Pygoscelid penguins

An abundance shift in sympatric breeding species

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Bachelor thesis 2010

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Abstract

Climate change at the Western Antarctic Peninsula includes increased mean annual temperature and snow accumulation, retreat of glaciers and shortening of the seasonal ice cover. These changes in the physical environment influence the biological environment and cause a shift in plankton species and krill stocks to decline. Because krill is a key item of prey to predators in higher trophic level of the food web, a decline in krill abundance impacts its predators.

Such an impact is demonstrated best for Pygoscelid penguins breeding near Palmer Station, West Antarctic Peninsula. The abundance of Adélie penguins has been rapidly declining whereas numbers of it congeners, the Chinstrap and Gentoo penguins have risen. Because krill stocks are declining and the Adélie penguin is a specialist feeder, it has a disadvantage to the other brush-tailed species. As sea ice covers are declining it becomes extremely difficult for ice-dependent Adélie penguins and especially their young to achieve their food requirements during the winter.

Photograph on front page: Gentoo Penguins and Chinstrap Penguins gather on an iceberg on the Western Antarctic Peninsula ©Steven Kaziowski / Barcroft Medi. http://www.dailymail.co.uk/news/worldnews/article-1258041/Incredible-pictures-giant-ice-sculptures-carved-sea-water-polar-winds.html#ixzz18vlA3cu3

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Introduction

The West Antarctic Peninsula (WAP) is one of three areas on Earth where rapid climate change occurs, but the WAP is the only one having a maritime climate (Schofield 2010). Along the peninsula the mean annual temperature increased 3.4°C and average midwinter surface atmospheric temperatures have increased 6°C since 1950 (McClintock 2008, Schofield 2010). Retreat of glaciers in this region (Clarke 2007), shortening of the seasonal ice cover and an increase of snow accumulation (Thomas *et al.* 2008) have also been noticed.

As regional warming reduced the extent and the duration of sea ice cover, the composition of the phytoplankton community changes in summer from diatoms to populations of cryptophytes in near-shore coastal waters. Low recruitment and increased predation are the two other factors causing Antarctic krill *(Euphausia superba)* to be outcompeted by salp *(Salpa thomsoni).* Because krill is a key link in the Antarctic food web and salp doesn't serve as food for others, so changes in higher trophic levels are a consequence (Moline *et al.* 2004, Schofield 2010).

The ice-reduction hypothesis introduced by Fraser *et al.* (1992) suggests that a decrease in winter sea ice in the West Antarctic Peninsula causes major long-term changes in the abundance of some regional krill dependent populations. This seems to be the case for Pygoscelid penguins breeding sympatrically near Palmer Station. Where the three species live sympatrically, their ecological segregation isn't caused by competition for food, but it seems to be that difference in adaptation to conditions in the center of their distribution. Does (Trivelpiece 1987).

Adélies penguins are the most southern breeders of the three species and are ice-dependant through the year, whereas Chinstrap and Gentoo penguins only arrived a few decades ago and are adapted to milder northern conditions and being ice-intolerant. (McClintock 2008). Climate change at the West Antarctica Peninsula has changed the environmental conditions to which the Adélie penguins have most adapted, favoring Chinstrap and Gentoo penguins. Data by Schofield (2010) show that populations of latter two species have increased near Palmer Station, Antarctica, whereas abundance of Adélies penguins have fallen.

There is currently a lot of literature on differences in life strategy, breeding performances, dietary and foraging behaviour available for Pygoscelid penguins breeding in relative nearby areas of Palmer Station. Using these articles this thesis will form a summary and speculation on the differences and similarities between brush-tailed penguins life strategies and behaviour and trying to link these to the physical climate changes occurring at the West Antarctic Peninsula. The main question of this thesis is therefore: *What causes Adélie penguins to be at a disadvantage to Chinstrap and Gentoo penguins at Palmer Station, Antarctica?*

McClintock (2008) reports of similar situation among seals; Weddell seals are like Adélies ice-dependent and their populations have decreased enormous, while the populations of ice-avoiding Fur- and Elephant seals have increased significantly. In contrast to Pygoscelid penguins only one species of seals in krill-dependent, so it seems that sea ice, rather than diet, is the main factor causing their difference in response to climate change.

Chapter 1, Brushed-tailed penguins

The genus *Pygoscelis*, or brush-tailed penguins, consists of three species; the Adélie penguin (*P. adeliae*), the Gentoo penguin (*P. papua*) and the Chinstrap penguin (*P. antarcticus*). Mitochondrial and nuclear DNA evidence (Fig. 1) suggests that around 38million years ago the genus split from other penguins. In turn, the Adélie penguins split off from the other members of the genus around 19million years ago, and the Chinstrap and Gentoo diverged around 14million years ago (Baker 2006).

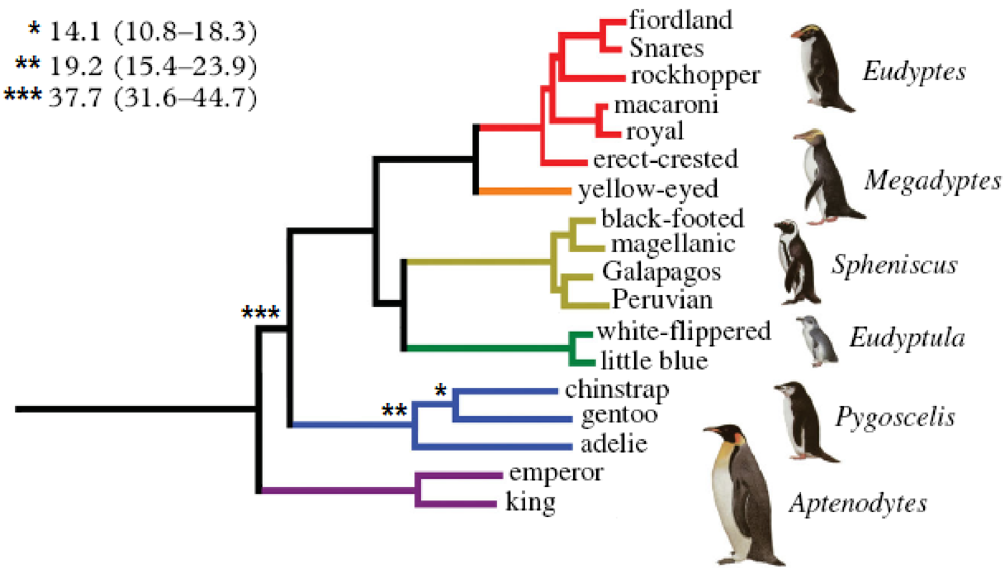


Figure 1: Phylogenetic relationships of modern penguins. Phylogenetic reconstruction was based on 2802 bp of RAG-1 and 2889 bp of mitochondrial 12S and 16S rDNA, cyt b and COI, excluding gaps and ambiguously aligned positions. Numbers above branches are estimates of divergence time (and 95% confidence intervals) in million of years ago for nuclear and mtDNA datasets combined (Baker 2006).

