Exceptional foraging plasticity in King Penguins (*Aptenodytes patagonicus*) from a recently established breeding site in Tierra del Fuego, Chile

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ABSTRACT

Animals constantly test the borders of their own ecological niche and tend to expand their range, which is now additionally challenged by global climate change. Following human exploitation throughout the Southern Ocean in the 19th and the beginning of the 20th century, numbers of King Penguin breeding pairs have increased and former breeding sites have been re-colonized. Since 2010 a breeding colony became (re-)established at Bahía Inútil, Strait of Magellan, Tierra del Fuego, Chile. The aims of this study were to study the foraging ecology of King Penguins at this new breeding site, which is characterized by a set of different environmental variables as it is located within the confined environment of the Magellan Strait, more than 300 km from the open ocean. During the course of this study, thirty-two birds were successfully equipped with external devices that recorded 206 foraging trips by breeding and non-breeding birds. With one exception, all birds foraged throughout the year exclusively in the Magellan Strait with the main foraging areas located within 100 km from the colony. The diving activities of 15 King Penguins were recorded during 59 foraging trips, the deepest dive was 160 m and the longest dive lasted 6.75 mins. Based on a representative subsample of 3000 dives, mean dive depth was 32 ± 34 m and mean dive duration 117 ± 84 s. Accordingly, foraging trip durations throughout the year were significantly shorter than those recorded for conspecifics elsewhere. In accordance with these changes in foraging behavior, stomach contents from seven birds showed a mix of fish and squid, with Falkland sprats *Sprattus fuegensis* as the main prey item present in all samples. The implications of these behavioral adaptations are discussed with regard to this unusual confined

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foraging environment and predicted changes in the performance of King Penguins breeding elsewhere following global change.

1. Introduction

Animals constantly test the borders of their own ecological niche and tend to expand their range when and where possible. Currently, this expansion is additionally driven by global climate change leading to a cascade of effects on their habitat, reproduction, diseases and food distribution and abundance (Grose et al., 2020). For example, Polar Bears *Ursus maritimus* in all but high-Arctic habitats are forecasted to become extinct due to a decreasing sea ice cover by 2100 under most global change scenarios (Molnár et al., 2020). On the other hand, Wandering Albatrosses *Diomedea exulans* have benefitted from a poleward shift and an increase in intensity of the westerly winds in the Southern Ocean by higher traveling speeds and thus shorter foraging trip durations (Weimerskirch et al., 2012). Even closely related species like the co-existing Adélie *Pygoscelis adeliae* and Gentoo Penguins *P. papua* can be affected by climate-related changes in opposing ways (Forcada et al., 2006; Forcada and Trathan, 2009). Foraging plasticity is an important mechanism for seabirds and other marine consumers to cope with environmental changes as well as intrinsic life history limitations such as the energetic constraints of each breeding stage and molt (Cherel et al., 2014).

King Penguins *Aptenodytes patagonicus* are circumpolar distributed and breed on sub-Antarctic islands in the vicinity of the Antarctic Polar Front (Fig. 1), from 46°S at Prince Edward and Crozet Islands to 54°S on South Georgia and Macquarie Island (Williams, 1995; Bost et al., 2013). Following human exploitation in the 19th and the beginning of the 20th century, numbers have increased again and even re-colonized former breeding sites from where it had disappeared, like Heard Island in the Indian Ocean (Budd and Downes, 1965) and the Falkland Islands (Otley et al., 2007; Pistorius et al., 2012). The global population was believed to have stabilized over the past decade (Bost et al., 2013), but recently it became evident that the largest King Penguin colony at Ile aux Cochons,
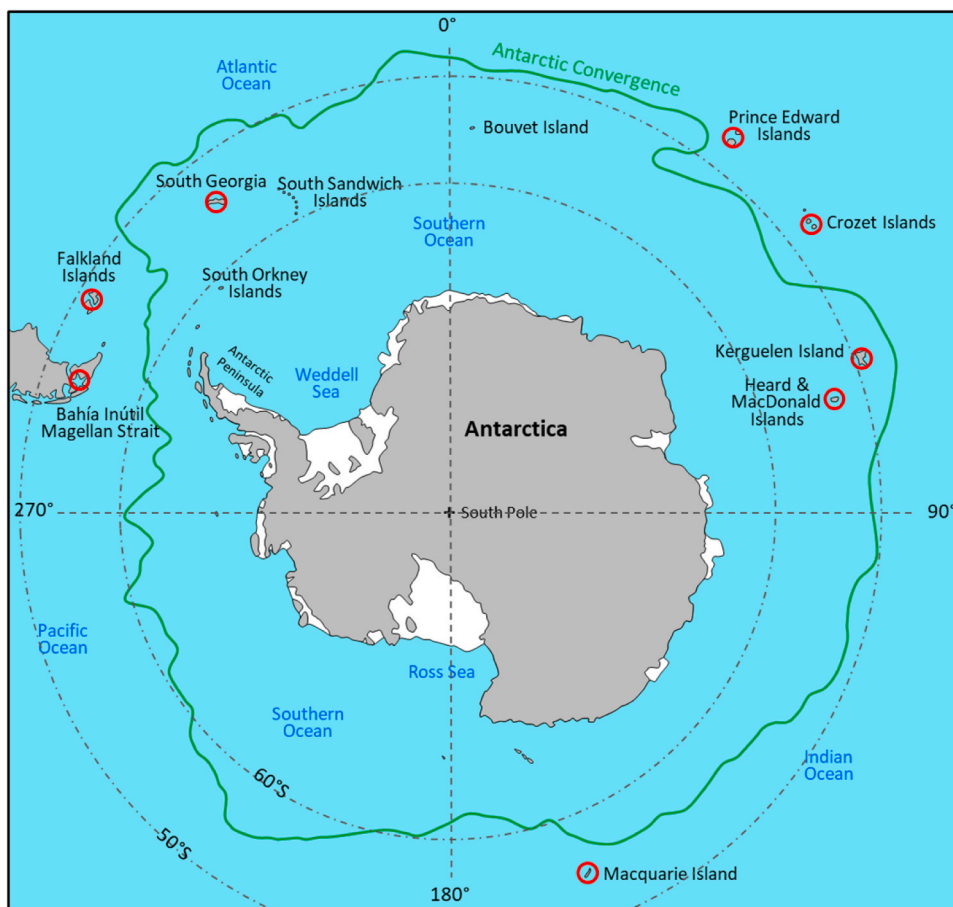

Fig. 1. King Penguin breeding sites (marked by red circles) in the Southern Ocean. For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.

Crozet Islands, has suffered a massive decline of 88% over the past 35 years (Weimerskirch et al., 2018). One potential reason for this decline may have been a southward shift of their main feeding ground, the Antarctic Polar Frontal Zone (APFZ), induced by the very same poleward shift of westerly winds beneficial for Wandering Albatrosses (Weimerskirch et al., 2012). This shift resulted in an increase in their foraging trip duration and subsequently reduced breeding success, indicating a projected reduction of breeding pairs on Crozet Islands (Le Bohec et al., 2008; Cristofari et al., 2018; Bost et al., 2015; Peron et al., 2012). However, this in turn could improve conditions for King Penguins breeding in South Georgia, which is situated east and south of the Antarctic Polar Front. Accordingly, there is evidence for a significant increase in the population on South Georgia over the past, which at least partly may be a consequence of climatic forces (Foley et al., 2018, 2020).

In addition to these well-established breeding sites, breeding attempts have been recorded over the past years at various locations in the South Shetlands and Sound Sandwich Islands, which were assumed to be linked to a southward range expansion following climate warming (Convey et al., 1999; Petry et al., 2013; Juáres et al., 2017; Gryz et al., 2018; Borowicz et al., 2020). In contrast, over the past 60 years King Penguins have also (re-)colonized the Falkland Islands (Pistorius et al., 2012), which, despite being located at 51°S, are climatically the most temperate breeding site (Pütz, 2002). Furthermore, there are also anecdotal reports of breeding attempts on Isla Hornos, Chile, and Isla de los Estados, Argentina, and with the laying of a first egg in 2010 a breeding colony became (re-)established at Bahía Inútil, Strait of Magellan, Tierra del Fuego, Chile (Kusch and Marín, 2012). In the following years, an increasing number of eggs were laid and chicks hatched, but the first chick only fledged in 2015 (pers. obs.). Since, the number of breeding attempts and chicks fledged has increased annually at a very slow pace, with ups and downs due to severe weather conditions, infectious diseases and terrestrial predation by introduced Gray foxes (*Lycalopex griseus*) and American mink (*Mustela vison*) (Godoy et al., 2019).

