LIMNOLOGY and OCEANOGRAPHY

Cyclical prey shortages for a marine polar predator driven by the interaction of climate change and natural climate variability

Amanda C. Lohmann [1]*, Joseph P. Morton [1,2], Oscar M. Schofield [3], Douglas P. Nowacek [1]
[1]Department of Marine Science and Conservation, Duke University Marine Laboratory, Beaufort, North Carolina, USA
[2]Department of Environmental Engineering Sciences, University of Florida, Gainesville, Florida, USA
[3]Department of Marine and Coastal Sciences, Rutgers University, New Brunswick, New Jersey, USA

Abstract

Between 1992 and 2018, the breeding population of Adélie penguins around Anvers Island, Antarctica declined by 98%. In this region, natural climate variability drives five-year cycling in marine phytoplankton productivity, leading to phase-offset five-year cycling in the size of the krill population. We demonstrate that the rate of change of the Adélie breeding population also shows five-year cycling. We link this population response to cyclical krill scarcity, a phenomenon which appears to have arisen from the interaction between climate variability and climate change trends. Modeling suggests that, since at least 1980, natural climate variability has driven cycling in this marine system. However, anthropogenic climate change has shifted conditions so that fewer years in each cycle now prompt strong krill recruitment, triggering intervals of krill scarcity that result in drastic declines in Adélie penguins. Our results imply that climate change can amplify the impacts of natural climate oscillations across trophic levels, driving cycling across species and disrupting food webs. The findings indicate that climate variability plays an integral role in driving ecosystem dynamics under climate change.

A growing body of theory suggests that climate variability can powerfully impact ecological responses to climate change (Jackson et al. 2009; Lawson et al. 2015; Terry et al. 2022) and that studies on longer-term climate trends may miss key dynamics if shorter-term climate variability is discounted (Thompson et al. 2013; Helmuth et al. 2014; Gardner et al. 2021). Climate variability comprises the natural fluctuations that occur in climate metrics (such as temperature, precipitation, and wind velocity) as a result of both stochastic and predictable processes in the Earth's climate system (Ghil 2002). This variability overlies longer-term means or trends. Some well-characterized modes of climate variability include named climate oscillations such as El Niño Southern Oscillation (ENSO) or the Southern Annular Mode (SAM), which can drive strong ecosystem responses (Stenseth et al. 2002). Thus far, most ecological work on the combination of shorter-term variability and longer-term trends has focused on responses of individual populations (Jackson et al. 2009; Lawson et al. 2015; Gardner et al. 2021). Connected responses across trophic levels, in contrast, are understudied (Vázquez et al. 2017; Terry et al. 2022). The ability to anticipate and respond to the ecological impacts of anthropogenic climate change necessitates a more robust understanding of the ways that climate change interacts with climate variability to drive changes across whole ecosystems (Chowdhury and Ndiaye 2017; Vázquez et al. 2017; Terry et al. 2022), particularly in marine environments in which climate oscillations are especially impactful (Stenseth et al. 2002, 2003).

A key mechanism by which climate variability influences ecosystems is by driving fluctuations in resource availability, which can shape ecosystem structure and functioning from the bottom up. A number of ecosystems rely on periodic pulses in primary productivity that result from interannual climate variability. In arid lands, for example, ENSO produces periodic rains that prompt eruptive plant growth (Yang et al. 2010). Similarly, North Atlantic Oscillation weather patterns influence tree masting (Ascoli et al. 2017, 2021) as well as coastal phytoplankton productivity (Tiselius et al. 2016), and some regions of the Southern Ocean experience unusually strong diatom blooms in response to periodic shifts in wind and ice related to the SAM (Saba et al. 2014; Soppa et al. 2016). Such episodic resource availability can lead to a variety of ecological impacts, including skewed population age structures, local extinctions, and species

*Correspondence: amanda.lohmann@duke.edu

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coexistence that would not otherwise be sustained (Ostfeld and Keesing 2000; Drinkwater et al. 2003; Tam et al. 2008; Yang et al. 2010; Edwards et al. 2010, 2013). For example, above average recruitment occurs in cod in the North Atlantic and Antarctic krill in the Southern Ocean as a result of periods of unusually high phytoplankton productivity in these respective systems, leading to skewed demography in these consumer populations (Drinkwater et al. 2003; Saba et al. 2014). As anthropogenic climate change intensifies, it is likely to alter the frequency, duration, and magnitude of peaks in resource availability in many systems. Such shifts may result in ecosystem-level responses that are fundamentally related to the variability itself, and thus poorly predicted by long-term averages alone (Yang et al. 2008; Schmidt et al. 2014; Czeszczewik et al. 2020).
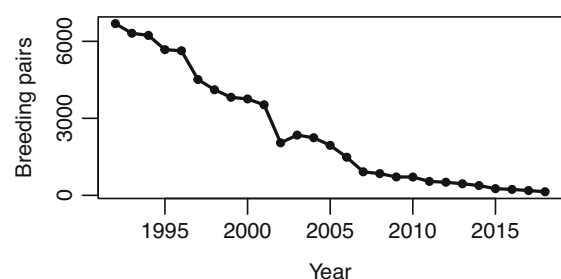
The marine region around the western Antarctic Peninsula is experiencing strong effects from both anthropogenic climate forcing and climate variability, making it an ideal system in which to study the interplay between these two drivers. Since the 1950s, the region has been one of the fastest-warming on Earth (Vaughan et al. 2003), with temperatures increasing by $0.54°C$/decade between 1951 and 2011 (Turner et al. 2014). Resource availability in this system has been strongly periodic since at least 1995. Summer primary productivity oscillates with ~ 5-year periodicity, mediated by a suite of abiotic factors that influence water column stability and combine to create "set-up events" that lead to particularly dense phytoplankton blooms roughly every 5 years (Saba et al. 2014).

As in many marine food webs, energy that reaches the upper trophic levels in the marine ecosystem along the western Antarctic Peninsula passes primarily through a single forage species (Cury et al. 2000; Bakun 2006; Padovani et al. 2012), in this case the Antarctic krill (*Euphausia superba*, hereafter "krill") (Atkinson et al. 2014). Krill are euphausiid crustaceans with lifespans of 6+ years (Reiss 2016). Krill spawn in summer; the larvae hatch that same season, then overwinter under sea ice before emerging as postlarval recruits in spring. Krill recruitment is heavily influenced by oscillations in primary productivity because krill feed heavily on diatoms (Saba et al. 2014; Steinberg et al. 2015). Peaks in summer primary productivity (related mainly to diatom blooms) that occur every ~ 5 years drive corresponding pulses in krill recruitment (Saba et al. 2014; Steinberg et al. 2015). The oscillations in krill recruitment lead in turn to oscillations in krill population size (the "krill cycle"; Saba et al. 2014; Steinberg et al. 2015). The impact of climate change on this process has become evident over the last several decades. Across the northern Southwest Atlantic sector of the Southern Ocean (latitudes 50°S to 65°S), average krill recruitment showed an overall decline between 1976 and 2014, mirroring a change in a dominant climate mode in this region (the SAM) thought to be driven by anthropogenic climate change (Atkinson et al. 2019). This shift in SAM has resulted in conditions that are warmer, cloudier, and windier, which may inhibit krill recruitment by reducing the prevalence of phytoplankton blooms on which krill feed (Atkinson et al. 2019) and

potentially by reducing sea ice habitat that larval krill rely on during winter (Meyer et al. 2017).

Adélie penguin populations along much of the Antarctic Peninsula have also declined in the last several decades (Hinke et al. 2007; Trivelpiece et al. 2011). The breeding population in the area around Palmer Station (Anvers Island, western Antarctic Peninsula) held mostly steady through the 1980s (Woehler et al. 2002) but decreased by 98% between 1992 and 2018 (Fig. 1). Adélies in this region feed primarily on krill (Trivelpiece et al. 1987; Palmer Station Antarctica LTER and Fraser 2020*a*). One hypothesis is that the Adélie decline is related to a decline in krill population that in turn is linked to increased temperatures and decreased sea ice (Lynnes et al. 2004; Hinke et al. 2007; Trivelpiece et al. 2011). However, studies based on data from the Palmer long-term ecological research (LTER) monitoring project have suggested that decreased krill availability is unlikely to be a cause of decline of Adélie colonies in the Palmer area. Despite evidence of decreased krill recruitment over the past 50 years in the north of the Southwest Atlantic sector (Atkinson et al. 2019), the krill population in the Palmer LTER study region along the western Antarctic Peninsula has oscillated around a roughly steady mean since monitoring began in 1993, prompting the conclusion that a stable krill population is unlikely to be a cause of decreases in the Adélie population (Cimino et al. 2016*a,b*). Additionally, a bioenergetic model indicated that the mean quantity of krill biomass, averaged across summers 1995 through 2006, was sufficient to support existing Adélie colonies (Sailley et al. 2013).