- Distribution and habitat

Penguins are social animals gathering in large colonies, which often consist of thousands of individuals. The benefits of colonialism include information transfer, anti-predator strategies and access to mating partners (Ainley *et al.,* 1995).

Adélie penguins are the most widely distributed *Pygoscelis* penguins, they are circumpolar distributed and are the most southern breeders. Their breeding area ranges from the Antarctic mainland along the Antarctic Peninsula to the South Orkney Islands. Outside this area some small populations can be found on the South Sandwich Islands (Forcada 2009).

Adélies are migratory birds; during winter they are obligate inhabitants of the pack-ice (Hinke 2007) and the marginal ice zone where they have access to food. During the warmer summer months, the penguins return south to coastal beaches in search of ice-free ground on the rocky slopes and pebbles to build their nests. The pebbles are needed to inhibit slope water and snow entering the nest and so prevent chicks to become hypothermic (Forcada 2006).

Chinstrap penguins inhabit the Antarctic Peninsula and the sub-Antarctic islands (Shetland, Orkney and Sandwich) where sea ice is minimal. In summer they breed on land that is free of snow and ice. Sea ice doesn't influence their habitat choice, only if it blocks their access to their breeding colonies (Forcada, 2006). Chinstrap penguins are not ice obligate because they need open water habitats during winter to collect food (Hinke 2007).

Gentoo penguins live the most northern of the *Pygoscelis* penguins. They mainly breed on sub-Antarctic islands and along the Antarctic Peninsula to approximately 65°S latitude with access to inshore waters. They are adapted in the northern regions to a milder climate with longer summers, than their congeners. Gentoo penguins breed on land in flat ice-free areas and feed in the open sea near their breeding colonies. During winter they don't migrate and remain close to their breeding grounds (Forcada 2009, Carlini 2009).

- Breeding cycle

To become a member of the breeding population, Pygoscelid penguins must successfully complete several stages of their breeding cycle, including hatching, fledging and juvenile recruitment. Adélies, Chinstraps en Gentoo penguins can breed sympatrically during the austral summer, because niche overlap is minimal due to differences in their breeding cycles and raising chicks.

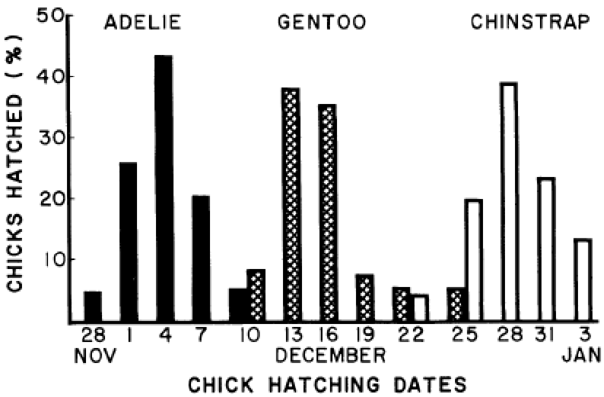
Species	Mean age at maturation (*A*)	Effective clutch size*	Incubation period (days)	Chick rearing (days)	Fledging period (days)	Breeding success	Mean adult survival (*S*)	Generation time†
Gentoo (*Pygoscelis papua*)	3–4	2	30–40	20–30	80–105	0.30–1.20	0.75–0.90	≥ 8
Chinstrap (*Pygoscelis antarctica*)	4–5	2	30–40	20–30	50–60	0.60–1.80	?	?
Adélie (*Pygoscelis adeliae*)	4–5	2	30–36	16–34	40–65	0.70–1.40	0.80–0.97	≥ 8

*Effective refers to the number of eggs that usually hatch.
†Generation time is calculated as $T = A + S/(1-S)$, where A is age at maturation and S is adult survival.
?Unavailable data.

Table 1: Life-history variation in Antarctic penguin species (Forcada and Trathan 2009).

After 30-40 days one or two chicks hatch in brush-tailed penguins nests. (table 1) (Forcada and Trathan 2009), but the breeding chronology differs per species (figure 2). According to (Trivelpiece 1987) differences in breeding time of Adélies and Chinstraps may reflect adaptation to early breeding in the harsh, short summer of the continental Antarctic, and adaptation of Chinstraps to later breeding in the milder sub-Antarctic. One would expect the Gentoo, the most northerly living species and also adapted to a milder climate to breed last. Breeding earlier than expected could be a result of needing more time to raise young ones (table 1) before the end of the summer season compared to its congeners.

Figure 2: The hatching chronology of Adélie, Gentoo, and Chinstrap penguins during the 1981/1982 breeding season at King George Island. Chicks are grouped into 3-d hatching intervals from 28 November, the first Adélie chick-hatch date, to 5 January, the last Chinstrap chick-hatch date (Trivelpiece, 1987).



After hatching (the guard stage), adults take turns attending the chick(s) at the nest while the other adult forages to feed for themselves and gather food for their offspring. Research by (Trivelpiece 1987) on nest relief interval by *Pygoscelis* penguins at King George Island shows different intervals; Adélie chicks received 0.99, Chinstrap chicks 1.44, and Gentoo chicks 1.92 feeding visits per day. During this stage, chicks replace their hatching feathering with a thick, downy plumage (Ainley 2002). At the end of the guard stage the energetic demands of growing chick(s) is so high that both adults must forage together and the unattended chicks gather in crèches. A second molt is needed to replace their downy plumage with waterproof feathering.

Finally, a few days prior to fledging, Adélie and Chinstrap adults stop feeding their chicks resulting in a short starvation period and chicks abandon their natal colonies in small groups over a short time (approx. 1 week). They must find suitable food without any foraging experience. In contrast Gentoo fledglings don't leave their natal colonies but enjoy a transitional time to independence of max. 3 weeks in which they make trips to the sea to food and receive extra food from their parents. This additional feeding may learn fledglings where and how to forage near their colony, as an advantage to the Adélie and Chinstrap juveniles (Hinke 2007).

