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RESEARCH ARTICLE

Contrasting bottom-up effects of warming ocean on two king penguin populations

 Émile Brisson-Curadeau^{1,2}  | Kyle Elliott¹ | Charles-André Bost²

¹Natural Resource Sciences, McGill University, Quebec, Sainte-Anne-de-Bellevue, Canada

²UMR 7372-CNRS, Centre d'Études Biologiques de Chizé, La Rochelle University, Villiers-en-Bois, France

Correspondence

Émile Brisson-Curadeau, Natural Resource Sciences, McGill University, 21111 Lakeshore Road, Sainte-Anne-de-Bellevue, QC H9X 3V9, Canada.
Email: emile.brissoncuradeau@mail.mcgill.ca

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Abstract

Breeding success is often correlated with climate, but the underlying bottom-up mechanisms remain elusive—particularly in marine environments. Consequently, conservation plans of many species often consider climate change as a unilateral threat, ignoring that even nearby populations can show contradicting trends with climate. Better understanding the relationship between climate and environment at different scales can help us interpret local differences in population trends, ultimately providing better tools to evaluate the global response of a species to threats such as global warming. We studied a growing king penguin population nesting at Kerguelen island (Southern Indian Ocean), hosting one of the largest colonies in the world. We used a unique dataset of foraging, breeding success, and climate data spanning over 25 years to examine the links between climate, marine environment, and breeding success at this colony. The results were then compared to the neighboring population of Crozet, which experienced the steepest decline for this species over the past few decades. At Crozet, penguins experienced lower breeding success in warmer years due to productive currents shifting away from the colony, affecting foraging behavior during chick rearing. At Kerguelen, while chick mass and survival experienced extreme variation from year to year, the annual variation was not associated with the position of the currents, which varied very little compared to the situation in Crozet. Rather than being affected by prey distribution shifts, we found evidence that chick provisioning in Kerguelen might be influenced by prey abundance, which seem to rather increase in warmer conditions. Furthermore, warmer air temperature in winter increased chick survival rate, likely due to reduced thermoregulation cost. Investigating the mechanisms between climate and fitness allowed us to predict two different fates for these populations regarding ongoing global warming.

KEYWORDS

breeding success, climate change, king penguin, marine ecosystem, ocean temperature, Southern Ocean

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1 | INTRODUCTION

Events of abnormally high ocean temperature have been reported in all oceans to affect the dynamic of currents, creating a cascading effect on the trophic chain (Frölicher & Laufkötter, 2018; Piatt et al., 2020). Increased occurrence of these warm events might be particularly devastating in the Southern Ocean, as it hosts around a quarter of the total fish biomass of the world (Dornan et al., 2022; Irigoien et al., 2014). This abundance of prey is mostly supported by unique circumpolar currents creating complex water mass interactions and distinctive surface and sub-surface dynamics, all of which are sensitive to ocean warming (Bost et al., 2009; Chapman et al., 2020). Yet, predicting the effect of climate change on this ecosystem is a difficult task, as complex currents result in complex interactions with wildlife.

The Polar Front is one of these important currents widely used by prey and top predators all around the Southern Ocean (Bost et al., 2009; Rayner et al., 2017; Scheffer et al., 2016; van Franeker et al., 2002). It is formed by the divergence of the cold <2°C Antarctic water (also called Winter Water) with the warmer Sub-Antarctic water, creating strong upwelling bringing prey such as myctophid (lantern fish) closer to the surface (Catul et al., 2011; Cotté et al., 2007; Marshall & Speer, 2012). However, the Polar Front is expected to contract towards the Antarctic continent with ocean warming (Fogt & Marshall, 2020; Péron et al., 2012). These spatial shifts may create a prey–predator mismatch for those central-place foragers, such as birds and pinnipeds breeding on islands, leading to population decline. At Crozet for example, located in the Southern Indian Ocean, three of the four species of breeding penguins, as well as some species of albatross, have experienced decline (Barbraud et al., 2020). While the causes of these declines are not always known, the Polar Front shifting southward and further away from the island has raised concern about the future of some species (Bost et al., 2015; Péron et al., 2012). For this reason, climatic models predicts that some of these front-associated species may soon face serious population threats in that region (Charrassin & Bost, 2001; Le Bohec et al., 2008; Péron et al., 2012). The main concern is that the Polar Front might migrate a critical distance away from the island—where food provisioning is no longer sustainable—leading to a strong decrease in chick feeding frequency and eventually high chick mortality (Péron et al., 2012).

Yet, even population trends of neighboring islands can be quite contrasting, showing that observed effects of climate change at a given site cannot be extrapolated without taking into account the location-dependant specifics. For example, most of the penguin species and albatrosses declining at Crozet have been stable or increasing at Kerguelen Island—its ocean neighbor located 1400km to the east (Barbraud et al., 2020). Some of these species also feed on the Polar Front there, but too few studies have linked global warming with the marine environment at Kerguelen to predict future population trends, or even explain why past trends differed from Crozet's. The Polar Front near Kerguelen is

also more constrained by strong bathymetric features, with less movement associated with warming temperature compared to Crozet (Pauthenet et al., 2018). Yet, no studies have looked at how this particularity might influence the life history of marine predators. In this context, comparative long-term studies are valuable to not only understand how two neighboring populations might show diverging responses to global warming, but also how these responses can be extrapolated to other populations.