Here, we first examine whether Adélie population dynamics are related to krill limitation, and we then interrogate the impact that climate change and climate variability together have on the Adélie population by driving bottom-up processes. We first find evidence that Adélie penguins around Anvers Island are krill-limited due to periods of very low krill recruitment, a phenomenon that may not be captured by analyzing the average ecosystem state across multiple years. We find that periodicity in the Adélie penguin population's growth rate tracks periodicity in both krill population size and

Fig. 1. Annual Adélie breeding pair census counts from the Palmer LTER project. Each census count indicates the total number of breeding pairs that nested on islands around Anvers Island during that year's breeding season. Between the 1992 and 2018 seasons, the number of Adélie breeding pairs declined by 98%.

primary productivity. Our analyses suggest that this shared periodicity occurs because intervals of low krill recruitment cause food limitation for Adélies, resulting in steep declines in the Adélie population. Modeling further suggests that primary productivity has oscillated with roughly the same frequency during the past ~45 years, but in recent decades climate change has pushed down the mean, decreasing the number of years in a cycle that prompt high krill recruitment and increasing the number of years in which penguins suffer prey shortages. In this way, climate change has amplified the ecological impact of climate variability, translating abiotic periodicity into offset oscillations across three trophic levels. Our results do not rule out the possibility that other abiotic or biotic factors are contributing to Adélie decline, but they indicate that Adélie penguins are krill-limited and that years of low krill represent serious prey shortages for these penguins.

Materials and methods

Monitoring data

We used monitoring data from the Palmer LTER project to examine three steps in a trophic chain from phytoplankton, through Antarctic krill, to Adélie penguins. Each dataset spanned between 22 and 26 years within the 1992–2018 time period. The Palmer LTER project collects data during the spring/summer season. We refer to these field seasons by their January year (for example, data collected in November 1991 are referred to as belonging to year 1992).

Ocean sampling grid

The Palmer LTER takes measurements of primary productivity and performs net tows in January–February on an ocean sampling grid, which is located along the western Antarctic Peninsula (Fig. 2). Following Steinberg et al. (2015), based on latitudinal shifts in biotic and abiotic factors we considered the grid to have three regions: north, south, and far south. Palmer Station (Anvers Island) is located near the northeast corner of the LTER sampling grid; we restricted analyses to the north of the grid (an area of 200 by 200 km) as this is the region spatially closest to and therefore likely to have the most biotic connectivity with the Adélie penguin colonies in our study. When we refer to the "sampling grid," we are referring to the northern sampling grid unless otherwise stated.

The northern grid has three sampling gridlines running perpendicular to the peninsula, spaced 100 km apart (gridlines 400, 500, and 600) (Fig. 2). Each gridline has a series of sampling stations spaced 20 km apart. We limited our analyses to nine stations along each line (Sta. 40, 60, … 200), as the resulting region was sampled reliably across all years in the Palmer LTER at-sea time series (1993–2017). In several cases, a particular station was sampled multiple times in a single year, sometimes weeks apart; in each case, we took only the data from the first sampling event to increase the comparability of data between years. In 2009, the LTER sampling grid was extended south along the peninsula (additional gridlines 100, 0, and −100 were added) and the density of stations sampled along each gridline was decreased, with the result that yearly means contain more samples in 1993–2008 than in 2009–2017.

Primary productivity data

The Palmer LTER measures primary productivity (the rate of carbon uptake in units of mg m^{-3} d^{-1}) via incubation of water collected at multiple depths in the water column at sampling stations. Full methods are available from Schofield et al. (2018). Primary productivity data (Palmer Station Antarctica LTER et al. 2020) spanned 1995–2017. The irradiance level chosen as the bottom of the euphotic zone (and therefore the cutoff for sampling) varied slightly between years. To avoid any resulting bias, we used primary productivity integrated linearly to 30 m depth, a depth that most CTD casts across the grid exceeded at least slightly. Casts that went to at least 28 m were included and extrapolated to 30 m, with the remaining depth to 30 m assumed to have the same primary productivity as the deepest sampled depth.
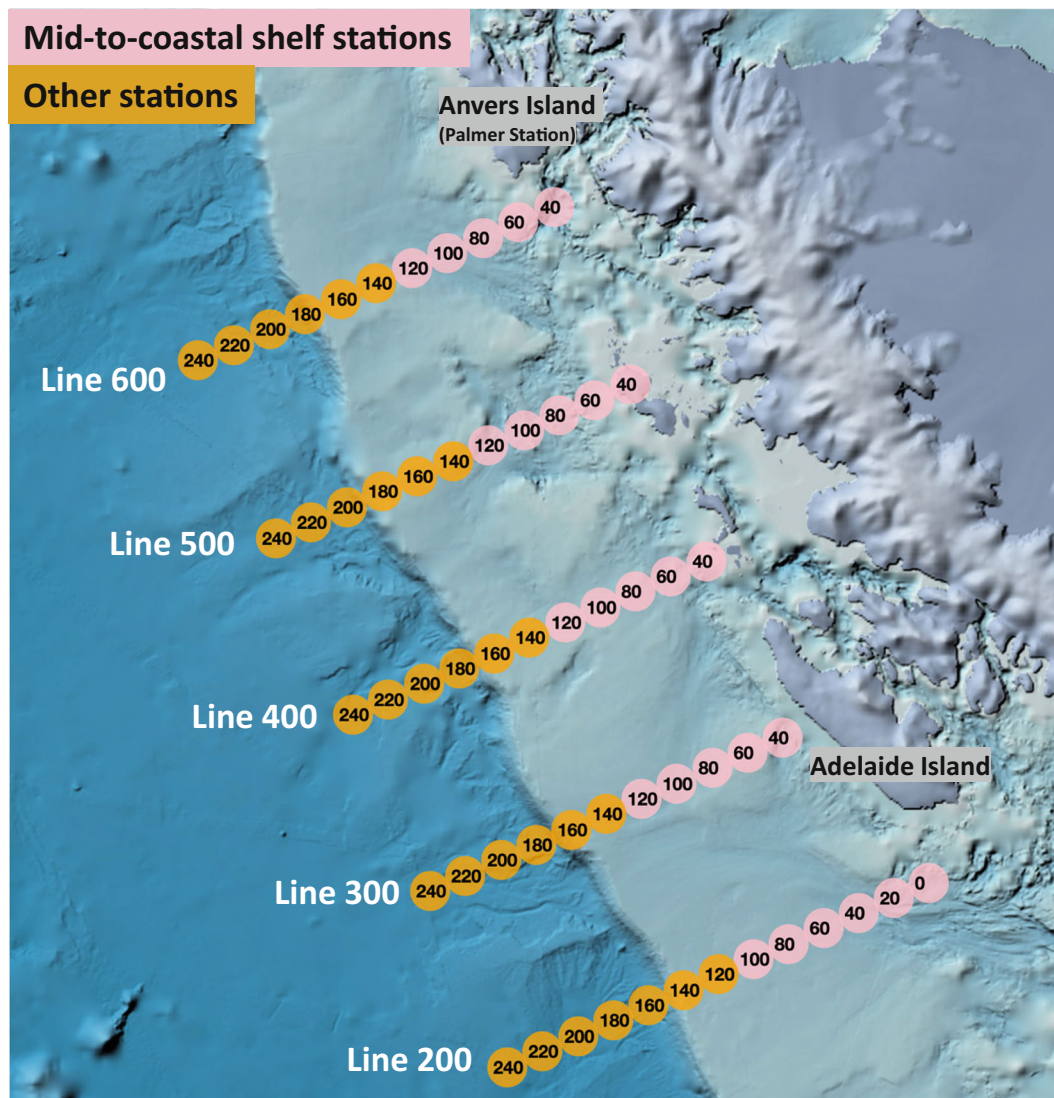
The number of stations at which primary productivity was measured ranged from 13 to 26 for 1995–2008, and 6 to 9 for 2009–2017. Primary productivity data were not available for 2016. For use in generating the spectral density (see Results and Discussion—Periodicity in the western Antarctic Peninsula marine ecosystem), this missing value was linearly interpolated based on the two adjacent values. For correlations/linear regressions, data from this missing year were not included.

Euphausiid density

Densities (number of individuals per 1000 m^3 of water) of *E. superba* and the smaller euphausiid *Thysanoessa macrura* were measured by the Palmer LTER at grid stations via net tows (Palmer Station Antarctica LTER and Steinberg 2020*a*). Full methods are described by Ross et al. (2008) and Steinberg et al. (2015). In brief, tows were performed with a square fixed-frame net with 700 μm mesh that measured 2 m a side. The net was towed obliquely from the surface to a depth of 120 m. A General Oceanics flowmeter mounted on the net frame measured the volume of water that was sampled. Net tow data spanned 1993–2017. The number of stations at which euphausiid density was measured ranged from 23 to 26 in 1993–2008 and 7 to 9 in 2009–2017.

To identify extremely high tow counts that would disproportionately affect the calculated means, we used interquartile range analysis. For each species, we pooled tows from all years (484 tows) and performed interquartile range analysis on the densities from all tows that contained at least one individual (459 tows for *E. superba*, 468 tows for *T. macrura*). We removed one major outlier for *E. superba*: a tow from 1993 that was 213 interquartile ranges above the third quartile.

Fig. 2. The Palmer LTER ocean sampling grid. Circles indicate sampling stations and are labeled with the station number. Stations are spaced at 20 km intervals along each gridline. Gridlines are spaced 100 km apart from each other. The grid is divided into three regions: north (gridlines 400 to 600), south (gridlines 200 to 300), and far south (gridlines -100 to 100, not pictured).