On the Antarctic Peninsula, Adélie and Chinstrap penguin chicks fledge on average 50-55 days after hatching, while Gentoo penguin chicks require on average 90 days (Forcada and Trathan 2009). According to Culik (1994) these inequalities are the result of adapting to different general habitat; Adélies breeding furthest South, Gentoo penguins breeding furthest North and under milder conditions, while Chinstrap penguins have an intermediate range. The amount of food delivered to Gentoo penguin chicks until fledging is two times the amount delivered to the chicks of the two other species enabled by a higher number of feedings per day, a longer fledge period and a higher need to stay warm compared to its better adapted congeners (Trivelpiece 1987). Once fledglings enter the water and leave the colonies, they typically do not return until they begin breeding. These returning chicks have successfully recruited into the breeding population (Ainley 2002).

- Food and foraging behaviour

During the breeding season the dominant prey of Pygoscelis penguins is Antarctic krill (*Euphausia superba*) although proportion varies by species and depending on geographic location. Hinke *et al.* (2007) calculated that the diet of sympatrically breeding Adélie, Chinstrap en Gentoo penguins at Admiralty Bay consists for 98, 96 en 94% out of krill. The remainder consists of various fish, squid and other Euphausiid species (Lynnes *et al* 2004).

Emslie and Patterson (2007) demonstrated that Adélies only recently (within the past 200 years) started to eat krill as their major food source of their diet. After a period of exploitation of baleen whales and krill-eating seals during the historic whaling era, a so-called 'krill surplus' became available in the Southern ocean. It was during this period that Adélie penguins modified their diet from especially fish (Rock cod, Dragon fish and Ice fish) to become a specialist feeder of krill. In contrast, its congeners are known to be opportunistic feeders, including squid and small fish in their diet at times of low krill availability.

Species that are competing for the same resource, in this case Antarctic krill, are considered able to co-exist if they occupy different niches. Wilson (2010) studied a group of sympatrically breeding Pygoscelid penguins, at King George Island, Antarctica, using deadreckoning loggers to examine foraging niche overlap.

The foraging area utilization by the three Pygoscelid penguins is shown in figure 3. The area close to the island was used for a distinguishable amount of time at sea by all the birds, being the areas close to the landing beaches, passed twice per foraging trip. Adélies used the sea area extending from about 28 km to 40 km south-south-east of Ardley Island, Chinstrap Penguins spent much more of their time between 8 and 24 km south-south-east of the island and Gentoo Penguins spent most of their time in a spot directly south-east of the island.

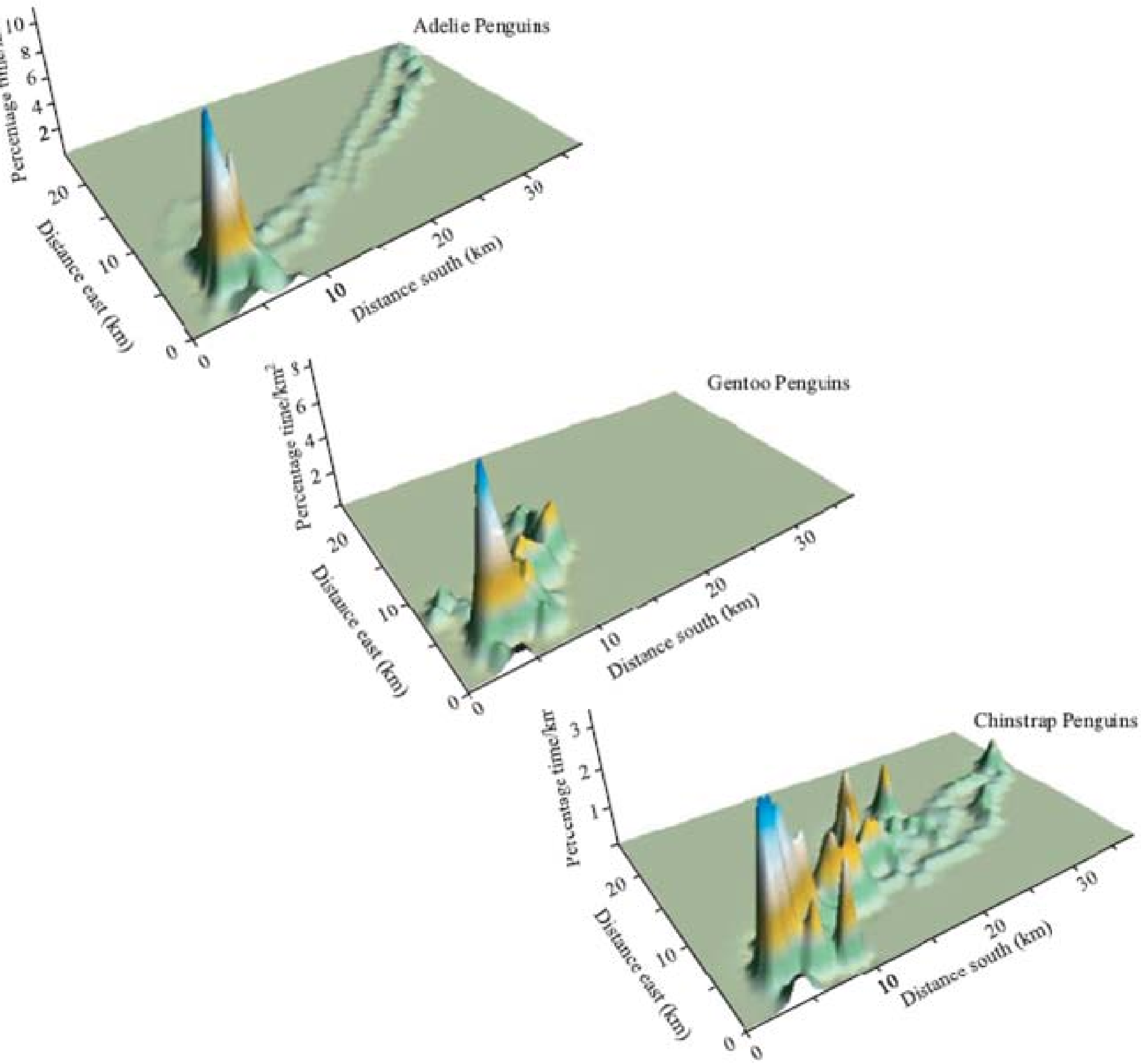
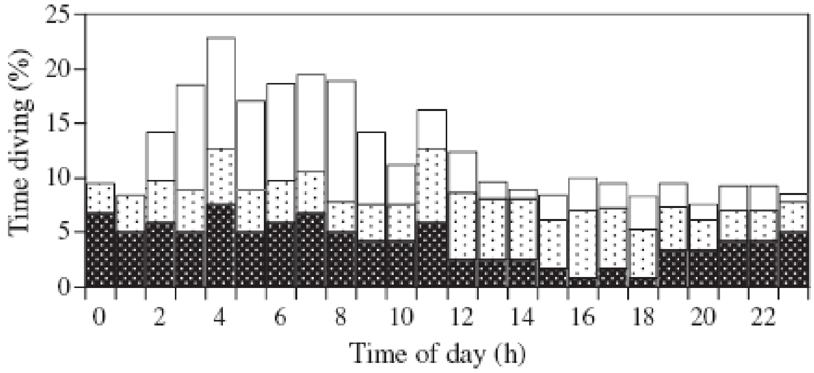


