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Title **CHINSTRAP PENGUINS: MISUNDERSTOOD AND VULNERABLE MONITORS OF ECOSYSTEM CHANGES IN THE SCOTIA SEA REGION OF ANTARCTICA**

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ABSTRACT Sea ice plays a critical role in structuring ecosystem dynamics throughout the Scotia Sea (SS) region, and variations in ice extent are hypothesized to affect predator populations in this area directly. A paradigm guiding recent research in the Western Antarctic Peninsula (WAP) region of the SS, the “sea-ice hypothesis”, suggests that declines in the seasonal extent and duration of sea ice, owing to climate change, have led to declines in “ice-loving” Adélie penguin (*Pygoscelis adeliae*) populations, while “ice-avoiding” chinstrap penguin (*P. antarctica*) populations have increased (1-5). However, 30 years of field studies in the WAP, coupled with more regional surveys throughout the Scotia Sea, refute this hypothesis; both Adélie and chinstrap penguin populations in this region are declining dramatically. Here, we present evidence supporting an alternative, more robust, hypothesis that explains both increases and decreases in penguin abundance as a result of changes in abundance of Antarctic krill (*Euphausia superba*) in the SS region. Linking trends in penguin abundance with trends in krill biomass can explain why populations of both Adélie and chinstrap penguins increased after seals and baleen whales were over-harvested (6) and, more recently, are decreasing in response to climate change. Thus, while the “sea-ice hypothesis” predicts that chinstrap penguins will benefit from climate change, the “krill-biomass hypothesis” leads to the contrasting prediction that chinstrap penguins are highly vulnerable to the current regime of climate warming.

SUMMARY OF FINDINGS AS RELATED TO NOMINATED AGENDA ITEMS

Agenda Item	
3.2	This paper links trends in penguin abundance with trends in krill biomass to explain why populations of both Adélie and chinstrap penguins increased after seals and baleen whales were over-harvested (6) and, more recently, are decreasing in response to climate change. It refutes the “sea-ice hypothesis” which predicts that chinstrap penguins will benefit from climate change, and presents data that support the contrasting prediction that chinstrap penguins are highly vulnerable to the current regime of climate warming.

Chinstrap penguins: misunderstood and vulnerable monitors of ecosystem changes in the Scotia Sea region of Antarctica

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Sea ice plays a critical role in structuring ecosystem dynamics throughout the Scotia Sea (SS) region, and variations in ice extent are hypothesized to affect predator populations in this area directly. A paradigm guiding recent research in the Western Antarctic Peninsula (WAP) region of the SS, the "sea-ice hypothesis", suggests that declines in the seasonal extent and duration of sea ice, owing to climate change, have led to declines in "ice-loving" Adélie penguin (*Pygoscelis adeliae*) populations, while "ice-avoiding" chinstrap penguin (*P. antarctica*) populations have increased (1-5). However, 30 years of field studies in the WAP, coupled with more regional surveys throughout the Scotia Sea, refute this hypothesis; both Adélie and chinstrap penguin populations in this region are declining dramatically. Here, we present evidence supporting an alternative, more robust, hypothesis that explains both increases and decreases in penguin abundance as a result of changes in abundance of Antarctic krill (*Euphausia superba*) in the SS region. Linking trends in penguin abundance with trends in krill biomass can explain why populations of both Adélie and chinstrap penguins increased after seals and baleen whales were over-harvested (6) and, more recently, are decreasing in response to climate change. Thus, while the "sea-ice hypothesis" predicts that chinstrap penguins will benefit from climate change, the "krill-biomass hypothesis" leads to the contrasting prediction that chinstrap penguins are highly vulnerable to the current regime of climate warming.

A current paradigm of Antarctic ecology is that sea-ice variability is a primary driver of penguin population trends. As sea-ice decreases in the SS region, the Adélie penguin, which favors pack-ice habitat in winter, should decline in population size, while the closely related chinstrap penguin, which forages in ice-free water in the winter, should increase (1-5). The foundation for this hypothesis was based on observed decreases in nesting populations of Adélie penguins and increases in chinstrap penguins following winters of low sea-ice in the South Shetland Islands (1, 7). Ice has been less extensive in recent years and Adélie penguin populations have declined, as predicted. However, in contrast to expectations, there is now overwhelming evidence that chinstrap penguin populations are also declining throughout the SS region.

