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

J. C. Xavier1,2,\*, N. Velez3, P. N. Trathan2, Y. Cherel4, C. De Broyer5, F. Cánovas3, J. Seco6,7, N. Ratcliffe2 and G. A. Tarling2

1- Marine and Environmental Sciences (MARE-UC), University of Coimbra, 3001-401 Coimbra, Portugal

2- British Antarctic Survey, High Cross Madingley Road, Cambridge, CB3 0ET, UK

3- Centro de Ciências do Mar (CCMAR), Gambelas, 8005-139 Faro, Portugal

4- Centre d´Etudes Biologiques de Chizé, UMR 7372 du CNRS-Université de La Rochelle, 79360 Villiers-en-Bois, France

5- Royal Belgian Institute for Natural Sciences, OD Taxonomy and Phylogeny, Rue Vautier 29, 1000 Bruxelles, Belgium

6- CESAM and Department of Chemistry, University of Aveiro, 3810-193 Aveiro, Portugal

7- Pelagic Ecology Research Group, Scottish Oceans Institute, University of St Andrews, St Andrews KY16 8LB, UK

\* JCCX@cantab.net

**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 theamphipod *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 (*Champsocephalus 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 lackof *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 (Lescroël et al. 2004; Williams 1995). Gentoo penguins *Pygoscelis papua*, have a circumpolar distribution and breed on the sub-Antarctic islands and the Antarctic Peninsula (46º - 65°S); approx. one third (26-28%) of the breeding population occurs at South Georgia (BirdLife\_International 2016; Williams 1995). At South Georgia, gentoo penguins are present year-round (Ratcliffe et al. 2014; Tanton et al. 2004), and variation in their diet, and the timing and success of breeding, is a product of local prey availability (Tanton et al. 2004; Williams 1990; Williams 1991). 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).

In terms of feeding ecology, gentoo penguins are typically opportunistic inshore feeders, know to dive, at least, up to 140 meters 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 (Bost et al. 1994; Cimino et al. 2016; Clausen and Pütz 2003; Croxall et al. 1988). Increasing Southern Ocean temperatures are likely to alter the distribution and availability of prey species (Constable et al. 2014; Gutt et al. 2015; Reiss et al. 2017; Trivelpiece et al. 2011) which could have negative impacts on how and where gentoo penguins forage, and consequently their capacity to survive and breed (Forcada and Trathan 2009; Forcada et al. 2006; 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 fishsouth 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; Takahashi et al. 2018; Xavier et al. 2017).

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 (Bowen and Iverson 2013; Libertelli et al. 2004; Trathan et al. 2012). 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) (Barrett et al. 2007; Reid and Croxall 2001) and even sex of some crustaceans can be carried out (e.g. on *T. gaudichaudii;* Xavier, unp. 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 analyzed them to (i) describe in detail the 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.

**Material 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) (CCAMLR 2014; Laws 2009). Material was taken to the laboratory within 2 hours of collection and analyzed 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 (Boltovskoy 1999; Kirkwood 1982). 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 (Bocher et al. 2001; Reid and Measures 1998). 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; Reid 1996; Smale et al. 1995; Williams and McEldowney 1990), and subsequently measured. Fish length was estimated by using otolith-total size relationships established by previous studies (Adams and Klages 1987; Hecht 1987; Reid 1996; Smale et al. 1995; Williams and McEldowney 1990). 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 (χ2) statistical test, for which p < 0.05 was considered significant, p < 0.01, highly significant and p ≥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 and 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 *Psychrotheuthis glacialis* (0.6%). The differences in the frequency of occurrence among all species of crustaceans, fish and cephalopods were significant (χ2= 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 sharply afterwards) and *E. superba* (abundant only in the second half of September and October, Table 2, Figs 2 and 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 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 and 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 (χ21= 3.75, P= 0.053)). However, sex ratios were significantly different between months (in total, females=85 %, males=15%) (χ210= 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, t12 = 0.727, P= 0.249). Detailed statistics of size frequency distributions by sex are given in Table 3.

*Importance of Euphausia superba in scats*

*E. 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, t244 = 6.747, P= 0.063), although the mean size was smaller in September (37.2 ± 2.2 mm of total length; n= 111) than in October (39.0 ± 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 =1.27g; for the other individual could not be estimated).