Figure 3: 'Foraging area utilization by the three Pygoscelid penguin species breeding at Ardley Island, King George Island, during 1991 ⁄ 2. The 3-d plots represents the fraction of total time spent per square kilometer in the vertical axis for all bird positions at sea. Ardley Island is located at the co-ordinates (5, 5)' (Wilson 2010).

The time that the penguins were actually diving during the time they were off the island showed there were inter-specific differences (χ^2 = 80.1, d.f. = 46, P < 0.01); Chinstraps foraged primarily at night, Gentoos during the morning and Adélies in the afternoon, figure 4). Due to physiological properties penguins exploited those depths that they were most efficient. For instance foraging efficiency was greatest for Adélie penguins diving near the surface (0-15m), while Chinstraps were most efficient at medium depths (15-60m) and Gentoos were most efficient at depths (>60m).

Figure 4: 'Percentage time spent actively diving as a function of time of day for Pygoscelid penguins bree-ding at Ardley Island during 1991 ⁄ 2. Darkest bars show Chinstrap, lightest Gentoo, and inter-mediate bars show Adélie Penguins '(Wilson 2010).



Aggregation of the measured parameters shows a minimal overlap between species (table 2), favoring the idea that penguin exploit different foraging niches in areas of sympatric breeding (Wilson 2010).

Overlap indices	Adélie - Chinstrap	Adélie - Gentoo	Chinstrap - Gentoo
Area use	0.29	0.44	0.40
Depth use	0.69	0.52	0.48
Foraging periods	0.47	0.26	0.40
Total	0.09	0.05	0.08

Table 2: Overlap indices of area use, depth use and foraging periods by Adélie, Chinstrap and Gentoo penguins at Ardley Island during 1991/2 (Wilson 2010).

Chapter 2, Climate change in the West Antarctic Peninsula

- Physical climate changes

The West Antarctic Peninsula (WAP), northwestern North America, and the Siberian Plateau are three areas on Earth where rapid climate change occurs, but the WAP is the only one having a maritime climate (Schofield 2010). The Southern Ocean circulation, surrounding the Antarctic continent is dominated by the Antarctic Circumpolar Current (ACC), figure 5. It is the largest, strongest and fastest current of all oceans currents and flows from west to east or clockwise seen from the South Pole (Ainley 2008). The ACC isolates Antarctica from temperate atmospheric conditions and warmer waters from northern latitudes, causing air and sea to cool. Due to gyres the ACC doesn't reach the continental shelves and coastal waters. And exception takes place at the West Antarctica Peninsula, where the ACC wells upward and floods onto the continental shelf, supplying the coastal waters with warmth and nutrients (Clark 2007, McClintock 2008).

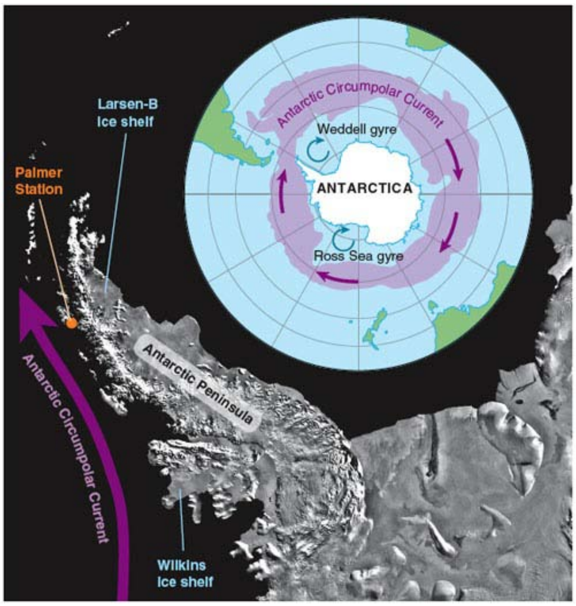


Figure 5: The Antarctic Peninsula (McClintock 2008).

In contrast to the rest of the Antarctic continent, where no noticeable warming has occurred in the past century, along the peninsula the mean annual temperature increased 3.4°C, average midwinter surface atmospheric temperatures have increased 6°C since 1950 (McClintock 2008, Schofield 2010) and the majority of glaciers in this region have retreated during the past 50 years (Clarke 2007).

In 2001 Smith and Stammerjohn reported a 40% reduction in annual mean sea ice extent over a 26-year period, caused principally by a reduction in the duration of winter sea ice. Research by Forcada and Trathan (2009) indicates a total decrease in the sea ice season at the WAP by 85 days due to an extensive sea ice retreat (over 30 days earlier) in spring–summer followed by a delayed sea ice advance (over 50 days later), caused by intensification of northerly winds.

According to Meredith and King (2005) a decline in winter sea ice, can be a cause, but also an effect of warmer seas in summer. Their data shows a rise in ocean summer surface temperature (figure 6), where the strongest warming occurs at the surface. Increased upwelling of heat to the coastal shelf and a lost of winter sea ice creates a positive feedback amplifying and sustaining atmospheric warming (Schofield 2010).