[Insert Figure 1 here]

At mixed species colonies in the South Shetland Islands, Adélie and chinstrap penguins have experienced >50% overall declines within the last 30 years (Figure 1A). Moreover, since 1987, inter-annual changes in Adélie and chinstrap breeding populations have been positively correlated (Pearson's $r = 0.7$, $p<0.001$, $n=20$). This contrasts with the negative correlation observed from 1977 to 1986 (7) that defined the "sea-ice hypothesis" ((1) (Pearson's $r=-0.80$, $p=0.03$, $n=7$, Figure 1B). During the first decade of our studies, approximately 40% of the penguins banded as fledglings recruited back to natal colonies, and first-time breeders constituted 20-25 % of the annual breeding population (Figure 1C and 1D). Analyses of cohorts, during these early years, revealed a strong effect of winter sea-ice on juvenile recruitment; young Adélie penguins recruited heavily to their natal colonies following cold, winters with extensive sea ice, while juvenile chinstrap penguins exhibited the opposite affinity, migrating to natal colonies following warm, ice free winters (8). When juvenile penguin survival rates were high, variability in winter sea-ice extent caused the strong, negatively correlated changes in breeding populations (1, 7). However, the survival rates of juveniles of both species declined dramatically in the late 1980s (8). Presently, only 10% of the penguins banded as fledglings survive to return to our study site (Figure 1d) and first-time breeders comprise <5 % of the annual breeding population (Figure 1c). Adélie and chinstrap penguin breeding populations are no longer dominated by the influx of large numbers of first-time breeders and thus, the impact of contrasting juvenile recruitment patterns on annual population estimates of the two species is now lost (Figure 1b).

[Insert Table 1 here]

Population declines at our study sites in the South Shetland Islands are not an anomaly; Adélie and chinstrap penguin populations have declined concurrently region wide (Table 1). Both species have experienced significant population declines during the past 30 years in the South Orkney Islands (9) and at colonies in the Antarctic Peninsula region (10). In the South Sandwich Islands, long considered the heart of the chinstrap penguin's distribution, both Adélie and chinstrap penguin populations have declined by more than 50% (11). Variability in sea ice remains a primary physical force in the SS region; however, we suggest that sea-ice is not directly driving penguin population trends; rather, it is one of several factors that mediate prey availability to penguins. Krill is the dominant diet item for nearly all vertebrates in the SS region, including Adélie and chinstrap penguins (7, 17-24). Large-scale changes in krill biomass alone explain both why populations of Adélie and chinstrap penguins increased via competitive release, following the harvesting of the whales and seals in this region (6) and, more recently, why they have decreased as a result of climate change. However, these larger populations of penguins were not sustained for long, and, as we have described herein, Adélie and chinstrap penguin populations are now declining (Table 2, and refs.). The recent declines may be a consequence of the return of whales and seals to the Southern Ocean in the present post-whaling and sealing era. Concomitantly, increasing temperatures and reductions in sea ice have altered the physical environment necessary to sustain large krill populations.

[Insert Table 2 here]

Abundance and biomass trends in krill populations in the SS region exhibit large inter-annual variability, owing to the infrequent occurrence of recruitment events (25, Figure 2A). Results from annual acoustic and net surveys of krill populations in the South Shetland Islands over this time period suggest that the magnitude of krill recruitment events has declined, while the average time between recruitment events (4-5 years) has remained fairly consistent (25; Figure 2A). The decline in recruitment strength is an important factor determining the amount and mean size of krill available for recently fledged penguins. Both Chinstrap and Adélie penguin fledging weights have declined (8) and therefore each has less of a buffer against low krill abundance as they depart their breeding colonies at the end of the summer. Sea-ice extent and duration have been correlated with the reproductive success of krill, and in years following winters with expansive ice area and temporal duration, krill reproductive success increases (26). Mean annual sea-ice extent in the SS region is inversely related to mean annual air temperature (Figure 2B) and the rapid warming experienced in the South Shetland Islands (12, 13) is correlated with regional declines in sea-ice extent and duration affecting krill productivity (27). Long-term climate driven declines in krill abundance are evident over the SS region; krill density has declined by almost 80% from the early 1970s to the present, and that the decline was associated with reductions in sea ice (27). The decline in reproductive capacity associated with the overall decline in sea-ice suggests that food resources for penguins and other predators will continue to decline in the near future.