**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 seabird 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, unp. 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 10-30km (Tanton et al. 2004). Our study provide 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 *Champsocephalus gunnari* was at times the most frequently consumed prey (Croxall et al. 1999; Kato et al. 1991; Waluda et al. 2017; Williams 1991), showing that not only the main prey species changed but also the main components (from crustaceans to fish). Some of these previous diet studies (Croxall et al. 1999; Kato et al. 1991; Williams 1991) were all conducted after fish species (e.g. *C. gunnari*) have been reduced in Scotia Sea waters due to commercial fishing (Kock 1992; Kock et al. 2012; Kock and Jones 2005). 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 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 penguins populations.

Our results contrast with those of previous studies at South Georgia (Croxall et al. 1988; Croxall and Prince 1980; Croxall et al. 1999; Kato et al. 1991; Williams 1991) 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 wintermay be due to their low abundance around South Georgia at that time, necessitating the foraging for alternative prey, such a *T. gaudichaudii* (Croxall et al. 1999; North and Murray 1992; 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 and 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. 2016; Xavier et al. 1999), 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 Cherel 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 (Bost et al. 1994; Thiebot et al. 2011; Williams 1991; Williams et al. 1992). This behavior 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 behavior, 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; Xavier et al. 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 (Fielding et al. 2014; Hill et al. 2009; 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, unp. 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 were 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).

*T. 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 regards 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 predador 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.

**Acknowledgments**

We thank Marcella Libertelli (Instituto Antárctico Argentino) for aiding the identification of small otoliths. Peter Ward for identifying zooplankton, Karim Erzini and Ian Staniland for guidance and revision and to Derren Fox, Stacey Adler and Ewan Edwards for supporting collecting the samples. Thank you to the editor Dieter Piepenburg and referees for the excellent contributions in improving the manuscript. This study is a contribution to the programs SCAR AnT-ERA, SCAR EGBAMM, ICED Dynamics and to the PROPOLAR (Programa Polar Português). JS was supported by Do\*MAR PhD FCT fellowship from Fundação para Ciência e Tecnologia (Portugal). JX was supported by the Investigator FCT program (IF/00616/2013). This study benefited from the strategic program of MARE, financed by FCT (MARE- UID/MAR/04292/2013).

**Compliance with Ethical Standards**

The authors have no conflict of interests

**References**

Adams NJ, Klages NT (1987) Seasonal variation in the diet of king penguin *Aptenodytes patagonicus* at Sub-Antarctic Marion Island. J Zool 212: 303-324

Atkinson A, Ward P, Hunt BPV, Pakhomov EA, Hosie GW (2012) An overview of Southern Ocean zooplankton data: abundance, biomass, feeding and functional relationships. CCAMLR Sci 19: 171-218

Barrett RT et al. (2007) Diet studies of seabirds: a review and recommendations. ICES J Mar Sci 64: 1675-1691

BirdLife\_International (2016) *Pygoscelis papua*. The IUCN Red List of Threatened Species 2016: eT22697755A93637402 <http://dxdoiorg/102305/IUCNUK2016-3RLTST22697755A93637402en> Downloaded on 04 September 2017:

Bocher P, Cherel Y, JP L, Mayzaud P, Razouls S, Jouventin P (2001) Amphipod-based food web: *Themisto gaudichaudii* caught in nets and by seabirds in Kerguelen waters, southern Indian Ocean. Mar Ecol Prog Ser 223: 261-276

Boltovskoy D (1999) South Atlantic zooplankton. Backhuys Publishers, Leiden, Netherlands

Bost CA, Koubbi P, Genevois F, Ruchon L, Ridoux V (1994) Gentoo penguin *Pygoscelis papua* diet as an indicator of planktonic availability in the Kerguelen Islands. Polar Biol 14 147-153

Bowen W, Iverson S (2013) Methods of estimating marine mammal diets: a review of validation experiments and sources of bias and uncertainty. Mar Mammal Sci 29: 719-754

CCAMLR (2014) CCAMLR Ecosystem Monitoring Program (CEMP) Standard Methods. CCAMLR, Hobart. <https://www.ccamlr.org/en/document/science/cemp-standard-methods>.