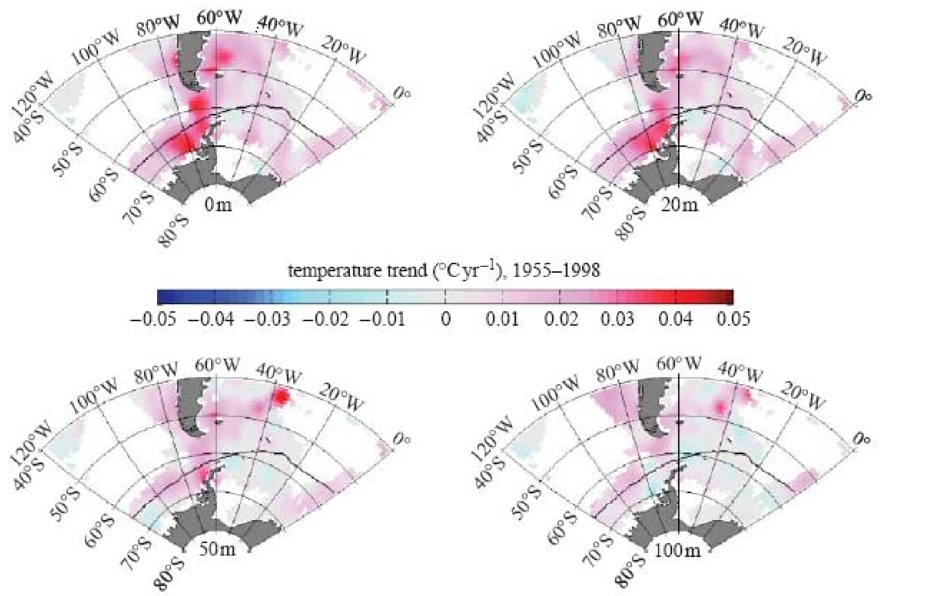


Figure 6: 'Trends in ocean summer surface temperature over the period 1955–1998, for four different depth levels (surface 20,50 and 100 m). Grid cells with no data are left white. Note that the marked warming trend observed close to the Antarctic Peninsula is strongly intensified towards the surface, and decays to almost 0 by 100m depth' (Meredith and King 2005).

According to (McClintock 2008), a decline in sea ice extent creates larger surface areas of open water exposed to the atmosphere, increasing levels of evaporation and cloud cover. This results increased snow fall. Thomas *et al.* (2008) analyzed a medium depth ice core drilled at a high accumulation site (Gomez) on the south-western Antarctic Peninsula (73.59°S, 70.36°W, 1400 m) and found a rapid increase of snow accumulation (measured in meters of water equivalent per year) in the latter part of the record with the mean accumulation rate from the mid-1970s onwards increasing to 0.95 mweq·y^{-1}, figure 7. Additional to his finding he states that the huge increase may be unique to the Gomez area, but other cores sites certainly show increases in accumulation as well.

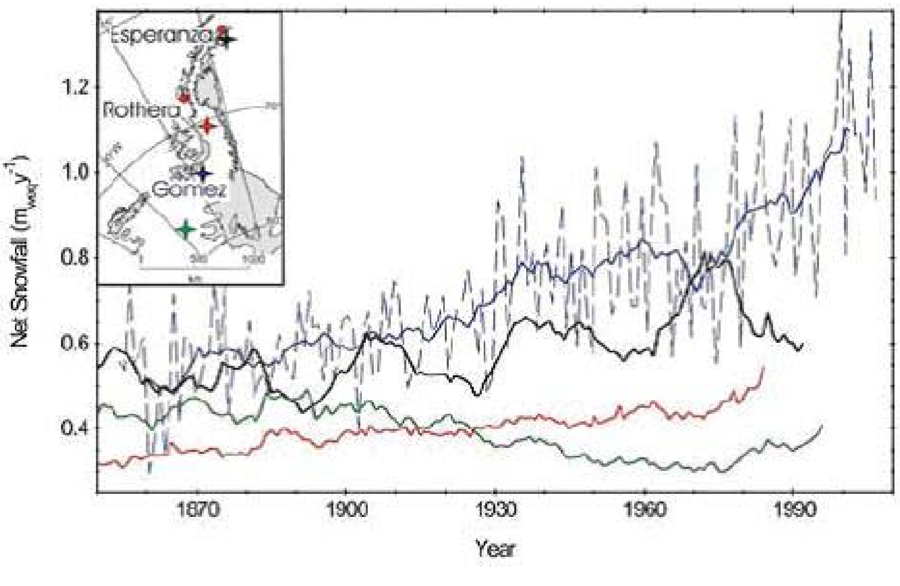


Figure 7: 'Annual accumulation at Gomez (dashed blue) and running decadal mean accumulation at Gomez (solid blue), Dyer Plateau (red), James Ross Island (black) and ITASE01_05 (green) in meters of water equivalent per year (mweq y-1) between 1850 and 2006' (Thomas *et al.* 2008).

- Ecosystem changes

The western coast of the Antarctic Peninsula is a highly productive ecosystem, partly due to the supplied warmth and nutrients by the ACC-upwelling. Large phytoplankton blooms in spring and summer are influenced by the annual ice cycle. During winter phytoplankton survives in pockets of liquid within the ice. When the ice melts in spring the phytoplankton is released in the water and exposed to increased sunlight. This stimulates their growth enormously and causes a bloom (McClintock 2008).

In 2004 Moline *et al.* reported of a consistent and repeated pattern in phytoplankton community composition and succession at Palmer Station, Antarctica: during spring the phytoplankton populations were dominated by diatoms, but during summer a transition from diatoms to populations of cryptophytes occurred. Simultaneously, a low salinity was measured, which was associated with glacial meltwater input at times when air temperatures were above freezing point (figure 8a-c).