[Insert Figure 2 here]

There is now overwhelming evidence to confirm significant declines in both Adélie and chinstrap penguin populations throughout the SS region and to refute the hypothesis that Adélie and chinstrap population changes are directly but inversely related to sea ice (1-5). If, as predicted, the warming trend continues (13, 42), winter sea-ice will be absent from much of the SS region, krill abundance will remain low and episodic (25, 26) and Adélie and chinstrap penguin populations will likely continue to decline. This is particularly critical for chinstrap penguins because this species breeds almost exclusively in the SS region where they have sustained declines in excess of 50% throughout their breeding range. Chinstrap penguins have no southern breeding refuges; unlike Adélie penguins, which, while experiencing similar declines as chinstrap penguins in the SS, are buffered by having large, stable populations in the Indian Ocean and Ross Sea sectors of Antarctica. Given the magnitude of their population declines, the predictions of increasing warming in this region (42) and the links between climate change and reductions in krill biomass (26), the obligatory food of the chinstrap penguin, we suggest that chinstrap penguin populations should be carefully monitored and their status regularly reviewed. Long thought to be ecological winners in the climate-warming scenario (1-5), the chinstrap penguin is instead among the most vulnerable species affected by climate warming.

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43. This research was conducted as part of NOAA's Antarctic Marine Living Resources Program(AMLR). It was supported by NOAA and by grants from NSF's – Office of Polar Programs. Further support and assistance was provided by the Lenfest Ocean Program of the Pew Charitable Trust and the Oceanites Foundation.

Figure 1.