Chessel D, Dufour AB, Thioulouse J (2004) The ade4 package-I-One-table methods. R news 4: 5-10

Cimino MA, Moline MA, Fraser WR, Patterson-Fraser DL, Oliver MJ (2016) Climate-driven sympatry may not lead to foraging competition between congeneric top-predators. Sci Rep 6: 18820

Clarke MR (1996) Cephalopods as prey.III.Cetaceans. Phil Trans R Soc Lond B 351: 1053-1065

Clausen AP, Pütz K (2003) Winter diet and foraging range of gentoo penguins (*Pygoscelis papua*) from Kidney Cove, Falkland Islands. Polar Biol 26: 32-40

Constable AJ et al. (2014) Change in Southern Ocean ecosystems I: How changes in physical habitats directly affect marine biota. Glob Chang Biol 20: 3004-3025

Croxall JP, Davis RW, Oconnell MJ (1988) Diving Patterns in Relation to Diet of Gentoo and Macaroni Penguins at South Georgia. Condor 90: 157-167

Croxall JP, Prince PA (1980) The food of gentoo penguins *Pygoscelis papua* and macaroni penguins *Eudyptes chrysolophus* at South Georgia. Ibis 122: 245-253

Croxall JP, Reid K, Prince PA (1999) Diet, provisioning and productivity responses of marine predators to differences in availability of Antarctic krill. Mar Ecol Prog Ser 177: 115-131

De Broyer C, Lowry JK, Jazdzewski K, Robert H (2007) Catalogue of the Gammaridean and Corophiidean Amphipoda (Crustacea) of the Southern Ocean, with distribution and ecological data. In: C. DB (ed) Census of Antarctic Marine Life: Synopsis of the Amphipoda of the Southern Ocean. Vol. I. , vol 77. Bulletin de l'Institut royal des Sciences naturelles de Belgique, Biologie, pp 1-325

Everson I (2000) Krill: biology, ecology and fisheries. Blackwell Science Ltd, Oxford

Fielding S et al. (2014) Interannual variability in Antarctic krill (*Euphausia superba*) density at South Georgia, Southern Ocean: 1997–2013. ICES J Mar Sci 71: 2578-2588

Forcada J, Trathan PN (2009) Penguin responses to climate change in the Southern Ocean. Glob Chang Biol 15: 1618-1630

Forcada J, Trathan PN, Reid K, Murphy EJ, Croxall JP (2006) Contrasting population changes in sympatric penguin species in association with climate warming. Glob Chang Biol 12: 411-423

Gutt J et al. (2015) The Southern Ocean ecosystem under multiple climate change stresses - an integrated circumpolar assessment. Glob Chang Biol 21: 1434-1453

Hecht T (1987) A guide to the otoliths of Southern Ocean fishes. S Afr J Antarct Res 17: 2-87

Hill HJ, Trathan PN, Croxall JP, Watkins JL (1996) A comparison of Antarctic krill *Euphausia superba* caught by nets and taken by macaroni penguins *Eudyptes chrysolophus*: evidence for selection. Mar Ecol Prog Ser 140: 1-11

Hill S et al. (2009) Multiple indicators suggest a strong ecosystem anomaly at South Georgia in 2009. WG-EMM-09/23:

Hill SL et al. (2016) Is current management of the Antarctic krill fishery in the Atlantic sector of the Southern Ocean precautionary? CCAMLR Sci 23: 31-51

Hinke JT, Trivelpiece WZ (2011) Daily activity and minimum food requirements during winter for gentoo penguins (Pygoscelis papua) in the South Shetland Islands, Antarctica. Polar Biol 34: 1579-1590

Irvine LG (2002) Sex differences in Antarctic krill (*Euphausia superba*) retrieved from Adelie penguin stomachs: implications for diet analysis. Polar Biol 25: 717-720

Kane JE (1966) The distribution of *Parathemisto gaudichaudii* (Guer.), with observations on its life-history in the 0° to 20° E sector in the Southern Ocean. Discov Rep 34: 163-198

Kato A, Williams TD, Barton TR, Rodwell S (1991) Short-term variation in the winter diet of gentoo penguins *Pygoscelis papua* at South Georgia during July 1989. Mar Ornithol 19: 31-38

Kindt R, Coe R (2005) Tree diversity analysis: a manual and software for common statistical methods for ecological and biodiversity studies. World Agroforestry Centre,

Kirkwood JM (1982) A guide to the Euphausiacea of the Southern Ocean. ANARE Res Notes 1: 1-45

Kock K-H (1992) Antarctic fish and fisheries. Cambridge University Press, Cambridge

Kock K-H et al. (2012) The role of fish as predators of krill (*Euphausia superba*) and other pelagic resources in the Southern Ocean. CCAMLR Sci 19: 115-169

Kock K-H, Jones CD (2005) Fish stocks in the southern Scotia Arc region—a review and prospects for future research. Rev Fisheries Sci 13: 75-108

Kock K-H, Wilhelms S, Everson I, Gröger J (1994) Variations in the diet composition and feeding intensity of mackerel icefish *Champsocephalus gunnari* at South Georgia (Antarctic). Mar Ecol Prog Ser 108: 43-57