Krill lengths

Body length data were collected by the Palmer LTER for a subset of Antarctic krill in tows for years 1997–2017, excluding 1998 and 2008 (Ross and LTER 2014; Palmer Station Antarctica LTER and Steinberg 2020*b*). Body length was measured from the tip of the rostrum to the blunt end of the uropod (standard 1 measurement, Mauchline 1980). In 2009–2017, if ≤ 100 krill were in a tow, body length was reported for all krill in the tow; otherwise, a random subsample of 100 krill were measured. Prior to 2009, a less systematic subset of krill was measured in some tows.

For population density estimates, we used only tows performed at predetermined grid stations to enhance the comparability of samples between years and to avoid bias from

unplanned tows performed to target an observed krill swarm. However, in analyses involving krill length, we included all tows within the sampling grid in order to broaden our sample size of individual krill and increase the accuracy of our size distribution. For density estimates, we used only tows performed at predetermined grid stations. We calculated the average length of krill in a given year as a weighted average based on the total number of krill in each tow and the mean length of krill in that tow.

We additionally used data spanning 1978–2010 from KRILLBASE, a compiled database of krill counts and body lengths from net tows performed across the Southern Ocean (Atkinson et al. 2017, 2020). To examine body length distributions over time, we combined krill length data from

KRILLBASE and the Palmer LTER project. We followed Atkinson et al. (2019) and used all measured krill body lengths from tows in the Southwest Atlantic sector (− 80° to − 20° longitude) below − 60° latitude. We excluded winter tows, using only tows performed in the months October through April. Tows with body length measurements were available for years from 1976 to 2017, except 1977. We used only years with at least 1000 krill body length measurements, which excluded 1980 and 1987. The majority of KRILLBASE lengths were taken using the "Discovery" measurement (AT) (Tarling et al. 2016), while the Palmer LTER takes lengths using the standard 1 measurement (S1). The two methods can differ by 1–2 mm, as the AT method measures from the anterior of the eye (as opposed to the anterior of the rostrum in S1) and to the tip of telson (as opposed to the posterior of the uropods in S1) (Siegel 1982, 2016). However, the two measurements are tightly correlated, and a linear equation derived empirically by Siegel (1982) can convert between the two. When combining with KRILLBASE, we converted the Palmer LTER measurements from S1 to AT measurements, though we found that not performing the conversion had such a small impact on our statistical results that it did not affect the values within the number of digits we reported.

Krill size classes

We defined recruits as krill < 31 mm in length (Saba et al. 2014). We defined "large krill" as krill ≥ 46 mm in length, approximately age 4+ (Fraser and Hofmann 2003; Reiss 2016).

Adélie census counts

Adélie breeding pair census counts (Palmer Station Antarctica LTER and Fraser 2020b) were taken annually by the Palmer LTER project at colonies near Palmer Station (Anvers Island, Antarctic Peninsula) once nests had been established for the breeding season. These data spanned 1992 to 2018. We calculated the proportional change in breeding population for each year n as $(c_{n+1} - c_n)/c_n$, where c_n indicates the census count in year n.

Adélie diets

The Palmer LTER project collects stomach contents via stomach lavage from a subset of birds returning from foraging trips (Palmer Station Antarctica LTER and Fraser 2020a). The weight of three prey types (*E. superba*, *T. macrura*, and fish) in each sample is reported (Palmer Station Antarctica LTER and Fraser 2020a). The body lengths of all *E. superba* in each sample are reported in 5 mm bins (Palmer Station Antarctica LTER and Fraser 2020c). We used Adélie stomach content data spanning 1992–2017. In most years, data were only taken in January and February; to avoid bias, we removed any samples taken outside of these months.

We calculated the overall proportions of *E. superba*, *T. macrura*, and fish in the diet by pooling the weight of all prey items from diet samples in a year and finding the proportion of

weight attributable to each prey item. Dietary proportions of *E. superba*, *T. macrura*, and fish therefore represent proportions by weight (not individuals). The dietary proportion of items besides krill was calculated as the proportion made up of *T. macrura* plus fish.

We also calculated the proportion of krill in a given body length bin in Adélie diets in a given year. We pooled all krill in Adélie diet samples from that year and calculated proportions for the pool. Antarctic krill size class proportions therefore represent proportions of individuals (not weight).

Because the diet samples reflect the stomach contents of Adélies upon their return to land from foraging trips, these samples represent the diet fed to chicks but likely undercount the fish consumed by adults at sea, as fish are digested much faster than krill (Karnovsky 1997) (see Results and Discussion—Importance of krill as a food source). For simplicity, we refer to the contents of these samples as the Adélie diet, but the amount of fish consumed by adults is likely underestimated by these samples.

Adélie reproductive success metrics

Each breeding season, the Palmer LTER project monitors the reproductive success of a subset of nesting Adélie pairs (Palmer Station Antarctica LTER et al. 2022a,b). Each egg is tracked from laying until either the resulting chick is successfully fledged, or death occurs. Fledging weight of the chicks is recorded. We used three metrics of reproductive success. Adélie nesting females will lay either one or two eggs, and the first metric was the number of monitored nests with one egg vs. the number with two eggs. The second metric was the proportion of laid eggs that resulted in a successfully fledged chick, and the third metric was the fledging weight of the chicks.

Sea ice

We used sea-ice data reported by the Palmer LTER project (Palmer Station Antarctica LTER and Stammerjohn 2020a,b). We examined eight sea-ice metrics as defined by Stammerjohn et al. (2008). These metrics are day of advance (first Julian day on which the sea-ice concentration exceeded 15% in that season's total sea-ice extent region for five consecutive days), day of retreat (first Julian day on which the sea-ice concentration fell below 15% and remained below that threshold for the remainder of the season), duration (elapsed time between day of advance and day of retreat), total sea-ice days (days between day of advance and day of retreat during which sea-ice concentration was above the 15% threshold), extent (size of region with at least 15% sea-ice concentration during that season's sea-ice maximum), area (size of area covered by sea ice during that season's maximum), and open-water area (area of open-water enclosed by the sea-ice edge, that is, extent minus area). We examined each of these eight metrics across four large-scale spatial extents (the entire western Antarctic Peninsula marine region, Antarctic Peninsula west coast to 80° W; the original Palmer LTER grid, lines 000–900; the original sampling grid,

lines 200–600; the new sampling grid, lines – 200-600); and the ∼ 50 km and ∼ 200 km penguin foraging areas around Anvers Island. Not all metrics were available for all spatial extents; in total, we used 45 combinations of metric and extent. We performed linear regressions between Adélie breeding pair change and each of these metrics over each of these extents.

Statistics

Data transformations

Prior to running parametric statistical tests, data that were strongly skewed were transformed to meet the assumption of normality.

We followed Steinberg et al. (2015) and, in analyses of primary productivity and euphausiid density, used the log anomalies of these variables, calculated as

$$A'_s = \log(\overline{A_y}/\overline{A})$$

where $\overline{A_y}$ is the mean density for year y, and $\overline{A}$ is the mean of the yearly means. We logit-transformed the proportion of *T. macrura* and fish in Adélie diets.

Calculations

All statistical calculations were performed in R, Version 1.0.143 (R Core Team 2020). Linear regressions were performed using the *lm()* function, cross-correlation was calculated using the *ccf()* function, periodograms were generated from the *spectrum()* function, and piecewise linear fits were calculated via the *piecewise.linear()* function in the package SiZer (Sonderegger 2020). All presented *p*-values are two-tailed.

Analyses

Longer-term krill recruitment consistency

As is the case with many species (Underwood and Keough 2001), the body size distribution of the krill population contains information about recent recruitment success (Quetin and Ross 2003; Saba et al. 2014). To extend our analysis of krill recruitment dynamics further back in time than the Palmer LTER dataset, we used krill body length data from net tow hauls recorded in KRILLBASE (spanning 1976–2010) combined with net tow data from the Palmer LTER (spanning 1997–2017). Using length distribution, we assessed whether the consistency of krill recruitment in the Southern Ocean's Southwest Atlantic sector has changed over time. As robust krill size distribution data were not available for several years between 1976 and 1990, we were not able to determine the frequency of recruitment events directly. Instead, we developed a metric to quantitatively describe the consistency of recruitment over time based on the body length distribution of the krill population in a given season (Supporting Information Fig. S1). The body length distribution captures the history of relative recruitment over the past ∼ 5–6 years (krill lifespan), as the size classes of strong cohorts will be over-represented while those of weak cohorts will be under-

represented. For a given season's body length distribution, if recruitment had been relatively consistent over the lifetime of the oldest extant cohort, then the length frequency distribution would resemble a wide normal distribution (Supporting Information Fig. S1a–c). This bell curve would span from the smallest size classes (∼ 20 mm) to the largest (∼ 65 mm). The spectrum of this distribution would be low frequency, with a wide wavelength. However, if there had been gaps in recruitment, the length frequency distribution would have higher frequencies in its spectrum, indicative of the narrow peaks created by gaps in recruitment (Supporting Information Fig. S1d–f). If there had only been 1 year of high recruitment, there would be a single, narrow peak, resulting in a smaller wavelength.