The breeding site in Bahía Inútil differs from all others in nearly every aspect since it is located in a confined environment about 300 km away from the open seas in the Atlantic and Pacific Oceans. First indications of a substantially changed foraging behavior were provided by Gherardi-Fuentes et al. (2019), who could show that during the early incubation period the duration of entire foraging

Table 1
Metadata of King Penguins studied at Bahía Inútil, Chile. Sex is mentioned when known. MK9 devices recorded dive depth, MK10 recorded dive depth and position (GPS) while Kiwisat and Seatag transmitted position (Argos). One adult (579-15B) and a juvenile (440-16) were excluded from analysis and treated separately.

Bird ID	Name	Sex	Breeding status Start/End	Device type deployed	Date of equipment (dd/mm/yy)	Duration (d)	Number of trips (n)
487-14		F	Incubating	MK10	03/12/14	4.6	1
490-14		F	Incubating	MK10	04/12/14	9.0	1
491-14		F	Incubating	MK10	05/12/14	12.0	1
492-14		F	Incubating	MK10	09/12/14	5.1	2
493-14		F	Non-breeding	MK10	16/12/14	2.2	1
696-14		F	Incubating	MK9	04/12/14	7.7	1
697-14		M	Non-breeding	MK9	25/11/14	19.4	13
698-14		M	Incubating	MK9	10/12/14	1.2	2
950-14		M	Non-breeding	MK9	30/11/14	14.5	11
953-14		F	Non-breeding	MK9	28/11/14	16.5	14
956-14		F	Incubating	MK9	01/12/14	19.6	2
973-14		M	Non-breeding	MK9	30/11/14	22.0	2
459-15	Rosmy	?	Non-breeding	Kiwisat	05/03/15	198.9	16
460-15	Paula	?	Chick	Kiwisat	13/03/15	45.0	4
461-15	Paul	?	Chick	Kiwisat	05/03/15	118.4	11
462-15	Leander	?	Non-breeding	Kiwisat	07/03/15	171.4	10
463-15	Cecilio	?	Non-breeding	Kiwisat	05/03/15	245.9	13
576-15		?	Non-breeding	Seatag	02/03/15	22.0	2
577-15		?	Non-breeding	Seatag	02/03/15	206.2	13
578-15		?	Chick	Seatag	03/03/15	41.3	3
579-15	O-Wawatay	?	Non-breeding	Seatag	05/03/15	28.8	4
580-15		?	Non-breeding	Seatag	04/03/15	97.2	7
436-16		F	Incubating/Chick	Seatag	09/12/16	101.1	9
441-16		M	Incubating	Seatag	22/12/16	104.9	7
442-16		?	Incubating/Chick	Seatag	31/12/16	133.9	14
444-16		M	Incubating/Chick	Seatag	16/12/16	146.9	17
459-16		?	Incubating	Kiwisat	19/12/16	86.5	6
460-16		M	Incubating/Chick	Kiwisat	10/12/16	90.4	12
487-16		?	Non-breeding	MK10	08/12/16	42.1	3
491-16		M	Incubating	MK10	11/12/16	26.1	4
493-16		F	Incubating	MK10	27/12/16	10.8	1
579-15	O-Wawatay	?	Non-breeding	Seatag	03/04/15	264.9	2
440-16	Juvenile	M		Seatag	21/12/16	70.4	2
						2051.7	207.0

trips and individual dives was much shorter, and dive depths shallower, than in conspecifics from breeding sites in the open ocean. This makes it highly likely that the birds have changed their foraging behavior as a response to the confined environment with a potential different quality and quantity of prey species, because it can be assumed that penguins do not commute on each foraging trip between the Magellanic Strait and the open ocean. The objectives of this study were a) to investigate the foraging ecology of King Penguins at this new breeding site, and b) to compare the findings to those obtained at other breeding sites. For this purpose, a set of different remote sensing devices was deployed to determine their foraging areas and ranges throughout the year, including characterization of their diving activities and diet during the incubation and early chick rearing periods.

2. Methods

2.1. Study site

This study was conducted at the King Penguin colony located in Bahía Inútil (53°27′42″S, 69°18′32″W) on the southeastern coast of the Magellan Strait in Tierra del Fuego Island, southern Chile (Fig. 3). The colony is located within the limits of the private park "Parque Pingüino Rey" (PPR) and covers an area of ca. 200 m^2 on a grassy plain just behind a chain of dunes, between the Marazzi River and the ocean (López, 2014). First individuals at this colony were recorded during the 1980s (Couve and Vidal, 2010) and about 50 individuals were counted in 2010 (Kusch and Marín, 2012), further increasing up to 156 during the 2014–2015 breeding season (C. Godoy, pers. obs.), Egg-laying at this colony was first observed in December 2010 (Kusch and Marin, 2012) and an increasing number of chicks hatched regularly since then. However, all chicks died before fledging until the first chick, amongst about 25 breeding attempts, successfully fledged in November 2015. Number of breeding pairs has since increased steadily, while the number of chicks fledged varied between two in 2019 and ten in 2017 (C. Godoy, pers. obs.; PPR, unpubl. data).

2.2. Fieldwork

Field work was conducted during three breeding seasons: 23 November to 24 December 2014, 2–4 March 2015 and 7 December 2016 to 19 January 2017. Birds were caught by hand and devices were attached to the middle of the back using black Tesa tape and epoxy glue following Wilson et al. (1997). Birds were individually marked using combinations of colored Tesa tape attached to the wings. All devices were streamlined to minimize potential effects of an increased drag underwater (e.g. Wilson and McMahon, 2006). During the whole procedure, which lasted between 10 and 15 min, the head of the bird was covered with a dark hood to reduce stress.

The colony was surveyed 2–3 times per day using 10 × 42 binoculars to monitor the breeding status and the presence/absence of the study birds. Devices were recovered by catching the study birds at the edge of the colony or at the beach. Some of the satellite tags deployed could not be recovered as they were lost at sea.

Overall, we deployed tracking devices on 32 individuals. In 2014, twelve adult individuals engaged in courtship (for subsequent breeding status see Table 1) were equipped with time-depth recorders (TDRs): seven Mk9 and five Mk10 TDRs (Wildlife Computers, Redmond, WA, USA). Between 2 and 4 March 2015, ten randomly selected birds were equipped with satellite transmitters (PTTs): five with KiwiSat 202 K2G 273 (Sirtrack, NZ) and five with SeaTags (Desert Star Systems, USA, 1st gen). In 2016, nine birds engaged in courtship were equipped with either TDRs or PTTs: three MK10 TDRs, two KiwiSat 202 and four SeaTags (2nd gen). In addition, one SeaTag was deployed on a juvenile just about to fledge. With the exception of eight satellite transmitters that were lost at sea, all other devices were recovered upon re-sighting of the study birds in the colony (for details see Table 1).

2.3. Devices used

MK9 devices (30 g, 72 × 19 mm, 64 Mb of flash memory) included sensors for depth (with a resolution of 0.5 m and an accuracy of ±1%), temperature (ranging from −40 °C to 60 °C with a resolution of 0.05 °C and an accuracy of ±0.1 °C), light intensity (with a logarithmic range from 5×10^{-12} W cm^{-2} to 5×10^{-2} W cm^{-2}) and a wet/dry sensor. MK10 devices (165 g, 86 × 55 × 26 mm, 1 Gb of flash memory) included the same set of sensors (depth, temperature, light intensity and wet/dry sensor) but provided also the position of the birds through a Fastloc GPS. Devices were programmed using MK9 Host and MK10 Host software, respectively. We programmed devices to record data only when wet (i.e. when the bird was underwater) at 3-s intervals (for depth and temperature) and at 5-min intervals for battery voltage and wet/dry sensor. GPS data were programmed to be collected every hour when dry and every 15 min or immediately thereafter at the subsequent surfacing when wet.

Two different types of satellite transmitters were used. The KiwiSat tags used in 2015 (n = 5) and 2016 (n = 2), weighed 105 g and had maximum dimensions of 87 × 39 × 24 mm (Bird nos. 459–463; Table 1). The antenna originated from the rear of the devices at an angle of 45° to reduce underwater drag (Wilson et al., 2004) and a saltwater switch prevented transmission when underwater. These tags were duty-cycled and programmed to transmit between 0100 and 0500 UTC and 1300 and 1700 UTC (corresponding to local time −3 hr). Five SeaTags were deployed each in 2015 (1st gen) and 2016 (2nd gen). The SeaTag (1st gen) weighed 25 g and had a cylindrical design of a maximum of 17 mm in diameter and a length of 101 mm. The tags were powered by two high-efficiency (22%)

solar panels providing 7.6 mA total at 3.4 V in full sunlight. The photovoltaic charge was stored in an ultra-capacitor and a single Argos transmission was emitted once the capacitor was charged, and the process repeated. The SeaTags (2nd gen) were slightly shorter (96 mm) but heavier (26 g), contained four high-efficiency solar panels and, in addition, measured and transmitted light intensity for light-based positional analysis. Photovoltaic charge was stored in a rechargeable lithium-ion battery. Light intensity was not considered for positional analysis due to the restricted movements of the study birds and the relatively large errors associated with each light-based positional fix.