As a circumpolar breeder, the king penguin *Aptenodytes patagonicus* is an ideal model species to study location-dependant effects of climate. It is a central-place forager feeding almost exclusively on myctophids and foraging mainly on the Southern edge of the Polar Front, where a wide zone of the Winter Water upwelling occurs (Bost et al., 2009; Charrassin & Bost, 2001). Furthermore, adult king penguins provision their chicks throughout the austral summer but leave them fasting at the colony throughout winter for up to 4 months, a unique behavior among birds. During this fasting period, chick mortality is at its highest, as they must survive on the fat reserve they have built throughout the summer (Cherel & Le Maho, 1985). Temperature changes in winter might therefore potentially impact their survival rate, providing an opportunity to also investigate direct climatic effects on this population. At Crozet, ambient temperatures outside of the −1 to 9°C range have been shown to affect chick metabolism, but no studies have looked at long-term climatic trends on the survival of chicks (Barré, 1976).

We used 25 years of unpublished data to understand the effects of climate on the foraging and breeding success of a seldom studied population of king penguins at Kerguelen Island. We used accelerometers to assess at-sea foraging success in relation to the Polar Front, while chick mass after the chick-provisioning period—or before the winter fast—will serve as a metric to assess the overall summer foraging success of adults. As pairs raise only one chick, and as most of the energy intake by the chick is invested in building fat reserves for the winter (rather than structural development; de Margerie et al., 2004), the pre-winter mass is likely a good indicator of the foraging success of adults in this species. We also test if summer air temperature at the colony affected the final pre-winter chick mass by increasing thermoregulation costs. Finally, we investigated the effect of winter air temperature on chick survival during the fasting period. We then compare our results with a decreasing king penguin population at Crozet, where bottom-up climatic-effects on their life history are well known.

2 | METHODS

All data was collected at Ratmanoff's colony in the Kerguelen archipelago (−49° 14' 33", 70° 33' 40"), which hosts approximately 80,000–90,000 breeding pairs of king penguins (Barbraud et al., 2020). During the chick rearing period, king penguins forage southeast of the island, between −49° S and −53° S and 70° E and 78° E, hereafter "foraging zone" (Bost et al., 2002; Scheffer et al., 2016).

2.1 | Chick mass and survival

Chick mass and survival was assessed yearly from 2002 to 2021, apart from 2007, 2009 and 2010 (i.e. 17 studied years). Randomly selected chicks were weighed and marked with fish tags (FloyTags) in April before the winter fast, except for 2008, where weighing occurred in May due to fieldwork constraints. The number of chicks marked annually varied from 28 to 55, with most years (11) having $n = 40$ chicks. The colony was again visited in October–December to relocate the marked chicks and assess winter mortality.

2.2 | Foraging behavior

A total of 148 foraging penguins were equipped during the brooding period (February–March) between 1998 and 2022 with GPS or ARGOS tags from various brands, except for 2010 and 2012 which contained no equipped penguins (23 years). For ARGOS tags, locations with a precision class of O, A or B (i.e. with >1500m precision) were removed. When the animal speed between two consecutive GPS or Argos locations was >10 km/h, we removed the second point, which was also likely imprecise.

From these GPS/ARGOS-equipped penguins, 60 penguins were also equipped with depth-loggers from either Wildlife Computer or Technosmart. The maximum distance of the foraging trip from the colony was computed for all individuals, while kernel densities of foraging dives (see Section 2.4.1) were processed for individuals equipped with both GPS and Depth-loggers. A foraging dive was defined as a dive with maximum depth >50m (Charrassin et al., 2002; Pütz et al., 1998).

During 2019–2022, 16 of the GPS-Depth-logger equipped individuals were also equipped with accelerometers (Technosmart). Acceleration data in each dive was then converted into prey capture attempts—a measure of foraging success—throughout the foraging trips using a machine-learning algorithm tested on wild penguins equipped with beak-opening sensors (Brisson-Curadeau et al., 2021).

We retrieved all biologging equipment after the individuals had returned from their foraging trip at sea, which typically lasted 4–12 days.

2.3 | Environmental data

Monthly air temperature data at the colony during the winter chick-fast (April–August) and summer brooding period (February–March) was extracted from the NOAA National Centers for Environmental Information (2021). The wind chill effect was then added using wind data retrieved from NOAA Physical Sciences Laboratory (Kalnay et al., 1996).

Daily sea-surface height (SSH) and multi-depth ocean temperatures during the brooding period were obtained through the E.U. Copernicus Marine Environment Monitoring Service (CMEMS) at a 0.083° resolution (<https://doi.org/10.48670/moi-00016>, <https://doi.org/10.48670/moi-00021>).

Temperatures were retrieved from the 0–266m depth range (28 depth points total) and from 2007 onward, as significantly different methodologies were used pre-2007 by CMEMS to extrapolate temperature data, making across-year comparisons impossible. From this dataset, the Polar Front position was calculated as the northernmost extent of surface/subsurface water temperatures <2°C (Park et al., 2014). We also calculated the depth of the Winter Water layer throughout the foraging zone and the thermocline depth, the latter being defined as the depth where temperature changes are maximal (Fiedler, 2010).

2.4 | Statistical analysis

2.4.1 | Foraging habitat selection at Kerguelen

To understand which zones near the colony are the most prolific for penguins, we made several linear mixed models predicting the average number of prey capture attempts in a dive (using the 2019–2022 accelerometry data). Explanatory variables were: thermocline depth, SSH, upper depth limit of the Winter Water, and sea surface temperature (SST) at the dive location (Péron et al., 2012; Scheffer et al., 2016). Distance of the dive from the colony was also added as a variable to detect any effect of prey depletion (“Ashmole's halo”, Birt et al., 1987). The individual was used as a random factor.

We also plotted the kernel density of foraging dives and polar front positions near Kerguelen for the whole period and compared it with the foraging maps at Crozet. The kernels for both locations were calculated using a 90% quartic kernel function (Silverman, 2018). The kernel foraging range near Crozet was made possible using metadata from the Bost et al. (2015) study, with permission from coauthors, while the kernel density near Kerguelen was calculated using the data described in Section 2.2. Only foraging data post-2007 were used to create both kernel maps (i.e. 2007–2010 for Crozet, 2007–2022 for Kerguelen), as this was the earliest year with accurate Polar Front data (see Section 2.3). While the yearly range and total sample size at Crozet ($n = 8$ individuals equipped with both GPS and depth loggers) was smaller than at Kerguelen ($n = 60$ individuals), it still provided an interesting visual contrast in the foraging range at the two locations, with regards to the Polar Front.