To calculate a metric of recent recruitment stability based on length frequency distribution, we first calculated the density function of each year's length frequency distribution using R's *density()* function. We then linearly interpolated the density function from 0 to 70 mm at intervals of 0.1 mm. We calculated the spectrum of this interpolated density function using R's *spectrum()* function. We then integrated the spectrum and found the length below which the spectrum contained 25% of its cumulative value. Body length distributions that reflect more gaps in recruitment would have spectra with more value at small lengths, while body length distributions that reflect consistent recruitment would have spectra with almost all value at higher lengths. We used this as a rough metric of whether recruitment had been steady over the history captured in the distribution, or whether there had been gaps (Supporting Information Fig. S1).
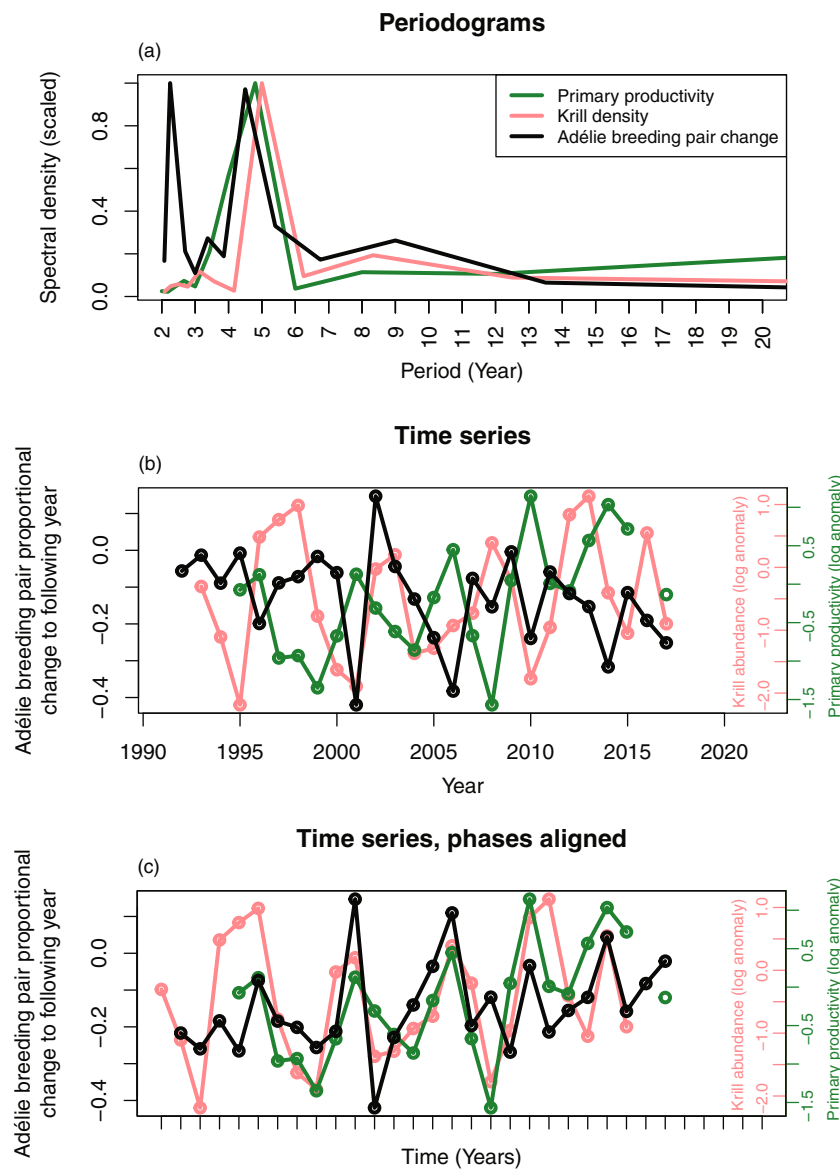
Longer-term modeled primary productivity

We modeled primary productivity from 1980 to 2017 based on available abiotic metrics, using variables identified by Saba et al.'s (2014) model of chlorophyll *a* (Chl *a*). We built linear models (no interactions) using monthly SAM from September to January, and the following ice indices for the original Palmer LTER grid (lines 0 through 600): day of sea-ice advance, day of sea-ice retreat, sea-ice duration, number of sea-ice days, sea-ice extent, and sea-ice area. We performed a stepwise model selection by AIC to find the best model. We then performed leave-one-out cross validation to check whether this model had predictive power for primary productivity.

Results and discussion

Periodicity in the western Antarctic Peninsula marine ecosystem

Our analyses of long-term monitoring data from the Palmer LTER (1993–2018) revealed that primary productivity, krill density, and the year-to-year proportional change in Adélie breeding pairs all showed ∼ 5-year periodicity (Fig. 3a). The cycles of the three measures were out-of-phase (Fig. 3b,c; Table 1). Primary productivity and change in Adélie breeding pairs were directly out-of-phase: when productivity was highest, Adélie

Fig. 3. (**a**) Unsmoothed, scaled periodograms showing similar periodicity in Adélie breeding pair annual proportional change near Palmer Station and the log anomalies of primary productivity and krill density on the north of the Palmer LTER ocean sampling grid. (**b**) Time series of Adélie breeding pair proportional change at colonies near Palmer Station, and log anomalies of primary productivity and krill density on the north of the Palmer LTER ocean sampling grid. (**c**) Time series of Adélie breeding pair proportional change, and log anomalies of primary productivity and krill density, with phases aligned based on cross-correlation (Table 1) to visually display shared periodicity.

Table 1. Correlations between Adélie breeding pair proportional change and log anomalies of primary productivity and krill density (Fig. 3). Lags determined by cross-correlation. Primary productivity and Adélie change are exactly out-of-phase; peaks in krill density lag both primary productivity peaks and Adélie change nadirs.

Variable 1	Variable 2	Lag of variable 2	Correlation direction	p	Adjusted R^2
Primary productivity	Adélie breeding pair proportional change	0 years	(−)	0.04 ($F_{1,20} = 5.049$)	0.16
Primary productivity	Krill	2 years	(+)	0.003 ($F_{1,19} = 11.867$)	0.35
Adélie breeding pair proportional change	Krill	2 years	(−)	0.03 ($F_{1,22} = 5.469$)	0.16

breeding pairs showed the steepest rate of decline from that summer to the next. Krill density was positively correlated with primary productivity with a lag of 2 years, and negatively correlated with Adélie breeding pair change with a lag of 2 years (Fig. 3).

To interpret this finding of shared ~ 5-year periodicity, we analyzed the relationships between these three trophic levels in greater detail. Combining these analyses with prior work, we find substantial evidence that the shared periodicity in primary productivity, krill density, and Adélie population change can be explained as follows. Primary productivity cycles due to underlying abiotic drivers (Saba et al. 2014). Cycling in primary productivity causes corresponding cycling, at a lag, in the krill population by driving recruitment (Saba et al. 2014; Steinberg et al. 2015). The cycle in krill drives a corresponding cycle in Adélies: when krill recruitment has been low for several years, Adélies become krill-limited, and they experience precipitously high overwinter mortality. We explore these ideas more fully in the following sections.

Abiotic source of periodicity for primary productivity

Using data from 1993 through 2011, Saba et al. (2014) found that abiotic conditions drove ~ 5-year cycling in Chl *a* in the waters around Palmer Station. High Chl *a* resulted from a confluence of factors, including high winter sea-ice extent and low spring wind speeds, that combined to create strong water column stability on a ~ 5-year cycle. Our study examined primary productivity across the northern Palmer LTER grid. In some systems, Chl *a* can be a useful proxy for primary productivity; we confirmed that summer primary productivity across our ocean sampling region was correlated with summer Chl *a* near Palmer Station as used in Saba et al.'s work (primary productivity vs. Palmer Sampling Station B Chl *a*, $p = 0.02$, adjusted $R^2 = 0.32$, $n = 15$, $F_{1,13} = 7.668$; primary productivity vs. Palmer Sampling Station E Chl *a*, $p = 0.008$, adjusted $R^2 = 0.36$, $n = 16$, $F_{1,14} = 9.454$) (Supporting Information Fig. S2). Our results suggests that similar forces drive phytoplankton growth in both offshore and nearshore waters along the western Antarctic Peninsula, and that the patterns that have driven ~ 5-year cycling in phytoplankton have continued after 2011 through at least 2018. We conclude that the observed cycling in primary productivity can be explained by the abiotic cycling elucidated by Saba et al. (2014).