2.4. Data analysis

Foraging trip durations, defined as the time period between departure and the subsequent return to the shore, were determined using either the dive records (TDRs) or positional fixes ashore in the vicinity of the colony (PTTs), complemented by daily sightings of equipped birds. For analysis of trip durations, the breeding cycle was divided into the following three main time periods: Incubation (1 November to 31 January), brooding (1 February to 30 April) and winter (1 May to 31 October). We analyzed and compared trip duration in each period for breeding and non-breeding penguins using one-way ANOVA test (Zar, 1984). In order to check for assumptions derived by ANOVA, we analyzed homogeneity of variance and normality using QQ-plot and Shapiro-Wilk test. All the analyses were performed in R studio (R Development Core Team, 2019).

All dives with a minimum depth of 3 m were analyzed (c.f. Pütz and Cherel, 2005) using *Instrument Helper* (Wildlife Computers, USA). The following parameters were determined for each individual foraging trip: trip duration, number of dives, amount of time spent diving in relation to total time spent at sea, vertical distance covered, maximum dive depth and dive duration. For the aim of this study, all dive data were pooled, irrespective of the breeding status of the study birds in order to provide a comprehensive account of the diving activity of birds in this newly established breeding site. A more detailed comparison of the diving behavior in breeding and non-breeding King Penguins, including the most commonly used dive parameters, has been published in Gherardi-Fuentes et al. (2019).

Apart from these parameters, we also calculated two variables indicative of foraging effectivity. Following Ydenberg and Clark (1989), diving efficiency (DE) was derived by:

DE = Bottom time / (Dive duration + Post-dive time)

Bottom time was defined as the time spent at 85% of the maximum depth (Pütz and Cherel, 2005). Post-dive time is dependent on the amount of oxygen used during the preceding dive. However, other factors may also contribute to this parameter, for example resting periods or oxygen deficits built up over a number of previous dives. In order to eliminate all but the purely physiological factors contributing to the surface time, calculation of diving efficiency was restricted to dives followed by a post-dive time of less than 1000 s (corresponding to about 2.5 × maximum dive duration).

Since we were not able to observe prey ingestion during dives, the feeding success was approximated through the proportion of the number of wiggles per unit bottom time. Wiggles are defined as sudden deviations from the mean dive depth and during the bottom time and believed to represent active movements following prey encounter and subsequent catching efforts (Wilson, 1995). They are also used to differentiate between so-called W-dives containing wiggles and U-dives without wiggles (e.g. Pütz and Cherel, 2005). The number of wiggles is a useful tool to quantify the feeding success in penguins (Simeone and Wilson, 2003; Bost et al., 2007). Subsequently, foraging success (FS) was calculated following Pütz et al. (2018):

FS = Number of wiggles / Minute bottom time

A sub-sample of 3000 dives (200 randomly selected dives from each bird using the *Random* function in *Microsoft Office Excel*) was used to derive maximum and overall means ± standard deviation of dive depth, dive duration, diving efficiency and foraging success. Results are presented as means ± standard deviation unless otherwise stated.

Locational data received from Fastloc GPSs and PTTs had varying accuracies associated with individual positions. Firstly, all positional data on land were deleted, then remaining data were filtered using maximum speed between two locations (10 km/hr) and turning angle (70°). With the exception of two birds (see below) all remaining positions were, irrespectively of breeding status and time of the year, within the Magellan Strait and adjacent channels and subsequently pooled. Kernel density was then calculated using R.3.3.1 (package adehabitat), Geospatial Modelling Environment (v. 0.7.2.0) and ArcGIS 10 with a search radius of 8000 m and an output cell-size of 800 m (c.f. Pütz et al., 2014), due to the foraging range of the species and the maximum distance reached (Hemson et al., 2005; Falabella et al., 2009). One bird that left the Magellan Strait during winter (KP 579–15B; Table 1) and the juvenile were analyzed in the same way but treated separately (see below).

2.5. Diet sampling

Between 8th and 11th December 2016, seven randomly chosen birds returning from the water were caught on the beach and stomach flushed using the water-offloading technique described by Wilson (1984) to determine most recent prey items. All birds
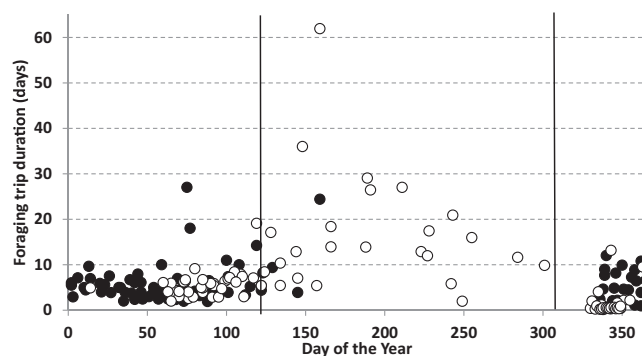
Fig. 2. Foraging trip duration of breeding (closed circle) and non-breeding (open circle) King Penguins from Bahía Inútil, Chile. Black vertical lines indicate 1 May (Day 120) and 31 October (Day 305), defined in the context of this study as onset and end of the winter period.

sampled were flushed only once. Stomach contents were drained and stored in plastic bags for later analysis. In all cases only few prey items were obtained, that were, with one exception, all little or only partly digested, indicating very recent ingestion. In one bird, only highly digested squid beaks were obtained, indicative of an ingestion at least some days ago (Piatkowski and Pütz, 1994). Stomach contents were qualitatively analyzed to the lowest taxon possible, either based on intact specimen or on otoliths extracted from fish skulls or loose otoliths (fish) and beaks extracted from squid heads as well as loose beaks (Clarke, 1986, Volpedo and Echeverría, 1999; Xavier and Cherel, 2009; Cerna et al., 2014).

2.6. Sex Determination

Immediately following device attachment, 1–4 ml blood was collected from the wing vein of the study birds using a syringe (21 needle). Blood samples were preserved in 0,5–1 ml alcohol 95% or in EDTA tubes (MiniCollect ®, Greiner Bio One International) and stored frozen until the laboratory analysis. DNA was isolated using a salt protocol from Aljanabi and Martinez (1997), modified by Vianna et al. (2017). For sex identification, we used the primer pairs P8 and P2 (Griffiths et al., 1998) to amplify regions of the CHD1 gene found on the sex chromosomes. All PCR amplification profiles and conditions were followed Valenzuela-Guerra et al. (2013). PCR products were loaded on 3% agarose gel electrophoresis with SB buffer and visualized with the UV transilluminator for the identification of one (male) or two (female) bands.

3. Results

Overall, thirty-two birds could be successfully equipped with external devices that recorded 207 foraging trips directed to the Magellan Strait for a total duration of 2052 days. Exceptionally, bird 579-15B spent 264 days outside of the Magellan Strait in the open ocean and South Georgia waters during two foraging trips. Furthermore, the juvenile 440-16 was tracked for 70 days (Table 1). A total of 19 penguins were sexed by molecular markers, 10 were females and 9 males (Table 1).

3.1. Foraging trip duration

About 85% of all trips performed during the course of the year by both breeding and non-breeding birds lasted 10 days or less (Fig. 2). Mean trip duration over the entire study period did not differ significantly between breeding (n = 98) and non-breeding (n = 108) penguins (5.6 ± 4.2 vs. 6.0 ± 6.9; F = 0.609, p = 0.436). However, we found that breeding periods had a significant effect on the foraging trip duration in penguins (F = 46.26, p = < 0.01).

At the beginning of the breeding season (1 November to 31 January) foraging trip duration in incubating birds (n = 36) was significantly higher than in non-breeding (n = 44) birds (5.4 ± 3.0 vs. 1.4 ± 2.4 days; F = 31.73; p < 0.01), whereas during the brooding period (1 February to 30 April) mean trip duration did not differ significantly between breeding (n = 57) and non-breeding (n = 38) birds (5.3 ± 4.2 vs. 5.5 ± 2.9 days; F = 0.8; p = 0.373). During winter months (1 May to 31 October), foraging trip duration was generally longer and the longest trip recorded lasting 62 days was performed by a non-breeding bird and started on 7 June 2015. Foraging trip duration in breeding birds (10.1 ± 7.5; n = 5) was less variable but not significantly different from birds of unknown breeding status (15.9 ± 12.4; n = 26; F = 2.18; p = 0.15).