Finally, to assess whether there was a temporal trend at Kerguelen in the mean foraging distance, we built a linear model with the variable “year” as the explanatory variable and compared it to a null model.

2.4.2 | Effects on chick growth

We made several linear regressions predicting annual chick mass before winter to assess which climatic variables influence inter-annual chick growth variations at Kerguelen ($n = 12$ years). These variables were: mean air temperature at the colony (accounting

wind chill), average SST in the foraging zone, and distance of the Polar Front from the colony. All these variables were computed for the February–March period, which is when chick-provisioning and hence chick-growth occurs. SST in the foraging zone with a time lag was also added as a variable to assess whether climatic events preceding the breeding period could influence prey abundance during chick-rearing and consequently affect chick-provisioning itself. Our preliminary results showed that SST with a lag of 1 year (i.e. in April the year before) showed greatest correlation with chick mass, and so $SST_{-1\text{ year}}$ was introduced in the model selection.

2.4.3 | Effects on chick survival

A beta-regression model selection was conducted to assess which factors influenced annual chick survival rate in the winter ($n = 17$ years). The three explanatory variables of interest to build these models were mean wind chill at the colony in winter (April–August), average chick mass before winter (April), and year (to detect temporal trends). We chose beta-regression to account for the response variable (annual chick survival rate) being a ratio, and not a continuous value.

The Akaike information criterion corrected for small sample size (AICc) was used to rank models in all model selections. Only models with $<2\Delta$ AICc were considered (Hu, 2007). All analyses were conducted in R (R Core Team, 2021).

3 | RESULTS

3.1 | General climatic trends at Kerguelen

Wind chill in winter was consistently higher in the last decade (2012–2021) compared to the first decade of the study (2002–2011), and a positive linear trend was significant throughout the study period (slope = $0.04 \pm 0.01^\circ\text{C}/\text{year}$, p value = .005, $R^2 = .38$). No such trend was detected in the summer, during the brooding period, where air temperature did not show any significant trend (slope = $0.04 \pm 0.03^\circ\text{C}/\text{year}$, p value = .13).

Similarly, the SST of the foraging zone during chick provisioning did not show any significant linear trends throughout the dataset (slope = $0.03 \pm 0.02^\circ\text{C}/\text{year}$, p value = .27). However, the last 5 years of the study (2017–2021) did show higher SST on average compared to the other years and included the three warmest years of the whole dataset (Figure 1). The position of the Polar Front varied little from year to year (range: 63–107 km from colony, $n = 16$ years, see Table 1 and Figure 2).

3.2 | Effects of climate on foraging and breeding success

3.2.1 | Foraging habitat selection at Kerguelen

From 1998 to 2022, penguins foraged on average 266 ± 98 km from the colony ($n = 148$ penguins). From year to year, the average foraging

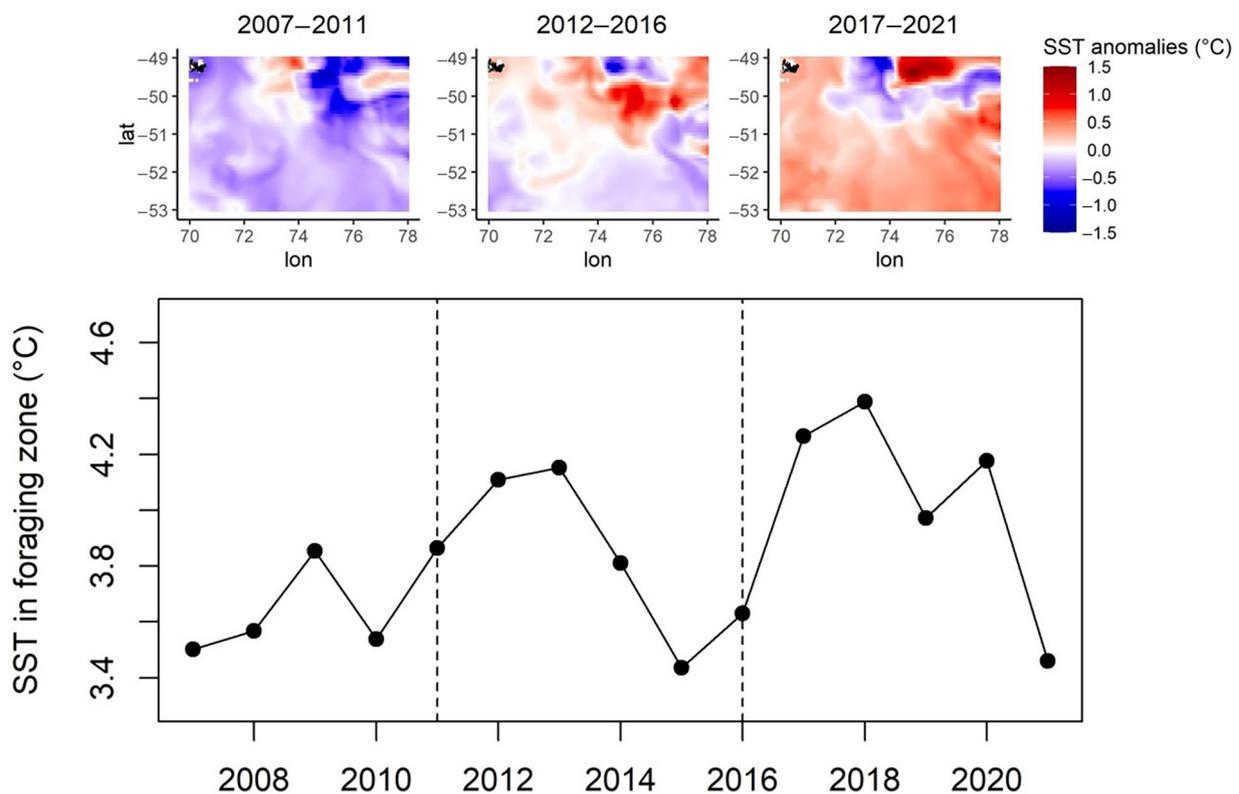


FIGURE 1 Sea surface temperature anomalies in the full extent of the foraging zone, with Kerguelen Island in the top left corner. Anomalies were calculated based on the 2007–2021 time series. Despite no significant trends, the last five years (2017–2021) were warmer on average compared to previous years of the study.