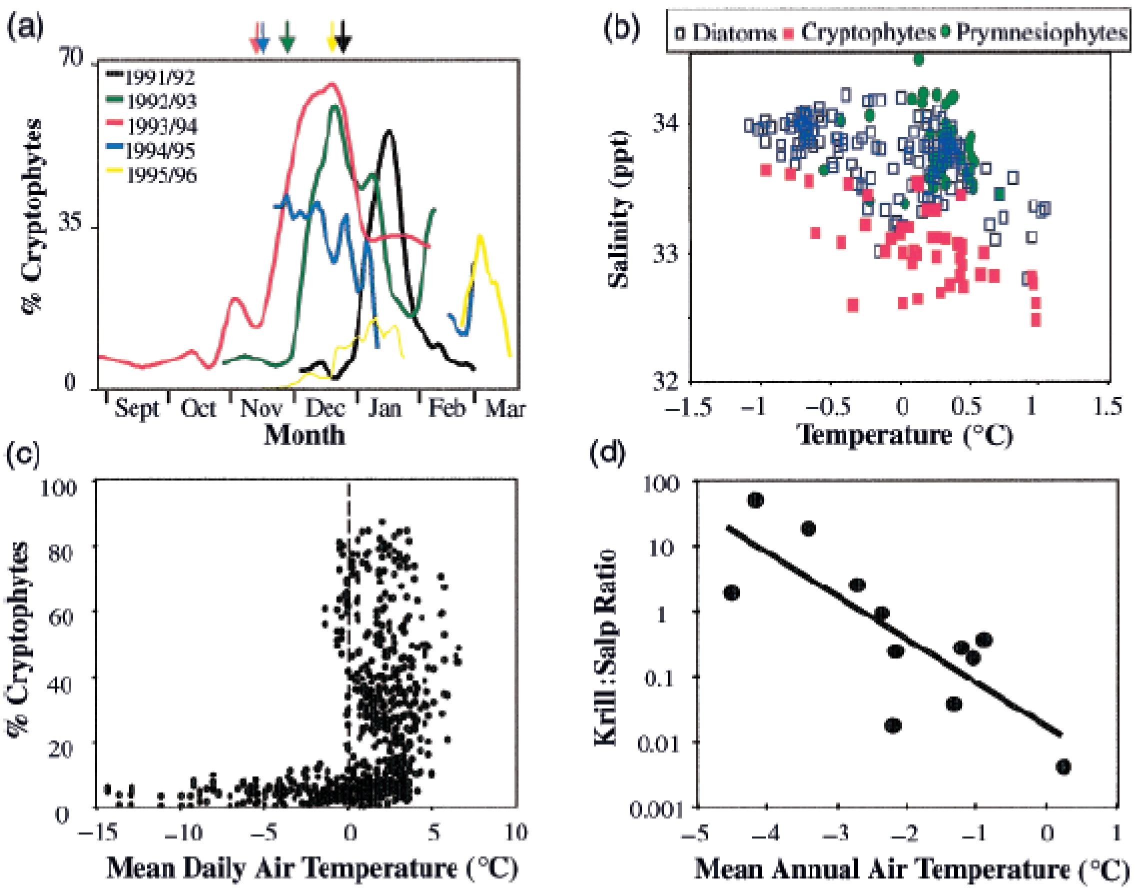


Figure 8: ‘(a) Seasonal changes in percent cryptophyte biomass during the spring and summer months off Palmer Station from 1991 to 1996. Arrows indicate the initiation of glacial melt-water input into the region during each year at Palmer Station. (b) Bivariate plot of temperature and salinity. Sample points indicate a >50% contribution to the total phytoplankton biomass by diatoms, cryptophytes and prymnesiophytes at Palmer Station from 1991 to 1994. (c) Percent cryptophytes from (a) shown as a function of mean daily air temperature at Palmer Station for the five sampling periods (n5696). (d) Relationship between mean annual air temperature (°C) measured at Palmer Station and the annual ratios of krill to salp abundance (r^2=0.63, n=12). Paired krill and salp data from the Antarctic Peninsula region were taken for 12 years between 1980 and 1996’ (Moline *et al.* 2004).

With a transition from diatoms to cryptophytes comes a decrease in the size class of the phytoplankton; diatoms range in size from 15 to 270 mm, whereas cryptophytes are just 8 ± 2µm long.

Antarctic krill *(Euphausia superba)* prefers diatoms as food, and can not graze cryophytes efficiently due to their small size (McClintock 2008). In contrast, salp (*Salpa thomsoni*) is efficient at grazing smaller cells and can outcompete krill when phytoplankton biomass is limited. Secondly, salp is a direct consumer of krill eggs and larvae, which intensifies the impact. Finally, a factor favoring salp blooms is low chlorophyll concentrations, although the mechanism behind this isn't well understood (Moline *et al.* 2004). Only in areas of high phytoplankton biomass salp thrives badly because its filtering apparatus can become clogged with negative consequences for growth and survival (Schofield 2010). If Atmospheric warming continues, the proportion of cryptophyte biomass to the total phytoplankton biomass is expected to raise, causing the krill : salp- ratio to decrease (figure 8d) (Moline *et al.* 2004, Siegel 2005).

Competition for food with and predation by salp is only part of the problem. As regional warming reduces the extent and the duration of sea ice cover, krill recruitment decreases. This is because the spawning behaviour of krill depends on sea ice in space an time. Under the ice krill juveniles assemble, eat algae that grows underneath it and use the ice habitat as a refuge from predators during winter (Atkinson 2004) So without sea ice krill can not complete their life cycle and breed successfully. Krill is a key link between primary producers, capturing energy and nutrients, passing it on to upper-level consumers. On the contrary salp has no natural predators and is a dead end in the food chain. A reduction in krill and substituted by salp, could have enormous implications for higher trophic levels of the food web.

Chapter 3, Possible causes for decline in Adélie penguins abundance

Changes in the higher trophic levels have been noticed most striking for Pygoscelid penguins breeding near Palmer Station on the West Antarctic Peninsula, figure 9 (Ducklow 2007, Schofield 2010). Compared to its congeners Adélie penguins occupied territory near Palmer Station for a much longer time, going back 700years, whereas the first Chinstrap colony was established in 1976 and Gentoo penguins arrived in 1994 (McClintock 2008). Research by Schofield (2010) shows that populations of Adélie penguins have fallen by 90%, whereas those of Chinstrap and Gentoo penguins have risen.