Primary productivity as a driver of recruitment and population density in krill

Steinberg et al. (2015), working with data spanning 1993–2013, found that primary productivity was positively correlated with the population density of krill two summers later. We found the same result when examining the period 1993–2017. Given the previously elucidated positive effect of primary productivity on krill recruitment (Saba et al. 2014), Steinberg and colleagues hypothesized that a summer of high productivity is followed by two summers of high krill recruitment, leading to a

spike in krill population density two summers after the peak in productivity. Our findings were consistent with this interpretation. Primary productivity was positively correlated with the proportion of recruits in combined KRILLBASE and LTER net tows both one summer later ($p = 0.0001$, adjusted $R^2 = 0.57$, $n = 21$, $F_{1,19} = 27.038$) and two summers later ($p = 0.01$, adjusted $R^2 = 0.25$, $n = 21$, $F_{1,19} = 7.570$). Similarly, primary productivity was also positively correlated with the proportion of recruits in Adélie diets both one summer later ($p = 0.01$, adjusted $R^2 = 0.25$, $n = 21$, $F_{1,19} = 7.719$) and two summers later ($p = 0.04$, adjusted $R^2 = 0.15$, $n = 21$, $F_{1,19} = 4.581$). While more research is needed to understand this phenomenon, we hypothesize that the observed 2-year lag relates to the impact of high primary productivity on the condition of both larval krill and mature female krill. High primary productivity represents high food availability to krill, as high primary productivity in this system generally reflects large diatom blooms (Saba et al. 2014), and diatoms are the phytoplankton taxon on which krill prefer to feed (Quetin and Ross 1985; Haberman et al. 2003), though we note that a limitation of our study is that we are not able to analyze the impact of different phytoplankton assemblages (Quetin and Ross 1985). The correlation between summer primary productivity and the proportion of recruits the following summer may occur because high summer productivity leads to larval krill entering the winter in good condition, leading to high overwinter survival and above-average recruitment. Additionally, female body condition is correlated with higher recruitment the following the year (Steinke et al. 2021). We speculate that the correlation between high summer productivity and the proportion of recruits two summers later may result from the following phenomenon: high summer productivity results in females entering the winter in good condition and emerging the following summer in good condition, which results in earlier spawning. Earlier spawning results in a longer timeframe in which larvae are able to grow and feed before winter, which results in higher overwinter larval survival and increased recruitment 2 years after the high productivity event. In summary, though more research is needed on the mechanisms behind the lag, we conclude that the ~ 5-year periodicity in krill density is driven at an offset by the ~ 5-year cycling in primary productivity, via the latter's lagged effect on krill recruitment.

Krill recruitment events as drivers of krill population density and size distribution

Saba et al. (2014) found that summers of anomalously high primary productivity, occurring approximately every 5 years, led to strong krill recruitment events. This pattern resulted in the well-documented skewed demography of krill along the western Antarctic Peninsula, in which one or two strong cohorts (the result of episodic strong recruitment years) dominate the population and drive the abundance of krill (Quetin and Ross 2003; Fraser and Hofmann 2003; Saba et al. 2014; Ryabov et al. 2017). The skewed demography resulting from

episodic strong recruitment can be seen in the size of krill consumed by Adélie penguins each year (Saba et al. 2014; Fig. 4).

While robust krill size distribution data are available from our ocean sampling region, data allowing population density estimates are limited. Due to krill's patchy spatial distribution (Tarling and Fielding 2016), a large number of net tow samples are needed to yield abundance estimates of high precision (Wiebe and Holland 1968); however, LTER net tow sampling is sparse (7–26 net tows each summer). The low precision of the resulting density estimates may mask important relationships. We therefore examined whether metrics of krill size distribution could serve as a useful proxy for krill population metrics.

Each strong recruitment year produces a krill cohort that persists for ~ 5–6 years (Saba et al. 2014). As the dominant cohort ages, two critical changes can be observed. First, krill abundance decreases as mortality and export remove individuals from the population (Quetin and Ross 2003). Second, individual krill grow, and thus the average size of krill in the cohort increases (Quetin and Ross 2003; Saba et al. 2014; Fig. 4). We examined the relationship between krill size and krill density. We found that krill density as estimated from tows was negatively correlated with the proportion of large krill (length ≥ 46 mm, age $\sim 4+$) in tows ($p = 0.001$, adjusted $R^2 = 0.42$, $n = 19$, $F_{1,17} = 14.243$) as well as with the proportion of large krill in Adélie diets ($p = 0.005$, adjusted $R^2 = 0.26$, $n = 25$, $F_{1,23} = 9.589$; Supporting Information Fig. S3b). A question that should be addressed is whether size-dependent net avoidance could drive this pattern, since larger krill are faster swimmers than smaller krill (Hamner 1984) and are likely better able to evade nets. However, work from the South Shetland Islands also found a strong negative correlation between annual average size of krill in tows and annual

krill biomass estimated from acoustic measurements, in which net avoidance is not a factor (Reiss et al. 2008). We conclude that the proportion of large krill is negatively related to krill population density. The proportion of large krill is a metric that further reflects the age of the dominant krill cohort and therefore how much time has passed since a strong recruitment event (Supporting Information Table S1).
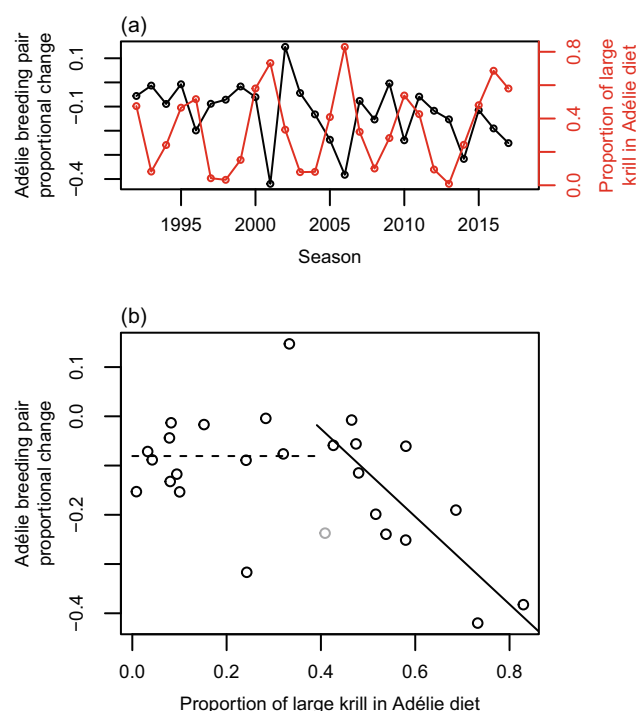
Cycling in krill as a driver of cycling in Adélie penguin breeding pairs

We investigated the relationship between Adélie breeding pair change and krill recruitment events. In the Palmer LTER time series, krill were the dominant prey item in Adélie diets during each summer sampling season, making up $94 \pm 10\%$ (mean $\pm$ SD) of the diet by weight. Our results indicate that Adélie breeding pairs decline more rapidly when several years have passed since a high krill recruitment event. Considerable evidence suggests that this relationship reflects the dependence of Adélie penguins on krill as a food source.

The Adélie population declined more rapidly during the later years of a dominant krill cohort, when most krill were larger, but the change in breeding pairs held roughly constant across the early years of a dominant krill cohort, when most krill were smaller. Adélie breeding pair change was negatively correlated with the dietary proportion of large krill for years in which large krill comprised at least 39% of the krill consumed ($p = 0.002$, adjusted $R^2 = 0.65$, $n = 11$, $F_{1,9} = 19.327$), as determined by a piecewise linear fit (Fig. 5). However, Adélie breeding pair change was not correlated with the dietary proportion of large krill when large krill represented $< 39\%$ of the krill consumed ($p = 0.3$, $n = 14$, $F_{1,12} = 1.029$). This breakpoint of 39% occurs roughly between year 3 and year 4 of a dominant cohort (Supporting Information Table S1). The change in

Fig. 4. Proportion of krill in each 5 mm-binned size class in Adélie diet samples, illustrating the relationship between recruitment and length distribution. Dominant cohort years are labeled qualitatively, with year 1 indicating the year in which a new dominant cohort recruits. The annual size distribution of krill in Adélie diets is well correlated with the annual size distribution of krill in net tows, so both datasets appear to provide a clear picture of krill size distribution (see Cycling in krill as a driver of cycling in Adélie penguin breeding pairs).

Fig. 5. (**a**) Time series of proportion of large krill ($\geq$ 46 mm in length) in Adélie breeding season diets and proportional change in Adélie breeding pair census counts from that breeding season to the next. (**b**) Dietary proportion of large krill vs. subsequent change in Adélie breeding pair census counts, showing a piecewise linear fit. One outlier (gray) was omitted before determining the piecewise fit change point (see Methods–Statistics). The fit for dietary proportion of large krill above the breakpoint (0.39) shows negative correlation ($p = 0.002$, adjusted $R^2 = 0.65$, $n = 11$, $F_{1,9} = 19.327$. No significant correlation occurs for dietary proportions < 0.39 ($p = 0.3$, $n = 14$, $F_{1,12} = 1.029$). A single linear regression across the dataset (with no outliers omitted) shows negative correlation ($p = 0.01$, adjusted $R^2 = 0.21$, $n = 26$, $F_{1,24} = 7.469$), but residuals appear nonrandom, so a piecewise linear regression was chosen.

Adélie breeding pairs was not significantly correlated with krill density as estimated from LTER net tows ($p = 0.3$, $n = 25$, $F_{1,23} = 0.959$; Supporting Information Fig. S3a), but, as previously mentioned, these density estimates are likely imprecise due to low sampling rates.