Variables compared	Kerguelen archipelago (this study)	Crozet archipelago (Bost et al., 2015)
Inter-annual range in Polar Front distance from colony	63–107 km ($n = 16$ years between 2007 and 2022)	217–642 km ($n = 16$ years between 1992 and 2010)
Inter-annual range in foraging distance	117–387 km ($n = 23$ years between 1998 and 2022)	290–580 km ($n = 16$ years between 1992 and 2010)
Inter-annual range in Southernmost latitude reached by foraging penguins	–49.9° to –51.3° ($n = 23$ years between 1998 and 2022)	–48.8° to –51.9° ($n = 16$ years between 1992 and 2010)

TABLE 1 Comparison of Polar Front position and king penguin foraging distance between the Kerguelen archipelago (this study) and Crozet archipelago (Bost et al., 2015)

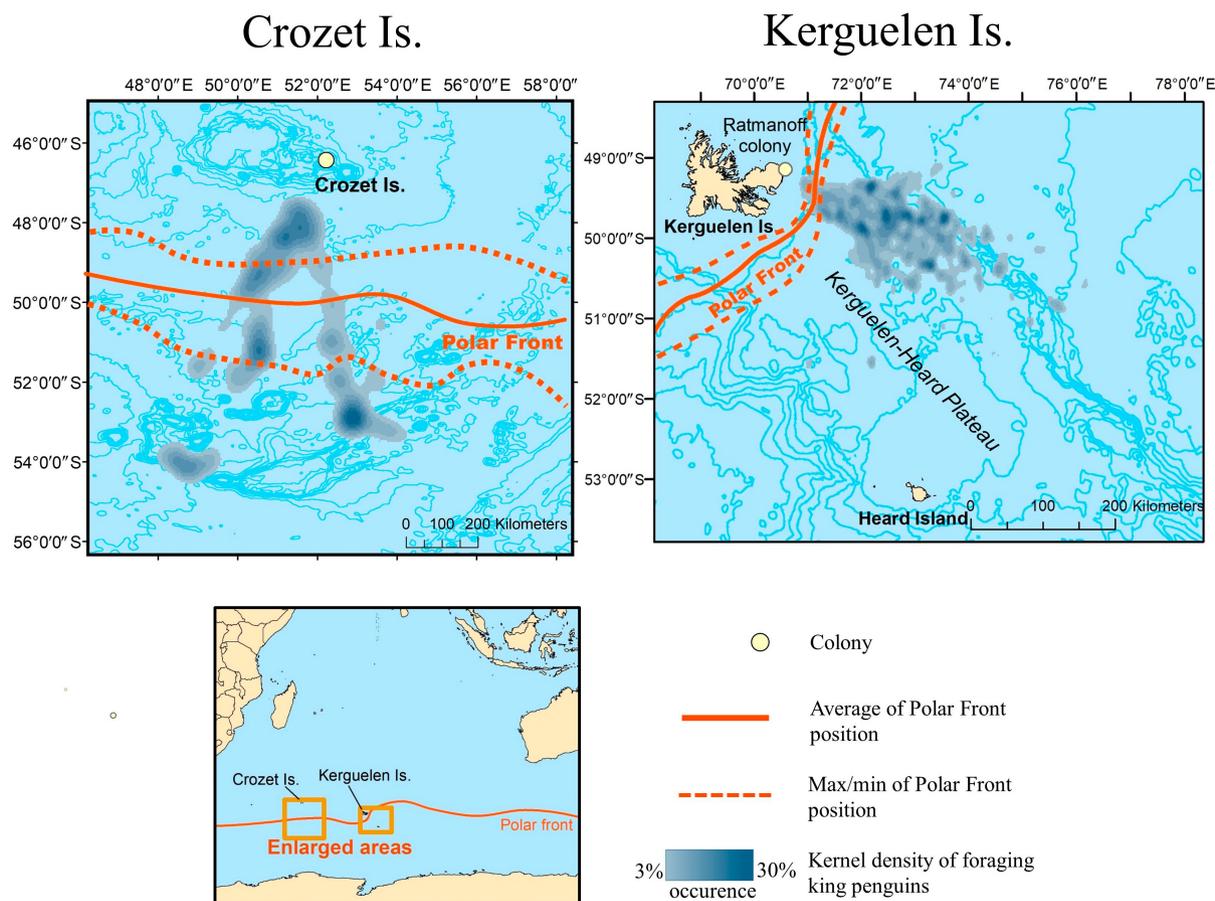


FIGURE 2 Between-location comparison of the polar front position and kernel density of king penguin foraging dives, for the 2007–2022 period. The base map is a 500m contour bathymetry. Notice how the Polar Front systematically passes close to Kerguelen—at the bathymetric frontier between the island and the Kerguelen-Heard Plateau—while it is much freer to move in the deep oceanic waters far off Crozet. This impacts the foraging distance of penguins, which is typically much further at Crozet (notice the different scale of the two maps). Polar Front position for both locations was calculated as the northernmost extent of the subsurface <2°C layer using E.U. Copernicus Marine Environment Monitoring Service data (spanning 2007–2022). Kernel density maps from Kerguelen were calculated using GPS and depth-logger data ($n = 60$ individuals, spanning 2007–2022), while kernels from Crozet were calculated using the Bost et al. (2015) foraging metadata, with authorization from coauthors ($n = 8$ individuals, spanning 2007–2010).

distance varied from 172 to 379 km ($n = 23$ years, see Table 1). The average southernmost latitude reached by penguins varied from –49.9° to –51.3° among years. There were no temporal trends in the foraging distance of penguins at Kerguelen (Table S1). The kernel density maps of foraging dives showed that penguins travelled south-east to where the Polar Front came the closest to the colony and started foraging at and beyond the front (Figure 2).