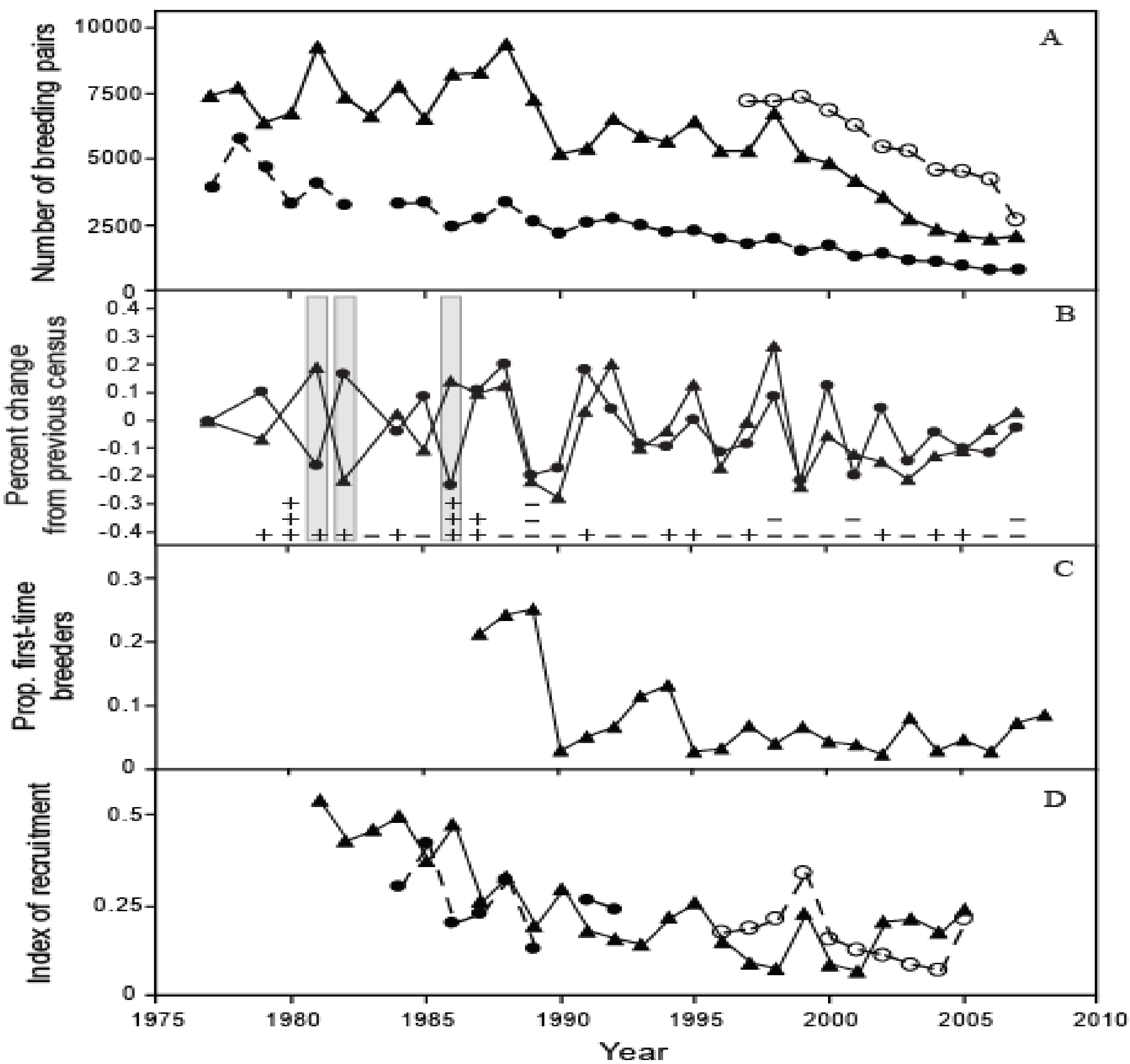

Figure 1. Closed circles (●) indicate chinstrap penguins in Admiralty Bay, King George Island (AB). Open circles (○) indicate chinstrap penguins at Cape Shirreff, Livingston Island (CS). Closed triangles (▲) indicate Adélie penguins in AB. A) Number of breeding pairs of Adélie and chinstrap penguins at all AB and CS colonies. These are CCAMLR-Ecosystem Monitoring Program data and include counts from other researchers and interpolations to estimate total abundance in some years. B) Percent change in breeding population size at AB colonies. The chinstrap data from 1978-1987 are from Copacabana colonies only (8). Data from 1988 to present are from all AB colonies. Grey bars highlight the years where the percent change in Adélie and chinstrap breeding populations exceed 10% in opposite directions. Horizontal line indicates the zero change. C) Proportion of first–time breeders in the population. D) Index of recruitment, based on analysis by (8). Chinstrap recruitment prior to 1984 is excluded in our analysis due to inconsistent resighting effort.

Figure 2.