3.2. Foraging areas

With one exception (bird 579-15B, see below), all adult King Penguins foraged within the Magellan Strait, irrespectively of their sex or breeding status (Fig. 3). Three high-utilization areas could be identified: One just off the colony in Bahía Inútil, another one at the
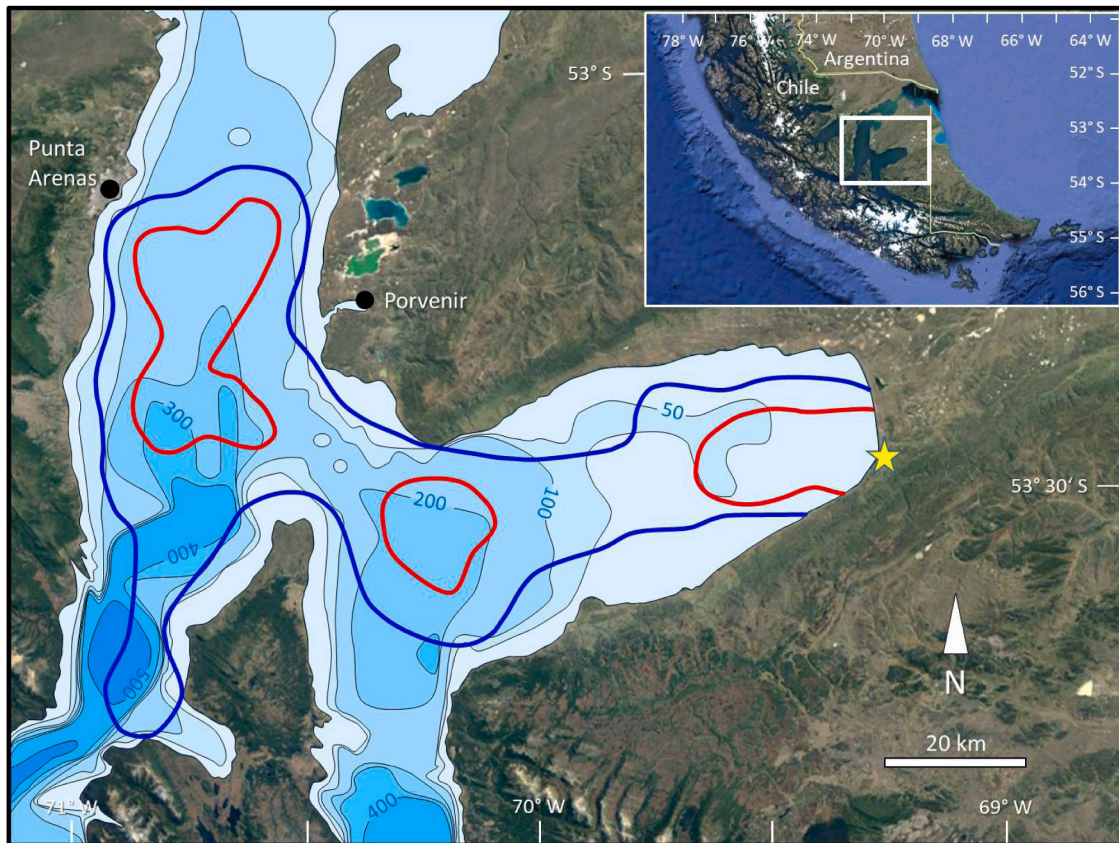
Fig. 3. Southern tip of South America (insert) with study area in the Magellan Strait. Kernels (blue = 90%, red = 50%) of adult King Penguins from the colony in Bahía Inútil, Magellan Strait, Chile (position indicated by yellow star). Water depth is indicated by shades of blue. Three high-utilization areas are visible, one just off the colony, one in the mouth of Bahía Inútil and one between Punta Arenas and Porvenir. For details see text. For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.

entrance of the bay and the third one in the Magellan Strait between Punta Arenas on the mainland and Porvenir on Tierra del Fuego. While the high-utilization area close to the colony contains also positions from traveling birds, three incubating birds spend several days exclusively in this area in 2014 (487-14, 492-14 and 493-14), indicating that this area was also used for foraging. Water depth in the latter two areas exceeds 200 m while the area in the vicinity of the colony had a maximum water depth of 54 m.

One bird, 579-15B, after performing four foraging trips within the Magellan Strait (as bird 579-15A), traveled more than 8000 km within two oceans in an eight months period. The bird left the Magellan Strait by the end of April in an easterly direction and turned south afterwards, traveling into the Drake Passage separating the South American and Antarctic continents (Fig. 4). By 12 May transmission ceased, but re-appeared on 8 August about 2000 km westwards in the Pacific Ocean. Subsequently, transmissions were again regularly received on a daily basis. The bird remained in the Pacific Ocean until 20 October, when he started traveling straight eastwards, past South America and heading straight to South Georgia, where it arrived on 24 November. In total, the horizontal distance covered within 35 days was 4000 km, and traveling speed was about 100 km per day in October and 125 km per day in November. After residing in King Haakon Bay on the southeastern coast for 12 days, the penguin started on 2 December a foraging trip of 23 days to about 650 km north of South Georgia, before returning to Fortuna Bay on the northeastern coast where transmissions ceased on 24 December 2016.

The other bird excluded from the general analysis was a fledged King Penguin juvenile entering the water for the first time on 21 December (Fig. 5). This bird remained in the Magellan Strait and the adjacent Chilean channels for the entire transmission period of 70 days, returning once to the colony on 30 January to stay for one week before leaving again. Transmissions ceased on 1 March while the bird was still exploring the Chilean fjords.
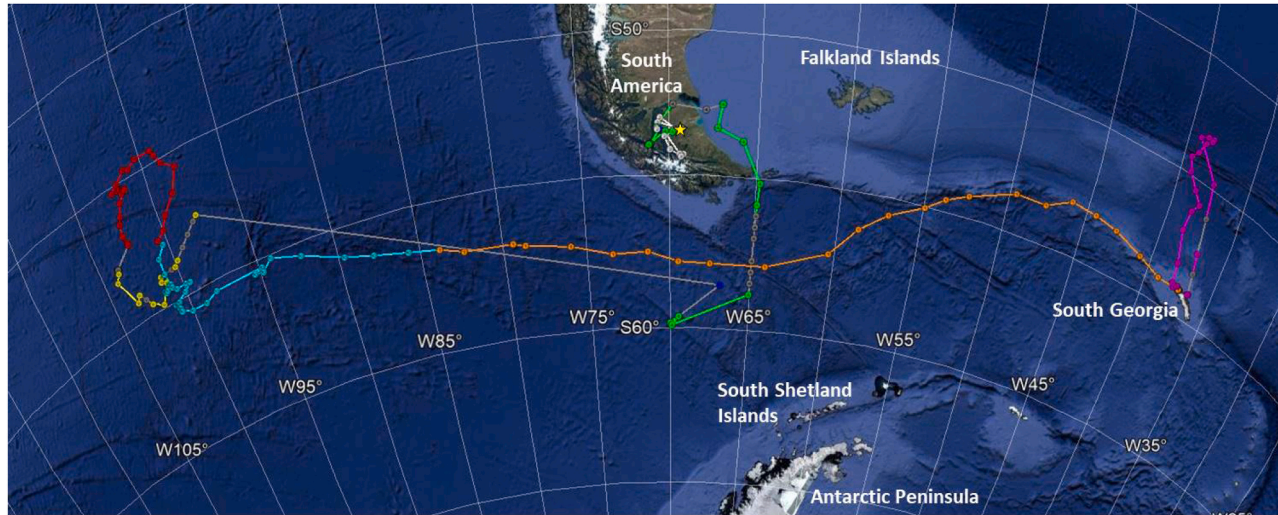
Fig. 4. Track of Penguin 579-15B. Symbol color indicates month (March = white, April = green, May = blue, August = yellow, September = red, October = cyan, November = orange, December = Purple). Interpolated daily positions are shown in gray. Location of breeding site is indicated by yellow star. For details see text. For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.
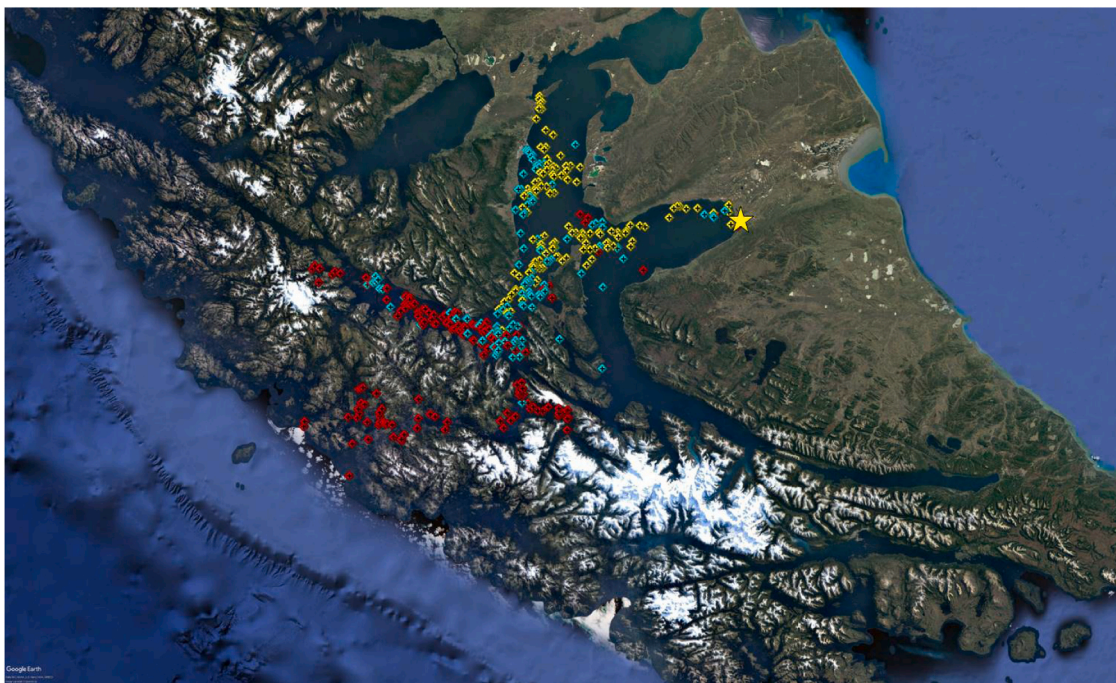
Fig. 5. Positions obtained from a King Penguin juvenile (440-16) from the colony at Bahía Inútil, Magellan Strait, Chile, between 21 December 2016 and 1 March 2017. Symbol colors indicate month (December = yellow, January = red and February = cyan). Location of breeding site is indicated by yellow star. For details see text. For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.