A final assessment of habitat selection was made using the 2019–2022 accelerometry data and model selection to determine which foraging zones are profitable to penguins. The model selection showed that SST and upper depth limit of the Winter Water layer were the two most important variables predicting prey capture attempts in a dive ($R^2 = .11$, Table S2). Both variables had a negative effect, with more productive dives occurring in cold SST water and

where the Winter Water upper-limit is shallower. When accounting for distance to the colony, only SST was present in the best ranked model ($R^2 = .12$, Table S3). Equipped penguins attempted 367 ± 112 captures on average per day at sea.

3.2.2 | Effects on mass before winter

The model with $SST_{-1 \text{ year}}$ as a unique explanatory variable scored the lowest AICc ($R^2 = .56$, Table S4). The effect of $SST_{-1 \text{ year}}$ was positive on chick mass, with higher $SST_{-1 \text{ year}}$ increasing chick mass (Figure 3).

3.2.3 | Effects on chick survival

Both average chick mass before winter and winter air temperature explained chick survival ($R^2 = .76$, Table S5). Both variables had a positive effect, with higher temperature and higher average chick mass increasing chick survival (Figures 4 and 5). Regardless of the year, individual chicks above 7 kg had high probabilities (>60%) of surviving the winter (Figure 4).

Both annual chick survival and annual chick mass varied considerably from year to year (survival rate range: 7%–98%, yearly chick mass range = 4.3–9.6 kg). This extreme variation was particularly strong during the first decade of the study, when winter temperature was lower on average, while chick survival rates stabilised in the last decade with a rise in air temperature (Figure 5).

4 | DISCUSSION

Global warming and the increased occurrence of extreme warm ocean events is expected to have a strong impact on the marine ecosystem, with cascading effects reaching top predators (Frölicher

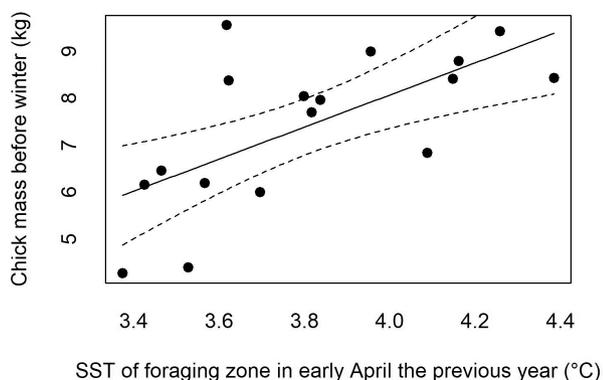


FIGURE 3 Relationship between average annual chick mass before winter (April) and SST-1 year. The solid line represents a linear regression ($\text{Chick mass} = 3.4 \times \text{SST} - 5.6$, $p = .004$, adj. $R^2 = .39$). The dashed lines represent the 95% confidence intervals. SST, sea surface temperature.

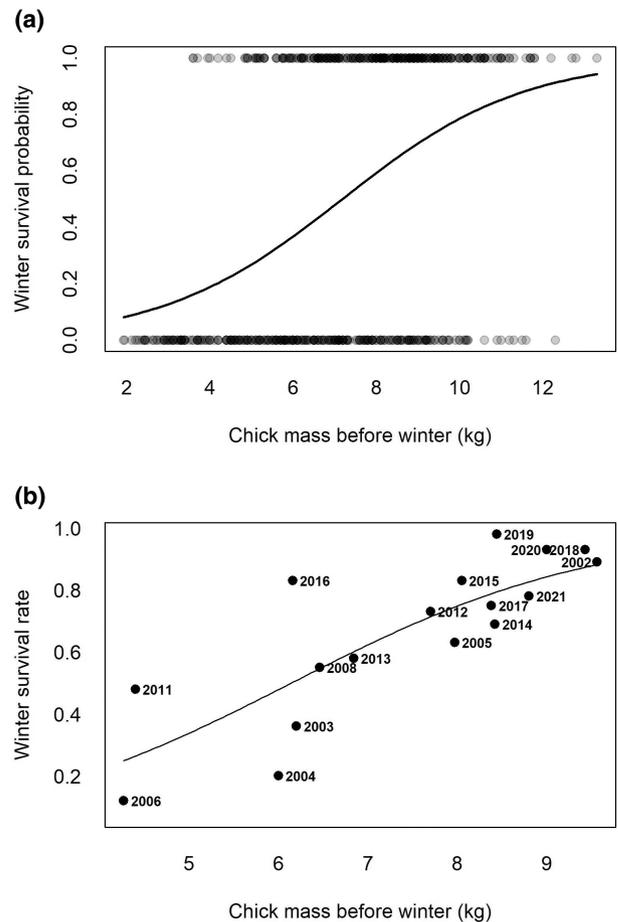


FIGURE 4 Effect of chick mass before winter on survival (a) at the individual level, where the solid line represents a logistic regression ($\text{survival probability} = 1/[1 - e^{-(0.65 \times \text{chick mass} - 4.1)}]$, p value < .001) and (b) across years, where the solid line represents a beta regression ($\mu = 0.6$, $\phi = 8.1$, p value < .001).

et al., 2018; Frölicher & Laufkötter, 2018). However, the mechanisms of these effects are often elusive, as long-term marine studies remain scarce. We used a unique dataset spanning over 25 years and looked at the interaction between the physical climatic variables and the fitness of a circumpolar predator and link these interactions with possible cascading effects in the food webs.

