
<i>?Gymnoscopelus braueri</i>															
May total	18	15	60	0.7	0.3	0.9	0.13	20.2	<1	34.7	7.36	0.2	0.06	0.38	0.077
June total	45	21	118	0.6	0.2	1.8	0.23	18.5	<1	87.0	12.82	0.2	0.04	6.28	0.576
July total	30	10	20	0.5	0.3	0.7	0.12	10.9	<1	23.0	6.74	0.1	0.06	0.20	0.042
August total	30	13	43	0.8	0.4	1.2	0.22	23.6	5.6	52.1	12.98	0.3	0.08	0.96	0.197
September total	30	17	43	0.8	0.5	1.1	0.16	28.5	11.4	46.3	9.18	0.3	0.11	0.70	0.155
October total	16	7	12	0.9	0.6	1.4	0.23	31.8	17.2	63.7	13.23	0.4	0.15	1.80	0.452
Total	169	83	296	0.7	0.2	1.8	0.21	21.1	<1	87.0	12.03	0.2	0.04	6.28	0.392
<i>Lepidonotothen larseni</i>															
May total	18	0	0												
June total	45	4	13	2.0	0.9	4.1	0.95	88.0	51.5	158.4	31.82	4.4	0.9	22.0	5.73
July total	30	2	17	1.4	0.6	2.5	0.45	69.2	41.5	104.9	14.88	1.7	0.7	4.5	0.86
August total	30	7	23	2.8	0.9	4.5	1.10	115.8	51.5	171.7	36.91	10.3	0.9	32.7	9.80
September total	30	5	6	1.5	0.9	2.0	0.39	71.5	51.5	88.2	13.02	1.8	0.9	2.8	0.65
October total	16	2	6	1.5	1.2	1.9	0.26	69.9	61.5	84.9	8.65	1.6	1.2	2.5	0.47
Total	169	20	65	2.0	0.6	4.5	1.02	89.7	41.5	171.7	34.03	5.3	0.7	32.7	7.37
<i>Muraenolepis microps</i>															
May total	18	0	0												
June total	45	6	13	1.115	0.8	2.2	0.38	46.1	28.8	112.8	22.66	1.3	0.2	10.6	2.86
July total	30	4	2	1.05	1.0	1.1	0.07	41.6	38.9	44.2	3.78	0.5	0.4	0.6	0.14
August total	30	12	14	1.100	0.8	1.5	0.21	44.6	28.8	67.3	11.32	0.7	0.2	2.16	0.56
September total	30	8		1.011	0.7	1.5	0.29	40.2	24.0	67.3	15.59	0.6	0.1	2.16	0.74
October total	16	5	8	1.113	0.7	1.4	0.30	45.6	24.0	61.3	16.27	0.9	0.1	1.6	0.70
Total	169	35	46	1.087	0.7	2.2	0.29	44.2	24.0	112.8	16.24	0.9	0.1	10.6	1.59

significantly lower with subsequent decrease in abundance (Kock et al. 1994; Main et al. 2009). Consequently, such links between the low abundance of *E. superba*, consequent low abundance of *C. gunnari* (and other *E. superba* predator species), fishing activities targeting both species and abnormal environmental conditions are likely to have an impact in gentoo penguin populations.

Our results contrast with those of previous studies at South Georgia (Croxall and Prince 1980; Croxall et al. 1988; Kato et al. 1991; Williams 1991; Croxall et al. 1999) as *E. superba* was present in much smaller proportions in the diet, and only relatively abundant at the end of winter/beginning of spring (i.e. late September and October).

The small amounts of *E. superba* in the diet during the 2009 winter may be due to their low abundance around South Georgia at that time, necessitating the foraging for alternative prey, such as *T. gaudichaudii* (North and Murray 1992; Croxall et al. 1999; Tarling et al. 2007; Watts and Tarling 2012). *T. gaudichaudii* was the most frequent prey for most of the winter, switching to *E. superba* that contributed highly only in September–October (Table 2, Figs. 2, 3) when sea surface temperatures got colder than the average for that time of the year (Xavier et al. 2017). The two krill species (i.e. *E. superba* and *E. triacantha*) made opposing contributions to the PCA analysis, which is consistent with our observation that the abundance of one

was inversely related to the other in the gentoo penguin diet (Table 2, Fig. 3).

Fish species occurred more consistently in the penguin diet during our study period and was present in 77.5% of the samples. However, there was some temporal variation in their dietary contribution; for instance, *G. braueri* was most frequently encountered in June. *C. gunnari* was more abundant in the diet during the earlier part of the study, while *M. microps* and *L. larseni* were increasingly abundant in the diet from July onwards. The consumption of the various species of fish during the study period does not seem to reflect any perceptible changes in sea surface temperature, with small numbers being consumed in comparison with crustaceans (Fig. 2). Even though the overall contribution of fish to the diet was lower than either crustacean species, *G. braueri* was more frequently consumed, as well as by number, than previously reported (Williams 1991). However, this species has comparatively some of the lowest individual biomass of all the fish species consumed (Fig. 2).