3.3. Diving behavior

The diving activities of 15 incubating King Penguins were recorded during 59 foraging trips with a total duration of 128 days (Table 2, Appendix 1). Overall, 35,772 dives >3 m were recorded, the deepest dive was 160 m and the longest dive lasted 6.75 mins. Based on a representative subsample of 3000 dives, mean dive depth was 32 ± 34 m and mean dive duration 117 ± 84 s. The frequency distribution of maximum dive depths showed a continuous decrease in the number of dives up to 70 m water depth, which included 84.3% of all dives (Fig. 6). Afterwards, number of dives varied only slightly up to 130 m before decreasing again towards the maximum depth of 160 m. Thus, most dives were performed in shallow waters and only about 15% of dives were deeper than 70 m.

The total time spent underwater and the bottom time duration were also higher in shallower waters than in deeper waters >70 m (Fig. 7). As in the frequency distribution of dive depths, both parameters increased again below 70 m water depths and exhibited a second small maximum at 110 m water depth. The relative proportions of time spent underwater and bottom time remained the same, irrespectively of maximum dive depth. Accordingly, the diving efficiency did not significantly differ over the various depth ranges and fluctuated around 0.4 throughout while it was on average 0.34 ± 0.20 over the entire depth ranges (Table 2, Fig. 7). In contrast, the foraging success increased with increasing maximum dive depth, indicating a higher proportion of wiggles during the bottom time, or, in other words, an increasing proportion of W-dives instead of U-dives. Over the entire depth range, mean foraging success was 1.03 ± 1.94 wiggles per minute bottom time.

3.4. Diet

Six out of seven (85.7%) stomach contents sampled from randomly chosen birds returning ashore contained fish (Table 3). The vast majority of fish were identified as Falkland sprats *Sprattus fuegensis*, which was present in all six samples. In addition, two Nototheniids *Patagonotothen* spec. could be identified in two samples, and two lantern fish *Myctophid* spec. in one sample. Squid was present in three out of seven samples (Table 3). However, one sample contained only heavily digested squid beaks (six Antarctic cranchiid squid *Galiteuthis glacialis* and four unidentified) and was thus not included in the list of fresh prey items In the two other samples with a fish-squid mixture, Patagonian squid *Doryteuthis gahi* was present, with additionally one specimen of *G. glacialis* in one sample.

One sample contained only highly digested squid beaks (6 *Galiteuthis glacialis* and 4 unidentified).

Table 2

Diving parameters of incubating King Penguins studied at Bahía Inútil, Chile. Subsample consists of 200 randomly selected dives from all 15 birds. Trip duration refers to total time at sea in birds studied over several foraging trips. For details on individual foraging trips, see Appendix 1.

| Bird	Sex	Trips	Total trip duration	Diving activity	Dives	Vertical distance	Dive depth (m)		Dive duration (s)		Diving efficiency	Foraging success
#		(n)	(days)	(%)	(n)	(km)	Max	Mean	Max	Mean ± SD	Mean ± SD	Mean ± SD
487-14	F	1	4.6	23	958	42.3	57	22.1 ± 16.3	261	94 ± 63	0.36 ± 0.21	1.97 ± 4.11
490-14	F	1	9.0	36	1884	171.2	133	45.4 ± 42.2	393	149 ± 99	0.37 ± 0.21	1.00 ± 1.56
491-14	F	1	11.2	33	3533	175.8	112	24.9 ± 24.4	264	90 ± 60	0.37 ± 0.19	0.95 ± 2.88
492-14	F	2	4.3	29	1929	52.1	52	13.5 ± 10.1	198	55 ± 41	0.28 ± 0.22	1.16 ± 2.91
493-14	F	1	2.1	27	477	22.4	54	23.4 ± 15.1	249	102 ± 62	0.32 ± 0.020	1.32 ± 2.26
696-14	F	1	7.7	33	1371	146.4	155	53.4 ± 49.3	357	162 ± 102	0.35 ± 0.18	0.98 ± 1.36
697-14	M	13	8.5	40	2683	123.3	113	22.9 ± 20.0	312	111 ± 70	0.32 ± 0.20	0.77 ± 2.36
698-14	M	2	1.3	42	588	18.2	54	18.4 ± 15.2	246	96 ± 67	0.35 ± 0.22	1.11 ± 1.87
950-14	M	11	8.1	37	3461	141.3	109	24.3 ± 21.0	285	90 ± 74	0.30 ± 0.23	1.21 ± 2.50
953-14	F	14	6.5	42	3636	123.8	64	17.0 ± 13.8	204	65 ± 51	0.26 ± 0.21	0.85 ± 2.23
956-14	F	2	7.0	37	1889	125.9	120	33.3 ± 29.1	300	119 ± 64	0.32 ± 0.19	1.00 ± 2.67
973-14	M	2	6.2	42	1214	129.6	160	53.4 ± 48.7	384	186 ± 61	0.36 ± 0.16	0.92 ± 1.85
487-16	?	3	27.6	39	6381	556.7	158	43.6 ± 42.6	363	147 ± 85	0.40 ± 0.17	1.01 ± 1.98
491-16	M	4	13.1	46	3666	250.4	147	34.1 ± 34.6	330	142 ± 75	0.41 ± 0.18	0.86 ± 1.85
493-16	F	1	10.8	37	2052	212.1	147	51.7 ± 46.9	405	169 ± 97	0.39 ± 0.17	1.15 ± 1.49
Sum		**59**	**128.1**		**35,722**	**2291.4**						
Subsample					**3000**		**152**	**31.7 ± 34.2**	**390**	**117 ± 84**	**0.34 ± 0.20**	**1.03 ± 1.94**
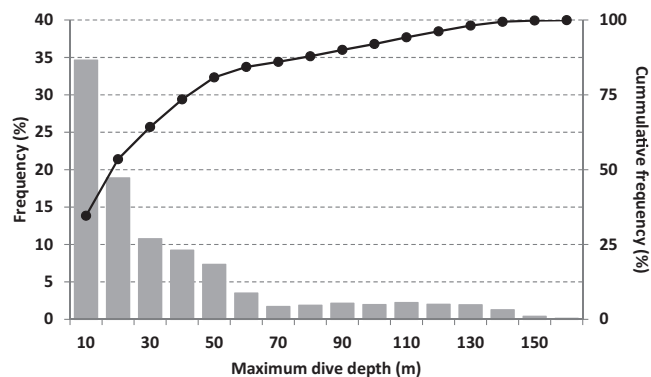
Fig. 6. Relative and cumulative frequencies of maximum dive depths of King Penguins from Bahía Inútil, Chile.
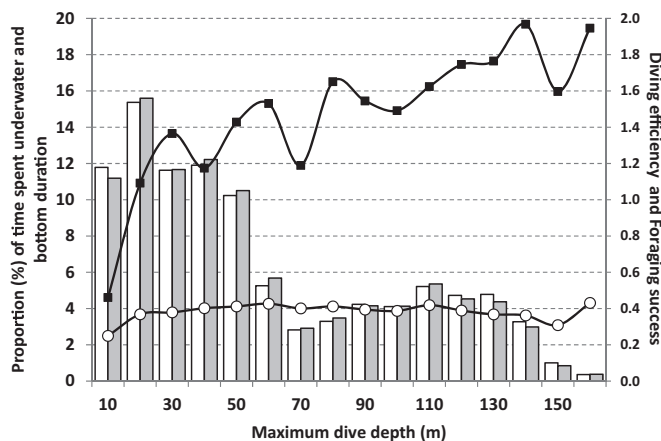

Fig. 7. Proportion of time spent underwater (white bars), bottom duration (gray bars), diving efficiency (open circle) and foraging effort (black squares) versus maximum dive depth in 10 m classes.