Kokubun N, Takahashi A, Mori Y, Watanabe S, Shin H-C (2010) Comparison of diving behavior and foraging habitat use between Chinstrap and Gentoo Penguins breeding in the South Shetland Islands, Antarctica. Mar Biol 157: 811–825

Labat J, Mayzaud P, Sabini S (2005) Population dynamics of *Themisto gaudichaudii* in Kerguelen Island waters, Southern Indian Ocean. Polar Biol 28: 776-783

Laws RM (2009) Antarctic seals: research methods and techniques. Cambridge University Press,

Lescroël A, Ridoux V, Bost CA (2004) Spatial and temporal variation in the diet of gentoo penguin (*Pygoscelis papua*) at Kerguelen Islands. Polar Biol 27: 206-216

Libertelli MM, Daneri GA, Piatkowski U, Coria NR, Carlini AR (2004) Predation on cephalopods by *Pygoscelis papua* and *Arctocephalus gazella* at South Orkney Islands. Polish Polar Res 25: 267-274

Main CE, Collins MA, Mitchell R, Belchier M (2009) Identifying patterns in the diet of mackerel icefish (*Champsocephalus gunnari*) at South Georgia using bootstrapped confidence intervals of a dietary index. Polar Biol 32: 569-581

Mori Y, Boyd IL (2004) Segregation of foraging between two sympatric penguin species: does rate maximisation make the difference? Mar Ecol Prog Ser 275: 241-249

North AW, Murray AWA (1992) Abundance and diurnal vertical distribution of fish larvae in early spring and summer in fjord at South Georgia. Antarct Sci 4: 405-412

Pakhomov E, Perissinotto R (1996) Trophodynamics of the hyperiid amphipod Themisto gaudichaudi in the South Georgia region during late austral summer. Mar Ecol Prog Ser 134: 91-100

Ratcliffe N et al. (2014) Love thy neighbour or opposites attract? Patterns of spatial segregation and association among crested penguin populations during winter. J Biogeogr 41: 1183-1192

Reid K (1996) A guide to the use of otoliths in the study of predators at South Georgia. British Antarctic Survey, Cambridge

Reid K, Croxall JP (2001) Environmental response of upper trophic-level predators reveals a system change in an Antarctic marine ecosystem. Proc R Soc B 268: 377-384

Reid K, Measures J (1998) Determining the sex of Antarctic krill *Euphausia superba* using carapace measurements. Polar Biology 19: 145-147

Reiss CS et al. (2017) Overwinter habitat selection by Antarctic krill under varying sea-ice conditions: implications for top predators and fishery management. Mar Ecol Prog Ser 568: 1-16

Smale MJ (1996) Cephalopods as prey. IV. Fishes. Phil Trans R Soc Lond B 351: 1067-1081

Smale MJ, Watson G, Hecht T (1995) Otolith atlas of Southern African marine fishes vol 1. Ichthyological Monographs of the JLB Smith Institute of Ichthyology. Grahamstown, South Africa,

Takahashi A et al. (2018) Migratory movements and winter diving activity of Adélie penguins in East Antarctica. Mar Ecol Prog Ser 589: 227-239

Tanton JL, Reid K, Croxall JP, Trathan PN (2004) Winter distribution and behaviour of gentoo penguins *Pygoscelis papua* at South Georgia. Polar Biol 27: 299-303

Tarling G, Cuzin-Roudy J, Thorpe S, Shreeve R, Ward P, Murphy E (2007) Recruitment of Antarctic krill *Euphausia superba* in the South Georgia region: adult fecundity and the fate of larvae. Mar Ecol Prog Ser 331: 161-179

Tarling GA (2003) Sex-dependent diel vertical migration in northern krill *Meganyctiphanes norvegica* and its consequences for population dynamics. Mar Ecol Prog Ser 260: 173-188

Thiebot J-B, Lescroël A, Pinaud D, Trathan PN, Bost C-A (2011) Larger foraging range but similar habitat selection in non-breeding versus breeding sub-Antarctic penguins. Antarct Sci 23: 117-126

Trathan P, Ratcliffe N, Masden E (2012) Ecological drivers of change at South Georgia: the krill surplus, or climate variability. Ecography 35: 983-993

Trivelpiece WZ, Hinke JT, Miller AK, Reiss CS, Trivelpiece SG, Watters GM (2011) Variability in krill biomass links harvesting and climate warming to penguin population changes in Antarctica. PNAS 108: 7625-7628