We examined whether a disproportionate importance of smaller krill in Adélie diets might explain our finding. For example, perhaps Adélies tend to forage in areas where smaller krill predominate, or perhaps Adélies eat a disproportionate amount of small krill because they are slower swimmers than large krill (Hamner 1984) and are thus easier to capture. We predicted that if Adélies feed disproportionately on smaller krill, then the average size of krill in their diets should be smaller than the average size of krill captured in tows. However, Adélies showed no selection preference for krill based on size compared to tows, and Adélies appeared to sample randomly from the krill size distribution available across the ocean grid as measured by tows: mean krill body length in LTER net tows was correlated with mean krill body length

in Adélie diets (coefficient = 1.00 ± 0.20, $p = 0.0001$, adjusted $R^2 = 0.56$, $n = 19$, $F_{1,17} = 24.142$). This result could also occur if Adélies are biased toward smaller krill *and* tows are biased toward smaller krill due to size-dependent net avoidance. If large krill (faster swimmers) avoid nets in greater proportions than small krill, tows might underestimate the average size of krill present in the sampling region. We are not able to rule out the possibility that larger krill are undercounted by tows. Our results suggest that either both Adélies and net tows are sampling roughly evenly from the available distribution, or that both Adélies and net tows have, on average, the same bias toward smaller krill. While we find the former to be a more parsimonious explanation than the latter, both are possible. Because the overall number of krill decreases so substantially as the proportion of large krill increases (Supporting Information Fig. S3b), we hypothesize that the relationship between Adélie population trends and krill size is mediated by the connection between krill size and krill availability in the form of krill abundance. However, it is possible that the size of krill plays into that availability, and that small krill may be more accessible to Adélies than large krill.
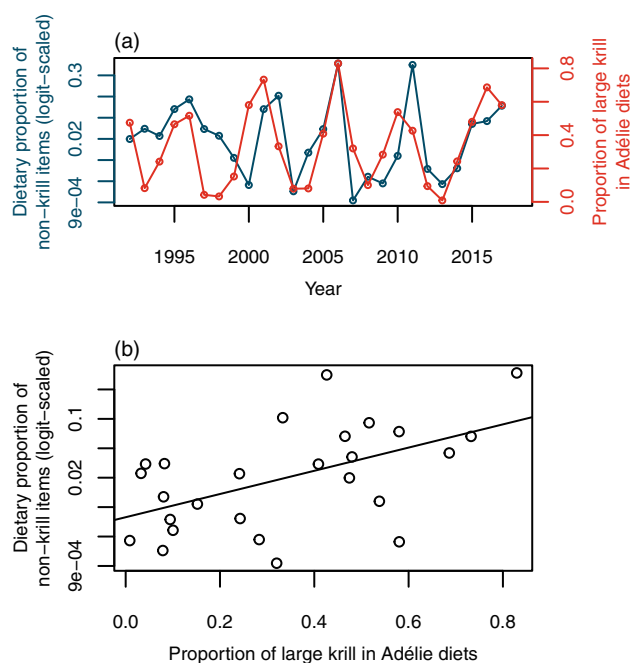
We also note that a difference in prey quality between small and large krill is unlikely to explain our results; percent lipid content (and therefore energy density) of euphausiids, including Antarctic krill at least up to 40 mm length, increases with increasing body length (Ruck et al. 2014).

In summary, our results thus suggest that when the proportion of large krill increases, krill availability decreases and krill become a limiting factor for Adélies, causing steep population declines. In the following section, we examine additional evidence for this idea.

Diet shifts in the later years of a cohort

Adélies showed shifts toward other diet items in years when most krill were large, further suggesting that krill availability for the penguins was low in these years. Prey in Adélie diet samples taken as part of the Palmer LTER project are separated into three categories: krill (*E. superba*), *T. macrura* (a smaller euphausiid), and fish. Krill dominated the diet samples in all years, indicating their importance as a food source; the mean proportion by weight of krill each year was $94 \pm 10\%$ (mean $\pm$ SD), but with a wide range, from 61% to 100%. This Adélie diet variability was related to krill demographics. The proportion of Antarctic krill that were large was positively correlated with the proportion of non-krill items in Adélie diet samples in a given year ($p = 0.005$, adjusted $R^2 = 0.26$, $n = 26$, $F_{1,24} = 9.600$) (Fig. 6). In particular, Adélies shifted to *T. macrura*. There were 15 years in which at least 1% of the diet samples by weight was composed of non-krill items; excluding one outlier year in which fish were heavily favored, *T. macrura* composed $92 \pm 8\%$ (mean $\pm$ SD) of the non-krill diet items in these years.

We checked whether Adélies might shift their diet toward *T. macrura* simply because the abundance of this species

Fig. 6. Proportion of Antarctic krill in Adélie penguin diets that are large (by individuals), and proportion of Adélie diets by weight consisting of non-krill items (*T. macrura* or fish) on a logit-scaled axis. The two are positively correlated ($p = 0.005$, adjusted $R^2 = 0.26$, $n = 26$, $F_{1,24} = 9.600$).

peaked when krill declined, but we found no evidence to support this idea. *T. macrura* density in net tows in a given year had no correlation with the proportion of *T. macrura* in Adélie diet samples ($p = 0.8$, $n = 25$, $F_{1,23} = 0.093$). We found no evidence of 5-year periodicity in *T. macrura* density (Supporting Information Fig. S4), nor was *T. macrura* density correlated with the density of krill ($p = 0.3$, $n = 25$, $F_{1,23} = 1.201$) or the proportion of large krill in the population ($p = 0.4$, $n = 25$, $F_{1,23} = 0.583$).

We conclude instead that shifts toward *T. macrura* in the diet when most krill are large indicate that Adélies are shifting to a less desirable prey item because krill availability is low. Although *T. macrura* are of good nutritional quality (Ruck et al. 2014), they are much smaller than *E. superba* (on the order of 20 times lighter by dry weight, Mizdalski 1988), and are therefore likely much less energy-efficient prey. This idea of decreased krill availability is further supported by previous work indicating that Adélies spend more time foraging for food during year 4 of a dominant krill cohort than they do in years 1–3 (Fraser and Hofmann 2003), which suggests that foraging conditions are more challenging for Adélies in year 4 than in years 1–3, and that the diet shifts revealed by our analysis represent a response to lowered prey availability.

Seasonality of krill limitation and effects on mortality

Theoretically, krill limitation could affect Adélie populations during summer alone, winter alone, or throughout the year. We reasoned that if krill were limiting during the summer breeding

season, then measures of reproductive success would correlate with krill availability. However, we found no evidence of summer limitation. The proportion of large krill was not related to egg-to-fledging success ($p = 0.5$, $n = 26$, $F_{1,24} = 0.452$), chick fledging weight ($p = 0.2$, $n = 26$, $F_{1,24} = 2.103$), or proportion of nests with two eggs vs. one ($p = 0.8$, $n = 26$, $F_{1,24} = 0.083$). Furthermore, none of these three metrics showed evidence of ~ 5-year periodicity (Supporting Information Fig. S5). While previous work (Fraser and Hofmann 2003) indicates that, in the later years of a dominant cohort, Adélies must expend more foraging effort, we do not see indications that this translates into prey limitation in the summer.

Instead, our results point to winter krill limitation. Under the more challenging survival conditions of winter, lowered krill availability in the later years of a cohort may threaten Adélie survival. The majority of Adélie adult mortality is known to occur in winter (Spurr 1975; Ainley et al. 1983). In the LTER sampling period, with a single exception, all years had a lower breeding population than the previous year; in other words, all year-to-year breeding pair declines except one were permanent, suggesting irreversible removal of individuals from the breeding population. Because larger declines in Adélie breeding pair numbers were correlated with the later years of a dominant krill cohort (when krill density was low), and because mortality is more common in winter, we suggest that the Adélies struggled to find enough krill to sustain themselves through the winter and there were thus fewer pairs available to breed the following summer.

The role of abiotic factors on periodicity of the Adélie population

Based on several lines of evidence, we posit that the periodicity in Adélie population change is a result of bottom-up regulation; however, the possibility that Adélie periodicity is driven directly by abiotic forces (such as those driving cycling in primary productivity) should also be explored. We examined this alternative hypothesis, but we did not find evidence to support it: the observed cycling lags did not match what we would predict under this scenario, nor did we find correlation between Adélie breeding pair change and sea ice, the major explanatory abiotic factor proposed in the literature.

Adélies are ice-obligate in winter, and previous work has suggested that declines in winter sea ice trigger declines in Adélies (Fraser et al. 1992; Forcada and Trathan 2009; Gorman et al. 2021). Therefore, we examined whether availability of sea ice could explain cycling in Adélie populations. We checked seven sea-ice metrics across eight spatial extents to determine whether overwinter sea ice could explain Adélie population changes from the previous summer to the following summer. With one exception, no metric across any of these spatial extents was correlated with Adélie breeding pair change at the level of $p \leq 0.1$, nor were nonlinear trends evident (Supporting Information Fig. S6). The exception was open-water area enclosed by ice across the entire western Antarctic Peninsula

($p = 0.08$), but this statistic was driven by a single extreme value without which no trend was detected ($p = 0.3$).

Furthermore, it is not clear how the sequence of cycling fits into the abiotic driver hypothesis. Since the icy winter and low-wind spring conditions that result in high summer primary productivity should benefit Adélies, while the low ice and high wind conditions that result in low productivity should be more challenging for them (Chappell et al. 1989; Ducklow et al. 2007; Bricher et al. 2008), we would expect to see that summer primary productivity was positively correlated with Adélie population change from the previous year. However, we found no evidence of correlation at this lag ($p = 0.6$, $n = 22$, $F_{1,20} = 0.297$).

We cannot rule out that unidentified abiotic aspects of the climate cycling are driving the cycling in Adélie growth rate. However, the dominant abiotic factor identified in the literature, sea ice, is not consistent with our data as the driver of cycling, nor is the sequence of cycling clearly explained by this hypothesis.