Table 3
Frequency of occurrence and abundance of fresh prey items identified in six King Penguin samples from Bahía Inútil, Chile. One sample not listed here contained only highly digested squid beaks (6 *Galiteuthis glacialis* and 4 unidentified).

	Frequency of occurrence		Abundance	
	(n)	**(%)**	**(n)**	**(%)**
Fish	**6**	**85.7**	**32**	**86.5**
Sprattus fuegensis	6	85.7	28	75.7
Patagonotothen (tessellata)	1	14.3	1	2.7
Patagonotothen (ramsayi)	1	14.3	1	2.7
Myctophid spec.	1	14.3	2	5.4
Squid	**2**	**28.6**	**5**	**13.5**
Doryteuthis (Loligo) gahi	2	28.6	4	10.8
Galiteuthis glacialis	1	14.3	1	2.7

4. Discussion

The recent extension of the distributional range of King Penguins into the Magellan Strait, Chile, was accompanied by a substantial change in their foraging habits, showing the species ability to display exceptional behavioral plasticity. Our results demonstrate that by adjusting to this unusual inshore environment, study birds, with one exception, foraged exclusively in inshore waters of the Magellan Strait and adjacent channels throughout the year. The animals did not dive deeper than 160 m and relied on a relative different set of

Table 4
Summary of foraging trip durations during incubation and in winter from various breeding sites.

Colony	Mean trip duration (d)	Status	Study
Bahía Inútil, Tierra del Fuego	5.4 ± 3.0	Incubation	Present study
Volunteer Beach, Falklands	14.6 ± 5.0	Incubation	(Otley et al., 2007)
Possession, Crozet Islands	15.4 ± 6.2	Incubation	(Bost et al., 1997)
	16.3 ± 5.0	Incubation	(Guinet et al., 1997)
	14.1 ± 2.0	Incubation	(Charrassin et al., 1998)
	18.0 ± 0.4	Incubation	(Gauthier-Clerc et al., 2001)
	12.8 ± 1.1	Incubation	(Charrassin et al., 2002)
Heard Island	14.8 ± 4.1	Incubation	(Wienecke and Robertson, 2006)
Macquarie Island	16.9 ± 2.2	Incubation	(Wienecke and Robertson, 2002)
	16.8 ± 3.6	Incubation	(Wienecke and Robertson, 2006)
Winter			
Bahía Inútil, Tierra del Fuego	10.1 ± 7.5	Breeders	Present study
	15.9 ± 12.4	Unknown breeding status	Present study
Volunteer Beach, Falklands	29.6 ± 25.7	Breeders (1996)	(Pütz, 2002)
	17.1 ± 14.7	Breeders (2011)	(Baylis et al., 2015)
Marion Island	120.1 ± 52.3	Breeders (2008)	(Pistorius et al., 2017)
	39.9 ± 21.2	Breeders (2013)	(Pistorius et al., 2017)
Possession, Crozet Islands	77.3 ± 41.2	Breeders (1994)	Pütz 2002
	16.1 ± 1.0	Successfull breeders (1998)	(Descamps et al., 2002)
	16.0 ± 1.4	Successfull breeders (1999)	(Descamps et al., 2002)
	13.6 ± 1.4	Successfull breeders (2000)	(Descamps et al., 2002)
	30.6 ± 3.2	Unsuccessfull breeders (1998)	(Descamps et al., 2002)
	20.8 ± 1.5	Unsuccessfull breeders (1999)	(Descamps et al., 2002)
	19.0 ± 1.6	Unsuccessfull breeders (2000)	(Descamps et al., 2002)
	28.4 ± 8.4	Non-breeding birds (1999)	(Descamps et al., 2002)
	32.9 ± 7.3	Non-breeding birds (2000)	(Descamps et al., 2002)
	91.5 ± 8.5	Breeders (1997 & 1998)	(Bost et al., 2004)
	60.4 ± 24.8	Unsuccessfull breeders	(Le Vaillant et al., 2016)
	36.2 ± 27.9	Previously once successful	(Le Vaillant et al., 2016)
	37.1 ± 24.8	Previously at least twice successful	(Le Vaillant et al., 2016)

main prey items in comparison to information available for other colonies. King Penguins are generally considered as oceanic foragers, feeding predominantly on myctophid fish and seasonally varying amounts of squid in water depths >150 m of the Antarctic Polar Frontal Zone (APFZ) in summer and even beyond in winter (Bost et al., 2013, Cherel et al., 2018). Thus, breeding sites are usually located within reach, less than 400 km away from the APFZ on sub-Antarctic islands between 45°S and 55°S. One exception from this general pattern has been a small colony in the Falkland Islands, which has produced the first fledgling by 1965 (Pistorius et al., 2012) and makes also use of the slope of the Patagonian Shelf (Pütz, 2002).

In the past, King Penguins have been sighted anecdotally in southern South America individually or in small numbers (Kusch and Marin, 2012). However, archeological evidence from Bahía Inútil clearly indicates the use of King Penguins body parts (e.g., bones, beaks) by indigenous people at least 500 years b.p. (Bahamondes, 2004), indicating a regular historical occurrence of this species at this location, albeit in unknown numbers. Furthermore, the scientific name of the King Penguin, *Aptenodytes patagonicus*, may also imply that this species was once numerous in southern South America. The first species description was made by the British illustrator John Frederick Miller in 1778, based on a sketch drawn by Sydney Parkinson, who accompanied James Cook on his first voyage (1768–1771), from a specimen collected by his colleagues Joseph Banks and the Swede Daniel Solander (Miller, 1778). As Cooks' first voyage took him around Cape Horn and into the Pacific, it is likely that this specimen was collected in Patagonia, especially as no further recently known King Penguin breeding site was visited during the entire voyage. It thus seems likely that King Penguins frequented the straits and channels in southern South America, but it remains inconclusive whether they ever occurred there in larger numbers or even had an established breeding colony.

In order to successfully colonize the Magellan Strait, King Penguins had to adapt to the confined environment. Their foraging areas are located not further away than 100 km from the breeding site and appear to provide predictable food sources and access throughout the year in shallower waters than usual. This results in much shorter trip durations and thus an increase in chick provisioning rates. At all other breeding sites, foraging trip duration during incubation is at least twice as long (Table 4), whereas our study birds, both breeding and surprisingly also non-breeding, stayed on average only 4.5 days at sea before returning ashore. Also, in winter, when King Penguins at other sites stay away for weeks or even months to forage at the APFZ or even beyond in Antarctic waters (Pütz, 2002; Bost et al., 2004; Cherel et al., 2018), foraging trip duration was much shorter not only in breeding (10.1 ± 7.5 days), but also in non-breeding (15.9 ± 12.4 days) birds. As a consequence, birds from Bahía Inútil spend much less energy to commute to their foraging

areas, return more frequently to the breeding site and consequently are able to provision their chick more regularly with food, which in turn should expedite growth rates and increase breeding success. While, for different reasons, it was not possible to take the body mass of the chicks in regular intervals, all chicks appeared well-fed (pers. obs.), supporting the assumption of high provisioning rates. Necropsies of dead chicks revealed other causes of death rather than starvation, mainly diseases or predators (C. Godoy, unpubl. data). For example, the mean weight of ten chicks taken by Gray Foxes between August and November 2017 was 6.7 kg (Godoy and Muñoz, unpubl. data), which is normal for chicks this time of the year (Stonehouse, 1960).