Our results show that the breeding success of a marine predator, the king penguin, varied dramatically from year to year, mostly due to differences in climate. However, the climatic variables influencing breeding success in Kerguelen were not the same as in Crozet, its closest neighbor. For instance, chick mass and survival were not influenced by shifts in the Polar Front position during warmer years, which was the case at Crozet. While chick-rearing king penguins at Kerguelen do feed at and beyond the Polar Front, the front displays inter-year position variation that is too small to affect chick-provisioning. Rather, we suggest that warmer climate might positively affect chick-provisioning penguins at Kerguelen by increasing prey abundance and/or growth. Winter wind chill at the colony also directly affected chick survival, with warmer conditions increasing survival rates. A graphical visualization of

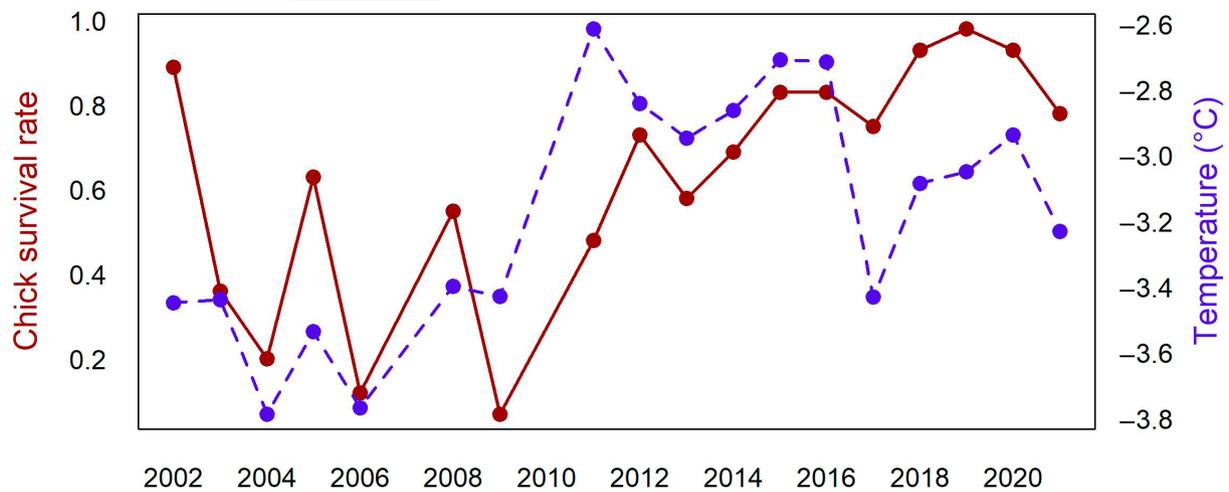


FIGURE 5 Temporal trends in the chick survival rate (in dark red) and the average winter temperature (accounting for wind chill, blue dashed line).

the air-temperature and ocean-temperature effects on the different stages of the king penguin reproduction cycle can be found in Figure 6. Our results help understand the mechanisms between climate and the fitness of a marine predator, as well as highlighting how these interactions can vary locally, creating distinct responses from different populations.

4.1 | Foraging habitat selection

Previous studies suggested that low SST and cold subsurface layers (Winter Water) originating from Antarctica, found around the Southern Ocean at and south of the Polar Front, is an important feature for the foraging of king penguins (Charrassin & Bost, 2001; Scheffer et al., 2016). Our results support this, as shallower 2°C layers and colder SST were associated with more productive dives.

Because there is an abrupt change in density between the deeper Winter Water and the warmer surface water, nutrients and plankton are thought to accumulate at the frontier of these two layers, creating favourable conditions for penguins' prey, that is myctophids (G. Duhamel, unpublished; Park et al., 2014; Scheffer et al., 2010, 2016). When these layers are particularly shallow, it might benefit the foraging success of the king penguins by bringing prey closer to the surface. Such is the case in the area South of the Polar Front—where an upwelling effect brings the Winter Water closer to the surface—and south-east of Kerguelen, past the Polar Front, where an offshore shoal deflects the Winter Water upward (Charrassin et al., 2002; Park et al., 2008). These two areas, the southern Polar Front boundary and the area to the south-east, were both targeted in all years by the foraging king penguins. Elsewhere around the sub-Antarctic region, king penguins also closely associated with these shallow cold layers upwelled by the Polar Front, as in South Georgia, Prince Edward Islands and Crozet archipelago (Bost et al., 2009; Pistorius et al., 2017; Pütz, 2002).

4.2 | Comparison with Crozet

At Crozet, the Polar Front position ranged from 217 to 642 km away from the colony in 16 years (Bost et al., 2015, Table 1). This variation ($\Delta 425$ km) is almost a 10-fold difference compared the one observed at Kerguelen in our study ($\Delta 44$ km) using the 16-year CMEMS dataset, and surely a significant difference for a species that can theoretically only travel ~ 170 km a day. The stability of the Polar Front near Kerguelen is likely caused by the strong bathymetric features occurring there: the front passes in a narrow trench, with Kerguelen's island forming the northern boundary preventing the front from shifting Northward, and the Kerguelen-Heard plateau forming the equivalent southern boundary (Park et al., 2014, also see Figure 3). No such bathymetric features are present at Crozet, and so the front can more freely move with annual sea temperatures there (Pauthenet et al., 2018). In addition, the Polar Front passed 3–6 times closer to Kerguelen than Crozet in all years of the study. The proximity and stability of the Polar Front at Kerguelen might explain why king penguins there do not have to travel as far as those at Crozet to reach the productive Winter Water zones during the brooding season (Table 1, also see Duhamel et al., 2019; Duhamel & Welsford, 2011). As the foraging hotspots are consistently accessible to penguins in Kerguelen, prey distribution shifts caused by warmer climate are not likely to be a limiting factor like at Crozet.