The gammarid amphipod *B. securiger* was also a commonly found prey type, particularly during June and July. Although Kato et al. (1991) previously noted this species in the winter diet of gentoo penguins, it made up < 1% of all specimens. These organisms were present in up to 40% of scats in July, making them an important dietary item, at least during the mid-winter period of the present study. *B. securiger* is mainly been found in benthic habitats, particularly those characterized by mud and sand at depth ranges of 67–405 m depth (De Broyer et al. 2007). Their consumption by gentoo penguins during the present study period indicates that the penguins were making frequent foraging trips to the sea bed to find this prey, as they are known to do for *E. superba* (Kokubun et al. 2010).

A few small cephalopod species also occurred in a total of 4% of samples. This is less than in previous studies [e.g. present in 54% of samples in the autumn study (Libertelli et al. 2004)]. This information is of particular interest as it may suggest the occurrence of juvenile *P. glacialis*, *K. longimana* and *S. circumantarctica* on the South Georgia shelf during the winter within 50 km radius of foraging gentoo penguins. These squid species are common in Antarctic waters (Xavier et al. 1999, 2016), and are part of the diet of a wide range of top predators in the Southern Ocean, including albatrosses, penguins, seals, whales and toothfish (Clarke 1996; Smale 1996; Xavier and Chereil 2009).

It has been suggested that gentoo penguins may not forage randomly but, through increasing trip length and range, head for more productive areas where they intensify the foraging effort to enable a more efficient exploitation of dynamic and patchy prey resources (Williams 1991, 1992; Bost et al. 1994; Thiebot et al. 2011). This behaviour has been observed in gentoo penguins at South Georgia (Tanton et al. 2004) and in Kerguelen islands (Thiebot et al. 2011)

outside of the breeding season when foraging ranges are comparatively larger. Our results suggest the same behaviour, and the observed shift in prey over the study period indicates that the penguins were searching widely for the most exploitable resources (Xavier et al. 2003, 2013). The density of *E. superba*, which usually comprises the main dietary item of gentoo penguins (Everson 2000), varies considerably from year to year (Fielding et al. 2014). Multiple indicators suggested a strong ecosystem anomaly in South Georgia in 2009, such as higher than average sea surface temperatures, extremely low *E. superba* abundances and a number of land-based krill-dependent predators populations producing under-weight offspring (Hill et al. 2009; Fielding et al. 2014; Xavier et al. 2017). Dead gentoo penguins were also found regularly on the beaches around Bird Island during the sampling period (Xavier et al. 2017) and the onset of the breeding season (i.e. the date at which 75% of nests have eggs) was delayed of 2–3 weeks in 2009 (Trathan, unpubl. data). This episode may reflect a low prey availability in the area for which gentoo penguins could not compensate with any extra foraging effort. Similarly, in 1994, when there was a ~90% decrease in prey mass among gentoo penguins, there was a corresponding 90% decrease in reproductive success (Croxall et al. 1999).

### Inferences on the population dynamics of *Themisto gaudichaudii*

The amphipod crustacean *T. gaudichaudii* was the most frequent species in the gentoo penguins' diet during the 2009 winter. This species is an important component of the zooplankton community in the region, and is particularly abundant around South Georgia (Atkinson et al. 2012; Watts and Tarling 2012). Our study allowed information to be gathered on the population dynamics of *T. gaudichaudii* around South Georgia. Although our data do not show significant differences in size of males and females in the diet samples, differences in the sex ratio were significant, with a higher frequency of females. In net studies near the Kerguelen Islands, the sex ratio was found to be of a ratio of 1:1 (Labat et al. 2005) or biased towards females (Bocher et al. 2001). Similarly, a substantially greater proportion of females *E. superba* in the diet of macaroni penguins (*Eudyptes chrysolophus*) at South Georgia, as also noted elsewhere (Irvine 2002), while net samples showed the females and males were present in equal proportions in the natural environment (Hill et al. 1996).

*Themisto gaudichaudii* recruits in spring (Watts and Tarling 2012), which means that females (as in the case of all peracarid crustaceans) will be gravid during the winter, making them energetically more nutritious. Indeed, gravid female *T. gaudichaudii* were found in September [Xavier, unpubl. data; see Xavier et al. (2017)]. The females may

also have a different behaviour than males, as their demand for energy intake differs, which may place them in more productive but riskier parts of the water column with regard visual predators (Tarling 2003).

Overall, our study shows that during the 2009 winter the diet of gentoo penguins was dominated by *T. gaudichaudii* as opposed to the more commonly consumed *E. superba* (Williams 1991). This anomaly in the gentoo penguin diet coincided with a year that was characterized by strong ecosystem anomalies in the area of South Georgia (Hill et al. 2009; Xavier et al. 2017). This is similar to other low *E. superba* seasons at South Georgia (e.g. 1994), when there was a 88–90% reduction in the mass of *E. superba* in predator diets, a switch from *E. superba* to amphipods, such as *T. gaudichaudii* (on *E. chrysolophus*) (Croxall et al. 1999). Although *T. gaudichaudii* may have some nutritional benefits (Pakhomov and Perissinotto 1996; Watts and Tarling 2012), such as its lipid reserves, it may not compensate numerically for the lack of *E. superba*. Our results imply that an increased frequency in strong ecosystem anomalies would be detrimental for gentoo populations in this region.

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## Compliance with ethical standards

**Conflict of interest** The authors have no conflict of interests.

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