Also, energetic expenditure during diving appears to be lower than in conspecifics from other sites, because food is located at much shallower depths. For example, mean dive depth and duration of King Penguins from the Falkland Islands during the brooding period were 55 ± 16 m and 159 ± 25 s, respectively (Pütz and Cherel, 2005), much deeper and longer than in our study birds with 32 ± 34 m and 117 ± 84 s. While diving efficiency is comparable, foraging success is higher than elsewhere, especially in deeper dives, while relation of time spent underwater and bottom time remain the same, indicating more W-dives in deeper water strata.

Additionally, birds have adjusted to the change in environment by changing their staple diet from myctophids to sprats, which has since been verified by stomach sample analysis of birds found dead (C. Godoy, unpubl. data). Throughout their distributional range the staple diet of King Penguins consists of myctophids and squid with abundance and diversity varying spatially and temporarily (e.g. Bost et al., 2013). In the confound environment of the Magellanic Strait no larger amounts of myctophids are available (Sielfeld and Vargas, 1999; Bernal and Balbontín, 2003) and thus birds may have switched to the abundant Falkland sprat.

However, the relatively low chick survival and breeding success observed for this colony suggests that there are trade-offs associated to these foraging dynamics. Firstly, recently established seabird colonies tend to have higher proportions of young unexperienced breeders, which may affect the ability to raise chicks successfully and therefore reduce productivity (e.g. Coulson and White, 1956; Bried and Jouventin, 2002; Tims et al., 2004; Hénaux et al., 2007; Lisnizer et al., 2014). The main problems, however, appear to exist on shore. As mentioned above, this breeding site undergoes an intense terrestrial predation by introduced predators (Godoy et al., 2019), which is lacking elsewhere. Furthermore, necropsies performed on dead chicks revealed the presence of different infectious diseases, like bacterial and virus diseases not recorded elsewhere for this species (Godoy et al., 2019). These terrestrial challenges may, at least partly, outweigh the observed advantages of successful foraging in a confined environment. Therefore, continuous monitoring of this breeding site is needed, ideally including research into potential competition with commercial (targeting fish but not Falkland Sprats) and artisanal (targeting mainly sea urchins and Southern King Crabs *Lithodes santolla*) fishing activities occurring in the Magellan Strait. In addition, there is a direct threat to the birds as they may become entangled in gillnets used to catch Chilean silverside *Odontesthes regia*.

Whether this recent (re-)colonization of a breeding colony in Tierra del Fuego and the associated behavioral changes described are a result of shifting oceanographic and climatic conditions due to climate change or other factors remains unknown. However, it is a exceptional finding that a top marine predator, such as the King penguin, is able to adjust its usual foraging strategies to remarkably different environmental conditions and even establish a breeding site. This strongly suggests that King Penguins may have the potential of foraging without dependence on the Antarctic Polar Frontal Zone, as has already be shown in King Penguins breeding in the Falkland Islands (Pütz, 2002; Baylis et al., 2015), and thus may be able to face the predicted global changes better than previously anticipated.

However, it remains to be seen whether the colony is able to significantly expand. Food availability in the confined foraging environment may eventually become a limiting factor, especially when taking into account interspecific competition with, for example, the abundant Magellanic Penguins *Spheniscus magellanicus* for the same main prey items (Radl and Culik, 1999), and artisanal fishery. Moreover, there have been plans to develop new fisheries, including one targeting Falkland Sprats (Zuleta and Rubilar, 2010) and expand existing ones in the area, including Salmon *Salmo salar* farming (Estrategia Regional de Desarrollo de Magallanes y Antartica Chilena, 2012–2020). On the other hand, oil pollution is one of the major anthropogenic-induced cause of death among penguins worldwide (Trathan et al., 2015). The intense ship traffic that frequents the Magellan Strait increases the probability of shipwrecks and oil spills, and given the vulnerability of penguins when they get oiled and the exposure they are facing by breeding and foraging within in the channel, their risk is exacerbated. While the prevalence of terrestrial predators is currently being controlled by the land-owners and park rangers (PPR, pers. comm.), any change in the management of this touristic site could have detrimental effects on the breeding success and, in the long-term, colony existence.

The question remains about the origin of the birds colonizing the Bahía Inútil area. The nearest breeding site in the Falkland Islands, ca. 800 km to the east-northeast, was established in the 1960s and now produces up to 800 fledglings per year (Crofts and Stanworth, 2020), whereas the population on South Georgia is much larger and numbers over 400.000 breeding pairs (Foley et al., 2020). An indication about the origin of the King Penguins in Bahía Inútil could be derived from study bird 579-15B that ended up in South Georgia following its winter migration. The lack of transmissions from this bird in mid-winter is assumed to be due to the lack of sufficient daylight to charge the battery. However, it remains unclear whether this bird was already mature and returned to its natal site on South Georgia or just explored potential breeding sites as immature. Genetical evidence suggests that migration between breeding sites is common in King Penguins and that there is little genetic differentiation among all breeding sites even though the South Georgia population is slightly different from all other colonies (Clucas et al., 2016). The lack of a population structure for King penguin at local (Cristofari et al., 2015) and global scales (Clucas et al., 2016; Cristofari et al., 2018) strongly limit the identification of origin of recently established colonies, different from other species of penguins with a marked population structure like Rockhopper

Penguins *Eudyptes chrysocome* (Lois et al., 2020; Frugone et al., 2018) and Gentoo penguins (Vianna et al., 2017). Thus, it was suggested that the recently founded colony in the Falkland Islands was probably established by migrants from Crozet Islands rather than from South Georgia (Clucas et al., 2016). In contrast to this suggestion, a fledgling banded at South Georgia in 1991 was recorded breeding in the Falklands for several years (Olsson 1997; Otley et al., 2007; Pistorius et al., 2012), indicating that migration occurs, albeit probably on a lower level. However, at present the origin of the King Penguins at Bahía Inútil remains highly speculative. In this context, the site fidelity exhibited by the single fledgling tracked from Bahía Inútil, which never left inshore waters and returned to its natal site at least once during the study period, is an interesting but inconclusive phenomenon. It may be assumed, however, that birds fledged in the Magellan Strait are likely congregating with other King Penguins in the area and adopt the foraging strategies exhibited by these birds and return breeding to their natal site upon reaching maturity. However, these assumptions are mainly based on anecdotal evidence and more thorough research is needed to determine the origin of the birds colonizing the Magellan Strait, to identify potential new breeding attempts and to study the evolution of these new breeding establishments.

Under the context of changing environmental scenarios, our study contributes to improve the understanding of how species can change their behavior in a way to allow them to prospect and thrive in new areas and ultimately redefine their breeding distribution range.

5. Conclusion

King Penguins have successfully established a breeding site on the shore of Bahía Inútil in the Magellan Strait, Chile. The confined environment with obviously predictable and sufficient food availability, in concert with a switch in their main prey items, allowed them to reduce foraging efforts compared to conspecifics breeding elsewhere. This resulted in much shorter foraging trip durations and presumably enabled birds to provision their chick more frequently throughout the year. However, these advantages in the marine environment appear to be at least partly compensated by terrestrial predation and diseases, which reduced breeding success over the past years. Whether King Penguins can survive or even flourish at this site in the longer term remains to be seen and is largely dependent on the adequate protection from terrestrial threats as well as a sufficient food supply in the Magellan Strait, which may limit colony growth.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Appendix. Foraging parameters for individual trips of King penguins from Bahía Inútil