Yet, there is still considerable annual differences in chick growth at Kerguelen, with the average mass before winter ranging from 4.4 ± 0.9 kg in 2006 to 9.6 ± 1.3 kg in 2002 (Figures 4 and 5). Such extreme differences suggest that adults can experience significantly different foraging conditions from year to year, despite what is shown by their foraging tracks. A possible explanation would be that, rather than being limited by prey distribution, the foraging success of brooding penguins at Kerguelen is dependent on prey abundance at the foraging location. Brooding penguins at Kerguelen primarily feed on 2-year-old myctophids *Krefflichthys andersonni* measuring between 40 and 55 mm (Bost et al., 2002;

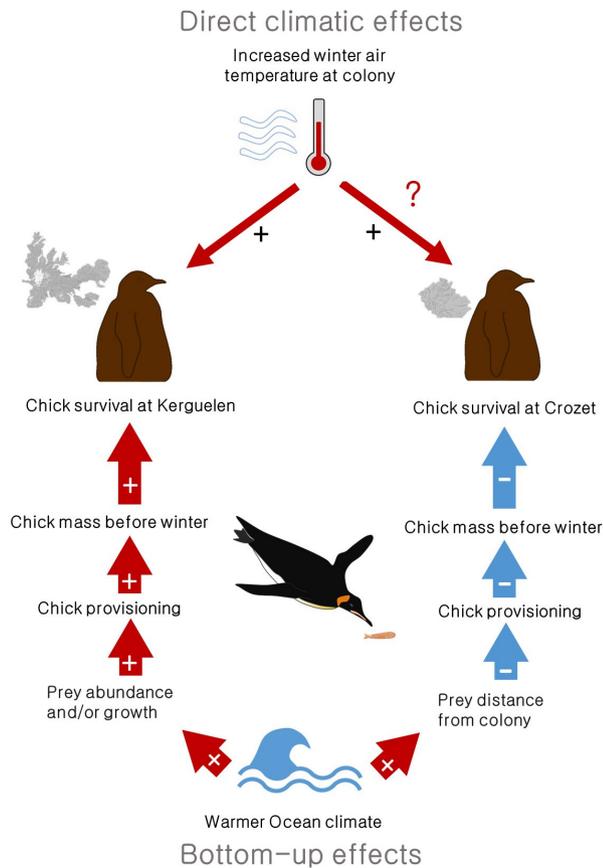


FIGURE 6 Conceptual diagram of the results at Kerguelen in contrast with the system at Crozet, with positive effects in red and negative effects in pale blue. Strong bottom-up effects dictate most of the variation of king penguin foraging and breeding success in both locations, but with opposite relationships to ocean warming. Top-down effects were also present at Kerguelen especially in winter, with warmer air temperature increasing chick survival. Although top-down effects on the long-term breeding success of penguins were never investigated at Crozet, the ambient temperature optimum for winter chick metabolism is higher than the current air temperature, suggesting that warmer temperatures would likely generate similar benefits as in Kerguelen. However, these effects would likely be offset by the negative bottom-up effects of ocean warming on chick survival.

Cherel & Ridoux, 1992; Lourenço et al., 2017; Saunders et al., 2020). The 2-year-old *K. andersonni* cohort of a given year exited the larval stage and entered its maximum growth period in April the year prior (Saunders et al., 2020). This is also the period when SST was correlated with chick growth the following year. We propose that higher SST in April the year before positively might influences the 1-year-old cohort growth and/or survival of *K. andersonni*, increasing foraging and breeding success of penguins the following year. It is not yet clear how exactly the mechanism of this correlation could operate, but a possible explanation is through the metabolic enhancement of fish. Growth of many cold water fish has been shown to increase with temperature (Brander, 1995; Imsland et al., 2006; Nytrø et al., 2014). In the North Atlantic, Atlantic cod *Gadus morhua* were larger following warmer temperatures, especially for younger

cohorts (Brander, 1995). Similarly, warmer conditions in Kerguelen could produce a larger 1-year-old *K. andersonni* cohort. The larger fish might also benefit from a better survival rate, and hence more food would be available for brooding penguins the following year when that same cohort is then 2 years old (Figure 7). This interpretation is further strengthened by the fact that the average size and abundance of *K. andersonni* can vary considerably between years (G. Duhamel, unpublished). It is also noteworthy that the maximum growth period of *K. andersonni* actually extends beyond April, and also occurs in May–July. While the correlation with chick mass was the highest with SST in April the year prior (when prey maximal growth starts), it was also significant in May and June, reinforcing this interpretation (Saunders et al., 2020). Further research using long-term prey data is needed to confirm this hypothesis.

4.3 | Population trend predictions

Many regions within the Southern Ocean have experienced warming in the last two decades (Bulgin et al., 2020). While the sea around both Crozet and Kerguelen have been spared from a steady temperature increase, the warmer episodes have been more dramatic in recent years. Worldwide, events of abnormally high ocean temperature have become more common, but little is known about how these extreme climatic events influence the ecosystem (Frölicher & Laufkötter, 2018).