Summary of factors influencing periodicity

In sum, the observed patterns of periodicity can be well-explained with krill as the direct driver of oscillations in Adélie breeding pair change. In years when most krill are large (recent krill recruitment has been low), Adélies decline more rapidly than in years when most krill are small (recent krill recruitment has been high). Krill limitation is a likely mechanism for this phenomenon, as the krill population decreases following low recruitment years, and krill are less available to Adélies in these years. We propose cycling occurs generally as follows. A summer of high primary productivity (Year 0) prompts 2 years of high krill recruitment, causing the krill population to increase and peak 2 years later (Year 2). Primary productivity falls after Year 0, reaching a nadir in Years 2–3, and so krill recruitment in Years 3–5 is low. Therefore, the krill population declines in Years 3–5, and then another summer of high primary productivity (Year 5) drives an increase in recruitment the following year (Year 6). Therefore, Year 5 in the cycle has high primary productivity and very low krill, which fits the observation that Adélie decline is steepest directly following summers of high primary productivity. The proportion of large krill, a proxy for recent recruitment failures, shows the expected correlations: the proportion of large krill is positively correlated with primary productivity with no lag ($p = 0.03$, adjusted $R^2 = 0.18$, $n = 22$, $F_{1,20} = 5.593$), negatively correlated at no lag with density of krill as estimated from tows ($p = 0.005$, adjusted $R^2 = 0.26$, $n = 25$, $F_{1,23} = 9.589$), and negatively correlated with Adélie breeding pair change to the following summer (Fig. 5). Our finding of diet shifts, combined with prior results from Fraser and Hofmann (2003) that indicate increased foraging times later in a dominant krill cohort, suggest that low krill recruitment negatively impacts Adélie foraging.
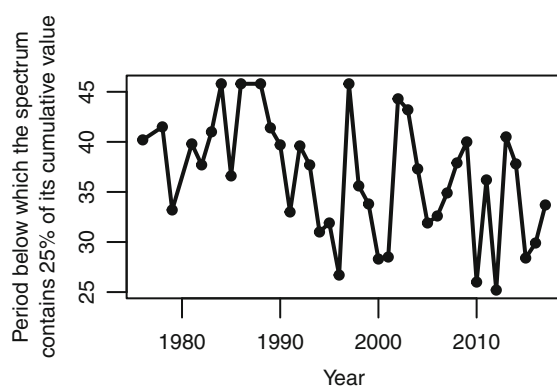
Decadal-scale changes and climate change

The Adélie population around Palmer Station was mostly stable during the 1980s, but began declining rapidly in the 1990s (Woehler et al. 2002). We suggest that climate change interacted with existing abiotic periodicity, resulting in years with high primary productivity becoming increasingly rare. This change in turn led to increasingly rare krill recruitment events, which negatively impacted Adélie populations.

We examined whether krill recruitment events have become more episodic over time. We observed a sizable decrease in krill recruitment consistency from the 1980s to the 1990s in the Southwest Atlantic sector of the Southern Ocean. Robust krill size distribution data were not available for several years before 1990, so we were not able to determine the frequency of recruitment events directly. Instead, we used a metric to quantitatively estimate the consistency of recruitment over the 5–6 years previous to a given year based on gaps in the krill size distribution of that year (see Methods— Longer-term krill recruitment consistency). This metric decreased significantly from 1976 to 2017 ($p = 0.006$, adjusted $R^2 = 0.16$, $n = 39$, $F_{1,37} = 8.3886$; when Palmer LTER lengths are not converted to AT, all statistics remain the same to displayed digits except $F_{1,37} = 8.534$) (Fig. 7). This decrease indicates that, as time went on, there were more gaps or "missing cohorts," suggesting more years of low recruitment. In the 1980s, the mean of this metric was 42 ± 4 (mean $\pm$ SD), while in the 1990s it was 35 ± 5, and from 2000 to 2017 it was 34 ± 6. This finding aligns with results from Atkinson et al. (2019), which showed a drop in mean krill density in the early 1990s based on population estimates constructed from historical net tows. These authors also found an increase in the early 1990s of mean krill length (indicating lowered average recruitment). Our results suggest that krill recruitment became rarer between the 1980s and the 1990s, leading to the current situation of krill limitation for Adélies in the years between strong recruitment events.

We hypothesize that strong krill recruitment events have become rarer over the past ~ 45 years because changes in abiotic conditions have reduced the likelihood of a year of high primary productivity. To test this idea, we modeled primary productivity over this time period based on available abiotic metrics, following Saba et al. (2014). Measures of two key variables (days of low wind and spring water column stratification) used by Saba and colleagues to model Chl *a* were not available before 1990. However, we reasoned that these variables could be modeled by sea-ice indices and spring/summer SAM phases; increased sea ice leads to stronger water column stratification, and SAM is a climate mode that impacts sea ice, temperatures, and wind speed, which in turn impact water column stratification (Saba et al. 2014). In particular, positive SAM is linked to warmer temperatures, reduced sea ice, and higher winds, all of which contribute to decreased stratification in the spring and summer, leading in turn to decreased primary productivity. We therefore modeled primary

Fig. 7. Metric of krill cohort consistency over time. Higher values indicate more consistent recruitment across the time period captured in the krill body length distribution ($\sim$ 5–6 years), while lower values indicate more gaps in recruitment. The metric has decreased significantly since 1976 ($p = 0.006$, adjusted $R^2 = 0.16$, $n = 39$, $F_{1,37} = 8.3886$).

productivity based on monthly SAM from September through January, and several sea-ice indices (see Methods—Longer-term modeled primary productivity). We found a linear model using January SAM ($p = 0.006$, negative coefficient), Julian day of sea-ice advance ($p = 0.04$, positive coefficient), Julian day of sea-ice retreat ($p = 0.2$, negative coefficient), and number of sea-ice days ($p = 0.1$, positive coefficient) contained information about primary productivity, though it tended to underestimate magnitude (model fit, $p = 0.007$, adjusted $R^2 = 0.43$, $n = 22$, $F_{4,17} = 5.017$; leave-one-out cross-validation, predicted vs. observed, coefficient $= 0.70 \pm 0.25$, $p = 0.008$, adjusted $R^2 = 0.27$, $n = 22$, $F_{1,20} = 8.7291$).

As expected, more negative SAM values correlated with increased primary productivity, as did a greater number of sea-ice days. A later day of sea-ice advance and an earlier day of sea-ice retreat were also linked to increased primary productivity. Number of sea-ice days is cross-correlated with day of sea-ice advance and day of sea-ice retreat, making it difficult to interpret the model coefficients of these three sea-ice variables. Years with a greater number of sea-ice days tend to have an earlier sea-ice advance ($p = 0.0003$, adjusted $R^2 = 0.47$, $n = 22$, $F_{1,20} = 19.644$) and a later sea-ice retreat ($p = 10^{-11}$, adjusted $R^2 = 0.72$, $n = 22$, $F_{1,36} = 94.6342$).

We note that on its own, number of sea-ice days shows evidence of a very weak positive correlation with primary productivity ($p = 0.1$, adjusted $R^2 = 0.06$, $n = 22$, $F_{1,20} = 2.4574$), while day of sea-ice advance shows no evidence of a relationship with primary productivity ($p = 0.8$, $n = 22$, $F_{1,20} = 0.0882$). Day of sea-ice retreat also shows evidence of a very weak positive correlation with primary productivity ($p = 0.1$, adjusted $R^2 = 0.07$, $n = 22$, $F_{1,20} = 2.6254$), indicating that, when the number of sea-ice days is not accounted for, a later sea-ice retreat correlates weakly with greater primary productivity. In light of this, we suggest the best interpretation of the model is that a greater number of sea-ice days is linked to greater primary productivity, and, for

a given number of sea-ice days, a later advance is linked to greater primary productivity, but that day of advance has little meaning on its own. Similarly, for a given number of sea-ice days, an earlier retreat is linked to greater primary productivity, but an earlier retreat on its own will not drive greater primary productivity.

All four of these abiotic variables (January SAM, number of sea-ice days, day of sea-ice advance, and day of sea-ice retreat) have changed over time (Supporting Information Fig. S7). In the Palmer LTER study region, winter sea-ice extent and duration declined from 1980 (first year of sea ice data) until $\sim$ 2010, at which point a period of sea-ice rebound began (Schofield et al. 2018). A piecewise fit split the number of sea-ice days into two regimes, with a breakpoint between 2010 and 2011; over years 1980–2010, the number of sea-ice days declined ($p = 0.004$, adjusted $R^2 = 0.22$, $n = 31$, $F_{1,29} = 9.559$), while over years 2011–2017, the number of sea-ice days increased ($p = 0.05$, adjusted $R^2 = 0.48$, $n = 7$, $F_{1,5} = 6.659$). Similarly, a piecewise fit of day of sea-ice advance identified a breakpoint between 2011 and 2012. Over years 1980–2011, the day of sea-ice advance moved later in the year ($p = 0.00008$, adjusted $R^2 = 0.39$, $n = 32$, $F_{1,30} = 20.807$), while over years 2012–2017, the day of sea-ice advance trended earlier ($p = 0.03$, adjusted $R^2 = 0.65$, $n = 6$, $F1,4 = 10.194$). A piecewise fit of day of sea-ice retreat, with the 1990 outlier year excluded, identified a breakpoint between 2011 and 2012, with sea-ice retreat trending earlier over the period 1980–2011 ($p = 0.004$, adjusted $R^2 = 0.23$, $n = 31$, $F_{1,29} = 9.820$) and no trend occurring in 2012–2017. January SAM from 1980 to 2017 showed a somewhat different trend, with a breakpoint identified between 1999 and 2000; across years 1980–1999, January SAM increased ($p = 0.004$, adjusted $R^2 = 0.34$, $n = 20$, $F_{1,18} = 10.883$), while across years 2000–2017, it showed no significant trend. January SAM data were available starting in 1960, and for the entire period of 1960–2017, January SAM increased significantly ($p = 0.008$, adjusted $R^2 = 0.097$, $n = 61$, $F_{1,59} = 7.467$).