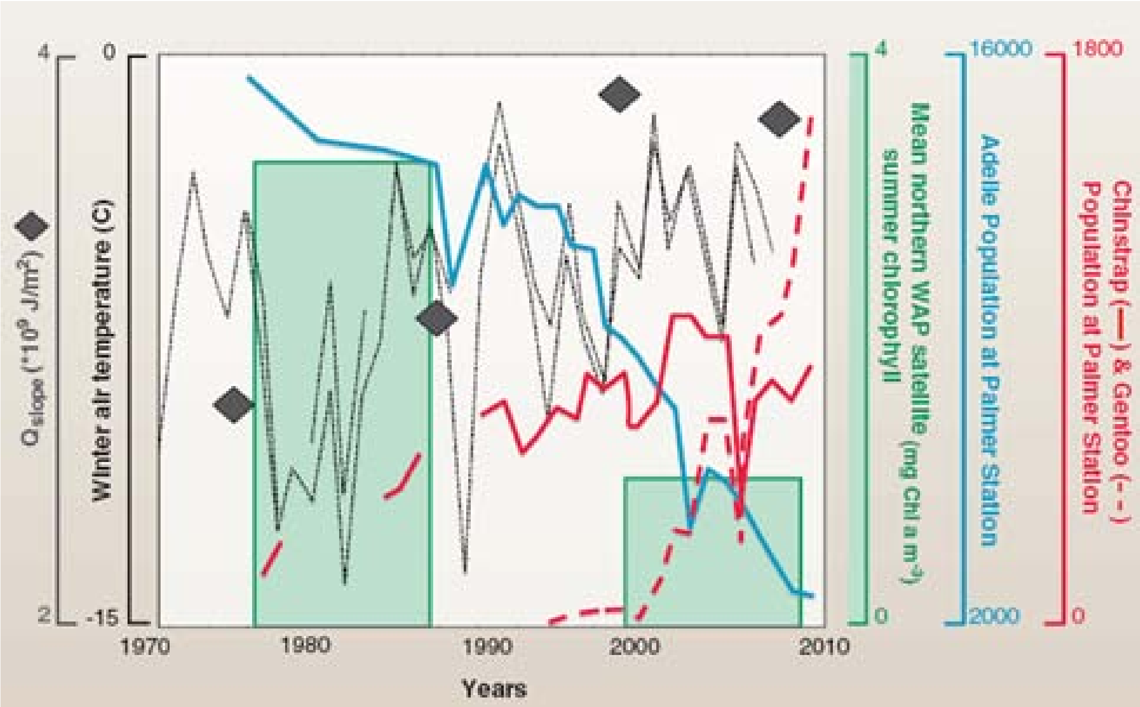


Figure 9: 'Changes observed along the WAP over the past 30 years. Annual average air temperatures at Faraday/ Vernadsky Station and Rothera Station have increased. There has been an increase in heat content (relative to freezing) of ACC slope water that had direct access to the WAP continental shelf (black diamonds). Average phytoplankton biomass declined between 1978–1986 and 1998– 2006 (between 1987 until 1997, no ocean color satellite imagery was available). There were also large shifts in the penguin populations at Anvers Island from 1975 to 2008' (Schofield 2010).

Data indicates that Adélie penguins are at a disadvantage to Chinstrap and Gentoo penguins. Through the years possible explanation for a declining Adélie penguin populations have been presented.

- Krill surplus hypothesis

Back in 1985 Wiley introduced the krill surplus hypothesis; suggesting that krill populations were restrained from growing in large numbers due the presence of baleen whales, but when these whales nearly exterminated in the 20th century due to hunting activities by humans, krill were no longer predated by these species. The resulting surplus should lead to a significant population growth in other krill-dependent predators.

- Increased nest flooding

According to (McClintock 2008), spring blizzards during the breeding season of Adélie penguins (November) have increased in number and severity at the Antarctic Peninsula. A large number of eggs and chicks is being killed when the snow is melting and floods the nest in the aftermath of the snowstorms. But this should not affect the breeding performance of Chinstrap en Gentoo penguins due to their sub-Antarctic breeding chronologies. Because they breed approximately three weeks later in ice free areas, the risk of nest flooding is less intense.

- Inaccessible food hotspots

In 1992 Fraser *et al.* introduced their ice-reduction hypothesis which suggests that a decrease in winter sea ice in the West Antarctic Peninsula is a major factor driving long-term changes in the abundance of some regional krill dependent populations. Another finding of the study by McClintock (2008) supports this hypothesis over a decade later; Adélie penguins find their prey during winter primarily at isolated 'hot spots'. Upwelling promoting gathering of krill and small fish occurs where the surface of the seabed creates impulses of warmer water from the Antarctic Circum Current.

To reach these areas of high krill abundance and thus making foraging efficient, Adélies depend on the zone of sea ice within 100km of the pack-ice edge, known as the marginal ice zone (MIZ) (Croxall *et al.* 2002). Because Adélies don't forage at night (Wilson 2010), they only have a short amount of time during the short polar winter days to find food and don't have time to travel far. So by moving over the sea ice can they stay close enough to their feeding grounds. As sea ice continues to retreat along the West Antarctic Peninsula, Adélie penguins lose access to their most productive winter foraging regions and starve due to a lack of proper food.

- Declining juvenile recruitment

Hinke *et al.* (2007) studied all three brush-tailed penguins species breeding sympatrically at King George Island (62°10`S, 58°30`W) between October and March from 1977/1978 until 2004. As shown in figure 10, the abundance of breeding Adélie and Chinstrap penguins both declined (Adélie -182 pairs year^{-1}, $F1{,}25= 40.7$, $P < 0.01$ and Chinstrap -132 pairs year^{-1}, $F1{,}25= 167$, $P < 0.01$), but there was no significant trend in abundance of Gentoo penguins (-9 year^{-1}, $F1{,}25= 0.89$, $P = 0.36$). Although breeding abundance is declining, maintenance of breeding success was observed in all colonies. According to Hinke *et al.* (2007) this suggests that most adult birds were able to require enough energy during winter to breed the next year and that food availability during winter had little effect on the breeding success.

Hinke *et al.* (2007) found that during summer the conditions at the shared colonies had similar effects on each penguin species, because I) fledging rates at all colonies were positively correlated, II) chick masses tended to decline for all species (although a bit weak for Gentoo penguins), III) food mass delivery to chicks was positively correlated at all colonies and IV) the mean size of krill ingested by birds at each colony was similar.