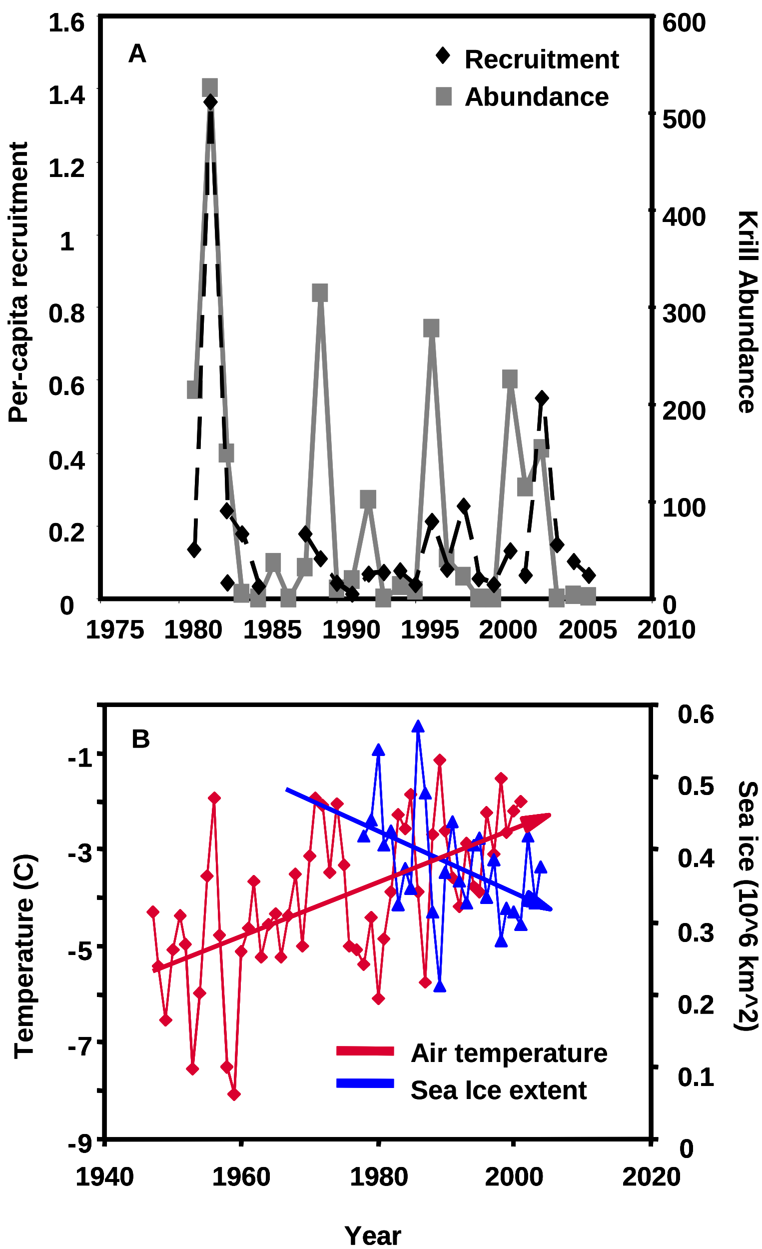

Figure 2. A) Time series of per-capita krill recruitment and krill abundance between 1980 and 2006 for the Elephant Island region of the South Shetland Islands, derived from annual net-tow surveys of the region (25). (B) Mean annual (January to December) temperature (°C) and sea-ice extent (>15% ice concentration) time series in the Antarctic Peninsula. Air-temperature and sea ice extent are significantly correlated ($r>-0.7$, $p<0.05$) over the 30 year times series.

Table 1. Average annual percent changes in the abundances of Adélie and chinstrap penguins from breeding colonies in the Scotia Sea. Averages are weighted by absolute changes in abundance and are limited to colonies where data exist from the mid 1970s to present with a minimum of 10 years between the first and last counts.

	Adélie	Chinstrap
Western Antarctic Peninsula	-0.22	-4.40
South Orkney Islands	-4.50	-1.90
South Sandwich Islands	-3.90	-4.40

Adélie colonies from the WAP are at Devil Island[10], Penguin Point[10], Berthelot Islands[10], Booth Island[10], Detaille Island[101], Fish Islands[10], Petermann Island[10], Yalour Islands[10], Penguin Island[35], Palmer Station[3], and Stranger Point[38]. Adélie colonies from the South Orkney Islands are at Shingle Cove[1], Watson Point[4], and Signy Island[9]. Chinstrap colonies from the WAP are Cecilia Island[10], Entrance Bay[10], Hannah Point[10], President Head[10], Eckener Point[10], Georges Point[10], Hydrurga Rocks[10], Orne Islands[10], Useful Island[10], Waterboat Point[10], Booth Island[10], Penguin Island[35], Chabrier Rocks[36], Palmer Station[3], and Harmony Point[38]. Chinstrap colonies from the South Orkney Islands are at Cape Robertson[38], Pirie Peninsula[38], Watson Peninsula[38], South Coast[38], Port Martin[38], and Signy Island[9]. Specific colonies from the South Sandwich archepeligo[11]are not identified.

Table 2. Harvesting levels and population trends for krill dependent predators in the Southern Ocean and Western Antarctic Peninsula (WAP) regions from the early 1800s to the present.

Take

SPECIES	LOCATION	1800-1900	1900-50	1950-75	1975-2000	2000-present	References
Small Baleen	S. Ocean	Low/Moderate	High		-	-	28, 29
Large Baleen	S. Ocean	-	High		-	-	28, 29
Fur Seal	WAP	High	-		-	-	30-32
Finfish*	WAP	-	-		High	Low	33

Population Trend

SPECIES	LOCATION	1800-1900	1900-50	1950-75	1975-2000	2000-present	References
Small Baleen	S. Ocean	Decrease	Decrease		-	Increase	28, 29
Large Baleen	S. Ocean	?	Decrease		-	Increase	28, 29
Fur Seal	WAP	Decrease	-	Increase	Increase	Increase/Stable	30-32
Finfish*	WAP	?	?	?	Decrease	Stable?	33
Chinstrap penguin	WAP	?	?	Increase	Decrease	Decrease	7-10, 14, 34-41
Adélie penguin	WAP	?	?	Increase	Stable/Decrease	Decrease	7-10, 14, 34-41

***Champsocephalus gunnari* and *Notothenia rossii*