Waluda CM, Hill SL, Peat HJ, Trathan PN (2017) Long-term variability in the diet and reproductive performance of penguins at Bird Island, South Georgia. Mar Biol 164: 39

Watts J, Tarling GA (2012) Population dynamics and production of *Themisto gaudichaudii* (Amphipoda, Hyperiidae) at South Georgia, Antarctica. Deep-Sea Res II 59: 117-129

Williams R, McEldowney A (1990) A guide to the fish otoliths from waters off the Australian Antarctic Territory, Heard and Macquarie Island vol 75. ANARE Research Notes,

Williams RL, Goodenough AE, Stafford R (2012) Statistical precision of diet diversity from scat and pellet analysis. Ecological informatics 7: 30-34

Williams TD (1990) Annual variation in breeding biology of gentoo penguins (*Pygoscelis papua*) at Bird Island, South Georgia. J Zool 222: 247-258

Williams TD (1991) Foraging ecology and diet of gentoo penguins *Pygoscelis papua* at South Georgia during winter and an assessment of their winter krill consumption. Ibis 133: 3-13

Williams TD (1995) The penguins: Spheniscidae. Oxford University Press, Oxford

Williams TD, Briggs DR, Croxall JP, Naito Y, Kato A (1992) Diving pattern and performance in relation to foraging ecology in the gentoo penguin *Pygoscelis papua*. J Zool 227: 211-230

Xavier JC, Cherel Y (2009) Cephalopod beak guide for the Southern Ocean. British Antarctic Survey,

Xavier JC, Croxall JP, Reid K (2003) Inter-annual variation in the diet of two albatross species breeding at South Georgia: implications for breeding performance. Ibis 145: 593-610

Xavier JC et al. (2013) Seasonal changes in the diet and feeding behaviour of a top predator indicate a flexible response to deteriorating oceanographic conditions. Mar Biol 160: 1597-1606

Xavier JC, Raymond B, Jones DC, Griffiths H (2016) Biogeography of cephalopods in the Southern Ocean using habitat suitability prediction models. Ecosystems 19: 220-247

Xavier JC, Rodhouse PG, Trathan PN, Wood AG (1999) A Geographical Information System (GIS) atlas of cephalopod distribution in the Southern Ocean. Antarct Sci 11: 61-62

Xavier JC et al. (2017) Sexual and individual foraging segregation in Gentoo penguins Pygoscelis papua from the Southern Ocean during an abnormal winter. PloS one 12: e0174850

**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). Lengths and corresponding standard deviation only applies to some species.

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

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

**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. “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”. “χ2” chi-square statistic and level of significance (“P”) values refer to test regarding significance in sex ratio.

|  |  |  |  |  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- | --- | --- | --- | --- |
|  | Samples collected | FO | Sex | N | Sex Ratio | Mean | SD | χ2 | 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 | - | - |

**Table 4.** *Euphausia superba* monthly samples, frequency of occurrence (FO), number (N) and mean total lengths. “χ2” stands for chi-square statistic value and (“p”) to p-value. “NS” stands for p > 0.05 (non significative), “ **·** ” for p < 0.05 (significative) and “ **¨** ” for p < 0.01 (very significative). The first 4 months of sampling had no measurable individuals (“UN” stands for unmeasurable).

|  |  |  |  |  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- | --- | --- | --- | --- |
|  | Samples collected | FO | N | Mean | Min | Max | SD | χ2 | p |
| 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 | 0.030 | NS |
| October total | 16 | 16 | 134 | 39.0 | 31.7 | 43.3 | 1.99 |

**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 (*Champsocephalus gunnari, ?Gymnoscopelus braueri, Lepidonothoten larseni* and *Muraenolepis microps*), by month, in the diet of gentoo penguins *Pygoscelis papua*.

|  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- |
|  |  |  |  |  |  | OL |  |  |  | TL |  |  |  | M |  |
| *Champsocephalus gunnari* | nº samples | Freq | n | Mean | Min | Max | SD | Mean | Min | Max | SD | Mean | Min | Max | SD |
| 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 |
| *?Gymnoscopelus braueri* |  |  |  |  |  | OL |  |  |  | TL |  |  |  | M |  |
| 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 |
| *Lepidonothoten larseni* |  |  |  |  |  | OL |  |  |  | TL |  |  |  | M |  |
| 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 |
| *Muraenolepis microps* |  |  |  |  |  | OL |  |  |  | TL |  |  |  | M |  |
| 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 |

Figures

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

**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.

**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.

**Fig 4.** Box & 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.