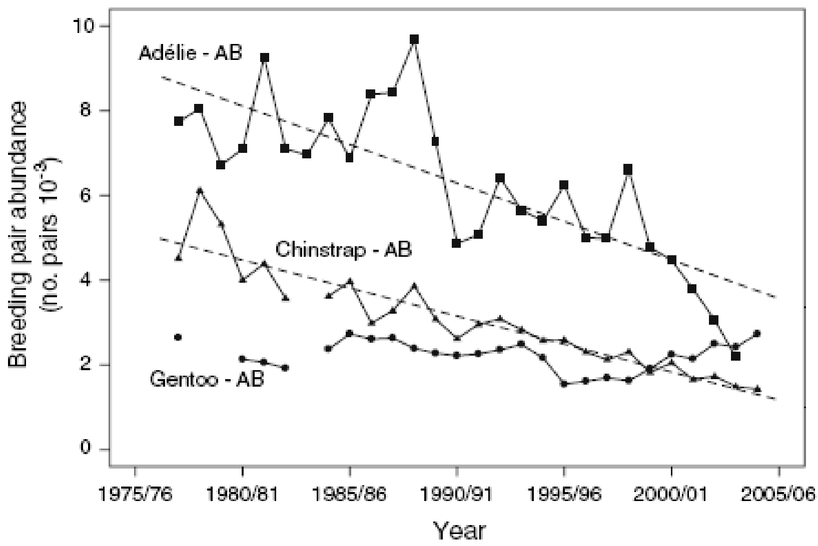


Figure 10: 'Number of breeding pairs of Adélie (*filled square*), Gentoo (*filled circles*) and chinstrap (*filled triangles*) penguins at Admiralty Bay (*AB*), King George Island, South Shetland Islands, Antarctica from 1977 to 2004. Linear regressions with significant, non-zero slopes are plotted as *dashed lines'* (Hinke *et al.* 2007).

But data on recruitment/survival differ per species, figure 11. First of all, cohort recruitment of Adélie penguins declined over the study period ($F1,19 = 65.3$, $P < 0.01$), there was no overall trend in cohort recruitment of Chinstrap penguins ($F1,10 = 1.96$, $P = 0.2$) and cohort recruitment of Gentoo Penguins did not trend ($F1,20 = 0.04$, $P = 0.84$). Secondly, total recruitment of Adélie penguins at Admiralty Bay declined significantly ($F1,19 = 19.8$, $P << 0.01$), and there was no such trend in recruitment of Chinstrap and Gentoo penguins.

Figure: 11: **'**Cohort and total recruitment based on first-time sightings of banded birds in their natal colony for Adélie, Chinstrap and Gentoo, and penguin colonies at Admiralty Bay. Cohort recruitment indices indicate recruitment from an individual cohort. Total recruitment indices indicate recruitment from multiple cohorts in single year. Linear regressions with significant, non-zero slopes are plotted as *dashed lines'* (Hinke *et al.* 2007).

According to Hinke *et al.* (2007), supported by (Carlini, 2009) and (Lynch 2010), the data shown above of declining populations breeding sympatrically, no noticeable food shortage in parents, similar breeding performances but different recruitment/ overwinter survival of juveniles favors the idea that a low recruitment is a good explanation for the decline in Adélie penguin populations.

Chapter 4, Discussion and conclusion

- Discussion

Although the colonies of Adélie penguins and the establishment of new species at Palmer Station have been monitored for a sufficient amount of time, almost thirty years, now hard data was available to investigate what causes the determined shift in abundance. Using outcome of research done on colonies relatively nearby, can be helpful, but doesn't give conclusive evidence.

The krill surplus hypothesis (Wiley 1985) doesn't seems to be fully sufficient to me. Krill is indeed a key component in the food web of the Southern Ocean and the main item of prey of many predators in higher trophic levels. But the krill surplus hypothesis doesn't fit in with populations trends in Pygoscelid penguins. The diets of all three species are dominated by krill, so with a surplus in krill similar trends would be expected among all three species and this is not the case.

Other data that I think is needed to get a better understanding of difference in relation to food is no just the amount of food that is taking, but also the nutritional value. Female krill just before spawning has a higher nutritional value than male krill (Chapman 2010). Dietary data of Adélies, Chinstrap en Gentoo penguins gives information on how much food is gathered and how much is given to the chicks, but no data is yet available on energetic values. It seems likely to me that these values differ per species.

Research by Wilson (2010) shows that penguin exploit different foraging niches in areas of sympatric breeding. Male krill live mostly in off shore areas, whereas female krill inhibits near-shore areas to spawn (Siegel 2005) Secondly, the diel migration of krill creates a difference in distribution and so food availability for foraging penguin species. Models by Chapman (2010) demonstrate that fledging mass positively correlates with juvenile recruitment. If fledglings start to forage for themselves, which to me is the most critical phase of the breeding cycle, and the nutritional values are at their peak, it would be a nice windfall for the young ones in addition to their inexperienced foraging strategy.

The idea of McClintock (2008) that an increase in spring blizzards (number and severity) and so increased flooding of nests due to glacial melt water during the breeding season of Adélie penguins is in my opinion a bluntly cause-effect statement and doesn't convince me that it is the main reason for the decline in Adélie penguins abundance at Palmer Station. Data to support this idea of nest devastation due to flooding, and supposedly finding a enormous amount of eroded nests (although pebbles could been taking by others to build new nests), dead chicks and lost eggs is not available (yet), neither has there research been done on the numbers of nest lost to support this idea.

Hinke *et al.* (2007), supported by (Carlini, 2009) and (Lynch 2010), state that difference in juvenile recruitment, is the best explanation for the abundance reduction of Adélies. Inexperience of the young ones in a time of changing circumstances, which leave little room for failure, could be the reason in their opinion to cause the decline. In my view, a reduced recruitment can also be the result of chicks not returning to their natal colonies, but becoming part of a different breeding colony. Another way for young not being able to join the breeding population is being predated by sea lions, leopard seals and orca's. A lack of data on the latter two options, makes it impossible to exclude them and so to me a decline in juvenile recruitment seems likely, but not the fact that this decline is caused by inexperience foraging.

Finally hardly any data was available on *Pygoscelis* penguins ecology and behavior in the winter period and what effects environmental change has on these birds during this season. The winter period lasts up to 8 months for Adélie, Chinstrap en Gentoo penguins, covering most of the year, but there is hardly data for this period. Data on dispersal patterns and diets, especially juveniles, could really more complete our understanding of how climate change impacts the life strategy of Pygoscelid penguins breeding on the West Antarctic Peninsula.

- Conclusion

The fact that the Adélie penguin is the only ice- obligated Pygoscelis penguin, gives it a disadvantage to Chinstrap and Gentoo penguins at Palmer Station. As sea ice continues to retreat along the West Antarctic Peninsula, Adélie penguins lose access to their most productive winter foraging areas. The trait of Adélie penguins finding their prey during winter only at isolated areas of high krill abundance in order to meet with their energy requirement during the short and cold winter days becomes a disadvantage, because they are specialist feeders as well. As their main item of prey becomes inaccessible they starve due to a lack of food and this impacts their abundance in a negative way.

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