Bird	Sex	Trips	Duration	Time submerged	Dives	Vertical distance	Dive depth (m)		Dive duration (s)		Diving efficiency	Foraging success
#		(n)	(days)	(%)	(n)	(km)	Max	Mean	Max	Mean ± SD	Mean ± SD	Mean ± SD
487-14	F	1	4.63	23	958	42.3	57	22.1 ± 16.3	261	94 ± 63	0.36 ± 0.21	1.97 ± 4.11
490-14	F	1	8.98	36	1884	171.2	133	45.4 ± 42.2	393	149 ± 99	0.37 ± 0.21	1.00 ± 1.56
491-14	F	1	11.24	33	3533	175.8	112	24.9 ± 24.4	264	90 ± 60	0.37 ± 0.19	0.95 ± 2.88
492-14	F	1	2.07	20	607	16.0	52	13.2 ± 9.2	177	58 ± 43	0.29 ± 0.23	1.44 ± 3.60
492-14	F	2	2.18	37	1322	36.1	50	13.7 ± 10.5	198	53 ± 40	0.28 ± 0.21	1.03 ± 2.53
493-14	F	1	2.14	27	477	22.4	54	23.4 ± 15.1	249	102 ± 62	0.32 ± 0.020	1.32 ± 2.26
696-14	F	1	7.68	33	1371	146.4	155	53.4 ± 49.3	357	162 ± 102	0.35 ± 0.18	0.98 ± 1.36
697-14	M	1	0.40	18	111	1.9	23	8.7 ± 6.6	171	55 ± 44	0.27 ± 0.24	0.88 ± 2.25
697-14	M	2	2.01	62	624	46.6	113	37.4 ± 28.5	312	171 ± 72	0.40 ± 0.17	0.78 ± 1.42
697-14	M	3	1.01	17	202	3.2	23	7.9 ± 5.0	237	75 ± 63	0.22 ± 0.19	0.28 ± 0.88
697-14	M	4	0.53	12	123	2.6	38	10.4 ± 9.2	159	44 ± 39	0.11 ± 0.15	0.37 ± 1.01
697-14	M	5	0.15	67	80	2.9	36	18.2 ± 8.8	159	113 ± 32	0.41 ± 0.17	0.38 ± 0.79
697-14	M	6	0.72	56	273	14.8	59	27.1 ± 15.4	243	127 ± 60	0.38 ± 0.19	1.16 ± 4.98
697-14	M	7	0.37	13	60	1.2	25	10.1 ± 6.3	132	69 ± 34	0.20 ± 0.17	0.21 ± 0.68
697-14	M	8	0.42	32	103	4.2	51	20.3 ± 12.6	210	114 ± 50	0.31 ± 0.19	0.79 ± 1.25
697-14	M	9	0.30	45	125	4.6	44	18.3 ± 10.9	174	94 ± 49	0.33 ± 0.19	0.54 ± 0.77
697-14	M	10	0.71	38	225	11.0	53	24.4 ± 16.0	231	103 ± 60	0.30 ± 0.19	0.94 ± 1.35
697-14	M	11	1.00	37	415	13.7	52	16.5 ± 11.9	234	77 ± 52	0.29 ± 0.19	0.69 ± 2.05
697-14	M	12	0.46	34	151	6.8	57	22.6 ± 14.8	210	91 ± 56	0.30 ± 0.21	1.57 ± 4.67
697-14	M	13	0.44	61	191	9.8	53	25.6 ± 13.9	225	120 ± 56	0.38 ± 0.19	0.72 ± 0.90
698-14	M	1	0.40	57	218	7.4	53	17.0 ± 15.9	237	91 ± 69	0.37 ± 0.22	0.56 ± 1.13
698-14	M	2	0.90	36	277	10.8	54	19.5 ± 14.6	246	100 ± 66	0.34 ± 0.22	1.55 ± 2.19
950-14	M	1	1.02	23	440	7.9	42	8.9 ± 7.6	246	47 ± 55	0.18 ± 0.20	1.13 ± 3.62
950-14	M	2	1.17	48	364	21.9	109	30.1 ± 24.9	279	134 ± 81	0.36 ± 0.23	0.82 ± 1.43
950-14	M	3	0.29	56	101	5.8	50	28.8 ± 15.1	234	139 ± 56	0.50 ± 0.18	1.03 ± 0.99
950-14	M	4	0.48	69	197	13.1	56	33.2 ± 17.2	228	146 ± 61	0.48 ± 0.19	1.12 ± 0.87
950-14	M	5	0.69	30	358	10.3	62	14.4 ± 16.1	273	49 ± 62	0.18 ± 0.20	1.08 ± 2.72
950-14	M	6	0.71	40	311	15.1	53	24.3 ± 19.9	258	80 ± 73	0.27 ± 0.22	1.14 ± 1.78
950-14	M	7	0.63	37	239	14.5	60	30.4 ± 20.1	204	84 ± 56	0.29 ± 0.21	1.63 ± 2.85
950-14	M	8	0.62	19	144	7.7	55	26.8 ± 18.3	165	72 ± 48	0.24 ± 0.19	1.94 ± 3.19
950-14	M	9	0.53	20	178	6.3	54	17.7 ± 16.4	168	52 ± 50	0.19 ± 0.20	1.37 ± 3.63
950-14	M	10	1.59	33	416	26.8	87	32.2 ± 24.7	285	109 ± 80	0.36 ± 0.22	1.24 ± 1.94
950-14	M	11	0.39	62	154	11.8	54	38.4 ± 16.6	219	134 ± 50	0.46 ± 0.17	1.49 ± 1.27
953-14	F	1	0.14	54	109	2.4	24	10.9 ± 7.2	156	61 ± 47	0.27 ± 0.22	0.79 ± 1.31
953-14	F	2	0.94	46	604	18.3	53	15.2 ± 14.1	201	62 ± 53	0.23 ± 0.20	0.46 ± 1.46
953-14	F	3	0.19	15	98	1.4	20	7.0 ± 4.5	96	25 ± 21	0.16 ± 0.19	0.72 ± 2.99
953-14	F	4	0.18	54	174	4.8	27	13.8 ± 8.0	132	49 ± 36	0.20 ± 0.17	1.10 ± 2.20
953-14	F	5	0.51	64	325	14.2	54	21.9 ± 14.5	198	87 ± 58	0.31 ± 0.20	0.78 ± 1.36
953-14	F	6	0.54	60	331	16.0	64	24.2 ± 16.2	183	85 ± 52	0.30 ± 0.21	1.18 ± 3.11
953-14	F	7	0.45	20	216	4.4	41	10.1 ± 9.2	132	35 ± 33	0.14 ± 0.17	0.92 ± 2.34
953-14	F	8	0.20	25	115	1.7	25	7.5 ± 5.5	129	37 ± 29	0.21 ± 0.20	0.64 ± 1.63
953-14	F	9	0.58	60	317	16.5	63	25.9 ± 16.8	204	94 ± 56	0.37 ± 0.19	1.02 ± 3.51
953-14	F	10	0.64	35	425	11.4	54	13.4 ± 10.7	174	45 ± 41	0.19 ± 0.19	0.97 ± 2.42
953-14	F	11	0.32	41	183	6.2	44	17.0 ± 10.5	165	63 ± 43	0.29 ± 0.20	0.92 ± 2.19
953-14	F	12	0.59	44	327	11.3	48	17.2 ± 12.5	186	69 ± 49	0.29 ± 0.20	0.84 ± 2.00
953-14	F	13	0.33	41	192	6.2	45	16.2 ± 11.4	147	61 ± 44	0.26 ± 0.20	1.01 ± 1.67
953-14	F	14	0.89	24	220	9.0	50	20.4 ± 15.2	186	84 ± 48	0.33 ± 0.20	0.84 ± 1.29
956-14	F	1	2.42	48	747	45.2	109	30.3 ± 25.9	300	135 ± 63	0.36 ± 0.19	0.77 ± 2.92

(*continued*)

Bird	Sex	Trips	Duration	Time submerged	Dives	Vertical distance	Dive depth (m)		Dive duration (s)		Diving efficiency	Foraging success
#		(n)	(days)	(%)	(n)	(km)	Max	Mean	Max	Mean ± SD	Mean ± SD	Mean ± SD
956-14	F	2	4.62	31	1141	80.7	120	35.4 ± 30.9	246	109 ± 64	0.30 ± 0.18	1.15 ± 2.48
973-14	M	1	4.05	50	851	102.8	160	60.4 ± 51.8	384	204 ± 89	0.38 ± 0.15	0.83 ± 1.60
973-14	M	2	2.18	28	363	26.8	136	36.9 ± 35.3	348	143 ± 83	0.31 ± 0.17	1.12 ± 2.31
487-16	?	1	13.16	31	2197	226.7	158	51.6 ± 43.1	363	163 ± 84	0.39 ± 0.17	1.12 ± 2.18
487-16	?	2	9.52	47	2783	209.7	158	37.7 ± 42.3	360	138 ± 87	0.42 ± 0.16	0.97 ± 2.00
487-16	?	3	4.90	47	1401	120.3	132	42.9 ± 40.4	327	142 ± 81	0.39 ± 0.17	0.94 ± 1.57
491-16	M	1	8.16	45	2078	171.5	147	41.3 ± 40.4	330	154 ± 82	0.40 ± 0.18	0.81 ± 1.19
491-16	M	2	1.05	63	429	24.4	65	28.4 ± 18.8	240	134 ± 67	0.38 ± 0.20	1.24 ± 2.77
491-16	M	3	0.95	52	375	20.0	65	26.6 ± 20.7	213	114 ± 50	0.40 ± 0.18	0.99 ± 2.29
491-16	M	4	2.92	39	784	34.5	101	22.0 ± 23.5	273	126 ± 63	0.44 ± 0.17	0.71 ± 2.33
493-16	F	1	10.78	37	2052	212.1	147	51.7 ± 46.9	405	169 ± 97	0.39 ± 0.17	1.15 ± 1.49
Subsample		**59**			**3000**		**152**	**31.7 ± 34.2**	**390**	**117 ± 84**	**0.34 ± 0.20**	**1.03 ± 1.94**

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