In the eastern Southern Ocean, these high temperatures might have, to a certain degree, a positive effect on myctophid growth and/or survival. However, for top predators breeding in archipelagos such as Crozet's, the distance of the Polar Front is expected to double in the next century, ultimately creating poor foraging conditions (Péron et al., 2012). With climate change, it is therefore expected that marine predators at Crozet and other northern localities (e.g. Marion-Prince Edward islands) will experience a decrease in foraging and breeding success. This trend might already be visible: king penguin colonies at Crozet have experienced some of the strongest population declines for this species in the last decades (Barbraud et al., 2020; Delord et al., 2004; Le Bohec et al., 2008; Weimerskirch, Le Bouard, et al., 2018).

In contrast, chick survival and total population at Kerguelen have increased in the last decades, in synchrony with both ocean and air temperature warming (Barbraud et al., 2020). We have shown that warmer air temperature in winter could benefit the survival of penguin chicks during these crucial months. The same effect is also expected to be present at Crozet, as the average wind-chill temperature in winter there (-3°C) is lower than the ambient optimum for metabolism of winter-acclimated chicks (between -1°C and 9°C , Barré, 1976). Yet, the strong bottom-up effects at Crozet might outweigh any positive effects of air-temperature, so that the predicted lower breeding success of its king penguin population still holds (e.g. Le Bohec et al., 2008; Péron et al., 2012). This is especially true for the summer dynamic, when no significant direct effects of air temperature were detected—in contrast with other species (e.g. Adelie Penguin *Pygoscelis adeliae*) that experience colder summers—so that bottom-up effects are dominating during this period (Salihoglu et al., 2001).

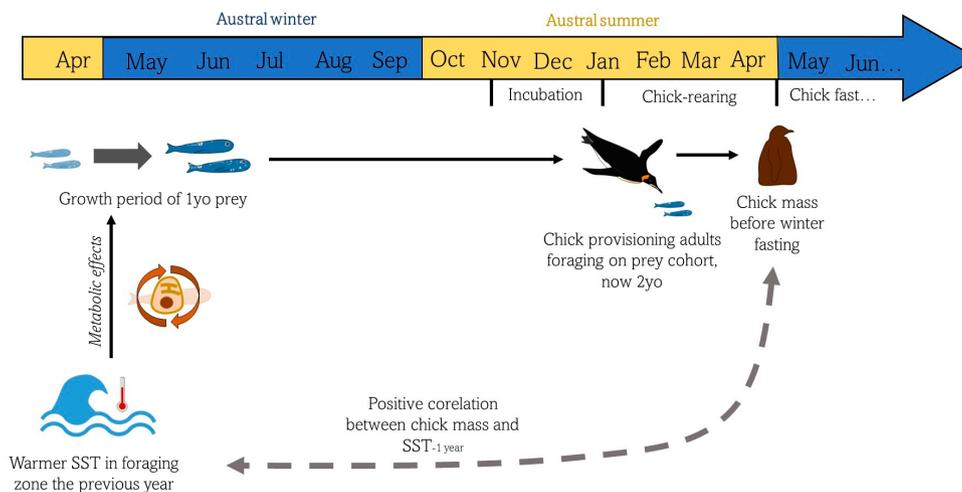


FIGURE 7 Proposed interpretation of the link between chick mass before winter and SST 1 year. High SST in April the year before could directly increase metabolism and positively influence the growth period of 1 year old prey (myctophid *Kreftlichthys anderssoni*) during late fall to mid-winter (Saunders et al., 2020). By the following February, brooding foraging king penguins—which feed on 2-year-old prey (Bost et al., 2002; Chérel & Ridoux, 1992)—will benefit from a more abundant prey cohort, positively influencing chick provisioning and ultimately chick mass. SST, sea surface temperature.

The Crozet archipelago and Kerguelen Island hold the two largest populations of king penguins in the Eastern Hemisphere (Barbraud et al., 2020). Before 1980, Crozet held the largest population of king penguins in the world, but has since inexplicably reduced by more than half (Delord et al., 2004; Weimerskirch, Le Bouard, et al., 2018). Further warming of the foraging zone might apply additional pressure to this population. We predict that Kerguelen Island will replace the Crozet Archipelago as the stronghold for king penguins in the Eastern Hemisphere, as its high chick survival rates and foraging zone stability will create good conditions for further population increase. Other marine predators associated with the Polar Front have experienced similar trends—that is, a decrease in Crozet but an increase in Kerguelen—like the black-browed albatross, but the exact reasons of the population trends are yet to be determined (Weimerskirch, Delord, et al., 2018).

For king penguin colonies located south of the Polar Front, as in South Georgia, we predict that populations will also increase. These colonies are not expected to be negatively affected by prey distribution shifts, as these shifts will occur towards the colonies rather than away as in Crozet. For this reason, colonies in South Georgia might benefit from the warming weather (increased chick winter survival, etc.) without the disadvantages, at least in the short term. Similar to Kerguelen, the king penguin population in South Georgia has experienced strong increase in the last decade (Foley et al., 2018).

Nonetheless, further monitoring at all colonies needs to be conducted, as the potential “beneficial” effects of warming might eventually be reduced, if not disappear completely, past a certain warming threshold. This is especially true for the ocean, where a certain degree of warming might approach the optimal conditions for prey, but further warming might bring the temperature away from that optimum. This might already be apparent in the Kerguelen

area, where the correlation between $SST_{-1 \text{ year}}$ and chick mass seems to have stabilised in the last 7–8 years (Figure 4). Air temperature warming could also eventually become detrimental for penguin chicks (e.g. Holt & Boersma, 2022). Maintaining the monitoring program in penguin colonies is needed to better assess any future non-linear association between marine predators of the Southern Ocean and climate change.

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CONFLICT OF INTEREST

All authors declare no conflict of interest for this study.

DATA AVAILABILITY STATEMENT

The data associated with the study has been deposited in Dryad and is available at <https://doi.org/10.5061/dryad.t76hdr84c>.

ORCID

Émile Brisson-Curadeau  <https://orcid.org/0000-0001-5795-9915>

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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