Based on our model as well as prior work, we would expect that the decreasing winter sea ice between 1980 and $\sim$ 2010 would correspond to decreasing primary productivity, and that primary productivity would begin to increase during the ice rebound period following 2010. Additionally, increasing January SAM from 1980 to 1999 would be expected to drive decreasing primary productivity, while the non-trended January SAM from 2000 to 2017 would not prompt any trend in productivity. We used the model to predict primary productivity for all years from 1980 to 2017 (Supporting Information Fig. S8). We found that modeled primary productivity decreased from 1980 to 1999 ($p = 0.04$, adjusted $R^2 = 0.17$, $n = 20$, $F1,18 = 5.03$; with 1990 outlier with Bonferroni $p = 0.03$ removed, $p = 0.01$, adjusted $R^2 = 0.29$, $n = 19$, $F_{1,17} = 8.203$). The mean predicted primary productivity in the 1980s was 0.24 (log anomaly, where 0 is the mean measured primary productivity 1995–2017; see Methods—Data transformations), and after 1990 it was $- 0.19$. In the Palmer

LTER dataset, above-average primary productivity years (anomaly above 0) tended to result in above-average krill recruitment and the establishment of a strong cohort. In the 1980s, 70% of years had a predicted primary productivity anomaly above 0 (the observed Palmer LTER dataset mean), while from 1990 onwards, only 39% of years did. In the observed primary productivity data (1995–2017), 41% of years had anomalies above 0. Additionally, modeled primary productivity in the 1980s shows two major peaks, 4 years apart, comparable to the ∼ 5 year cycling observed in the measured 1995–2017 data. While these modeled estimates contain large uncertainty due to inaccuracy in the model and the fact that it is being applied to a time period for which data are not available to validate it, they align with the ideas that (1) ecosystem variability with a ∼ 5 year cycle has been a factor in this system since at least 1980, and (2) years of conditions good for krill recruitment were rarer from 1990 to 2017 than in the 1980s. Currently, in a single primary productivity cycle, only 1 or 2 years prompt high krill recruitment, whereas in the 1980s, our model predicts that most years yielded high krill recruitment. Examining the impact of the ice rebound that began around 2010 is outside the scope of this work, but future research should investigate the effect of this ice rebound on the trophic dynamics of this system.

Importance of krill and fish as food sources

In our dataset, Adélie survival fluctuated with krill availability, indicating that krill were a critical prey species for these penguins during the study period. However, across much of Antarctica including the western Antarctic Peninsula, Adélies historically ate a greater proportion of fish than they do at present, with a shift away from fish occurring sometime within the last 200 years (Emslie and Patterson 2007). It has been proposed that the loss of forage fish species, particularly the Antarctic silverfish (*Pleuragramma antarctica*), may be a major driver of overall Adélie declines on the western Antarctic Peninsula in the past 50 years (Chapman et al. 2011; Sailley et al. 2013; Ainley et al. 2018), and that krill may be more important to Adélies now given the loss of fish.

The impact of fish in the diet on Adélie population trends has not been clearly elucidated. Modeling work has suggested that more fish in the diet promotes Adélie chick growth and survival (Chapman et al. 2011), but existing empirical work exploring this hypothesis is limited. Research spanning the summers of 2008–2010 found that chicks located at a more southern colony on the western Peninsula, where they were provisioned with a higher trophic level diet (i.e., a greater ratio of fish to krill), had higher fledging weights than chicks around Anvers Island (Gorman 2015). However, within each site, the proportion of fish in the diet had no relationship with chick fledging weight. Additionally, the body condition of adults returning to nest was unrelated to the trophic level at which they had been feeding, and the study does not rule out north–south differences in krill availability as a factor.

Work by Whitehead et al. (2015) in the Ross Sea found that a greater proportion of fish in the diet was related to larger chick size, while work by Ainley et al. (2018) in the same region found no relationship between the ratio of fish to krill in the diet and the fledging mass or recruitment success of Adélie chicks; however, at one colony, overall decreasing trends in both mean proportion of fish and mean fledging weight were observed, and the authors hypothesized these trends were related. There is at least one report indicating that Adélie penguins around Anvers Island ate a greater proportion of silverfish in the early 1970s than they did in the 1990s (Sailley et al. 2013), which might mean a decrease in silverfish consumption corresponded with overall Adélie decline, though these data have not been explored in detail. Silverfish decreased precipitously in the waters along the western Antarctic Peninsula around Anvers Island between 1990 and 2010 (La Mesa et al. 2015; Mintenbeck and Torres 2017); however, as this decline likely corresponds with declines in krill (Atkinson et al. 2004, 2019), it is difficult to separate the two when examining Adélie population trends.

Our dataset can provide only limited information on the role of fish in the diet, but we analyzed whether there was any obvious indication that the proportion of fish in the diet is too low to support a successful population. Because the diet samples were taken from adults upon their return from foraging trips, the samples reflect the stomach contents fed to chicks, but likely undercount fish consumed at sea as fish lack an exoskeleton and are digested much faster than krill (Karnovsky 1997). In our study, krill made up an average of 94 ± 10% (mean ± SD) of the diet samples collected each year, while fish made up an average of 0.3 ± 0.3% (mean ± SD, with one outlier year, discussed in detail below, excluded). We examined whether earlier studies from the Antarctic Peninsula region suggest that stable Adélie populations ate more fish. Prior work indicate that at least under some circumstances, Adélie populations have been stable or increased in size when the stomach contents of returning foragers had a similar composition to that observed in our study. Studies from the northern Antarctic Peninsula region indicate that krill have made up ≥ 99% by weight of diet samples taken from foragers returning to land in the South Shetland Islands since at least 1978, while fish made up ≤ 0.1% (Volkman et al. 1980; Trivelpiece et al. 1987; Juáres et al. 2018; Panasiuk et al. 2020), and Adélie populations in this area were stable throughout the 1980s (Antarctic Treaty System 2009; Southwest Fisheries Science Center 2019). Further north at Signy Island in South Orkney, the Adélie population increased from the late 1970s until about 1990 (Dunn et al. 2016), and diet data from 1981 and 1982 indicate that foragers returned to land with stomach contents of > 98% krill and 0.4–1.4% fish by weight in these summers (Lishman 1985). We therefore find no evidence that the ratio of fish to krill in the diet of Adélie chicks in our study is categorically too low to support a successful population. However, this does not rule out the possibility that the declining silverfish population has negatively impacted Adélies; as both

fish and krill populations have declined, the ratio of fish to krill could stay roughly constant while the overall amount of prey consumed decreased. Additionally, we lack diet data from outside the breeding season.

We examined whether there was evidence that a greater proportion of fish in the diet promoted Adélie survival in our dataset. We found that in general, a greater proportion of fish in the summer diet samples correlated with a steeper overwinter Adélie population decline to the following summer (with outlier removed, $p = 0.002$, adjusted $R^2 = 0.31$, $n = 25$, $F_{1,23} = 11.9857$) (Supporting Information Fig. S9). As discussed, the diet samples may underestimate the amount of fish consumed, but we hypothesize that the ratio of fish to krill in the diet samples is correlated with the ratio of fish to krill that the penguins consume at sea, and we expect it is reasonable to interpret the proportion of fish in diet samples as a relative proxy for the proportion of fish consumed. We attribute the steeper Adélie population decline in years with a higher proportion of fish consumption to Adélies eating a greater proportion of non-krill prey in years with low krill availability, which in this period translates to low overall prey availability. However, there was one notable outlier year (Bonferroni $p = 0.005$): in 2002, fish made up 12% of the diet, while in all other years fish were ≤ 1% of the diet. 2002 to 2003 was the only year-to-year step over which the Adélie population increased. 2002 was also a year of high krill recruitment, with the krill population having increased substantially since the previous year; perhaps the synergy between high fish availability and high krill availability provided an excellent prey field for the penguins. This single outlier year provides insufficient data to draw conclusions, but it hints that fish may be important in Adélie recovery and that this possibility should be investigated with additional historic data and in colonies in which fish make up a larger part of the diet. In conclusion, while our time series offers an intriguing datapoint hinting that years of increased silverfish availability may promote Adélie survival, existing work remains inconclusive and future work is needed to understand the role of fish in Adélie population trends.

Conclusions

Abiotic conditions have changed in the waters along the western Antarctic Peninsula over the past 45 years, with predictors of primary productivity becoming less favorable for high production: average SAM phase has increased and average sea-ice season has decreased. Our results suggest that primary productivity has cycled every ~ 5 years across this time period, but that mean primary productivity has decreased over time. In the LTER primary productivity dataset (1995–2017), only one or two years out of every ~ 5-year cycle led to high krill recruitment; by contrast, our model implies that in the 1980s, most years in a cycle prompted high krill recruitment. Analysis of region-wide krill length distribution data suggests

that krill recruitment has become more episodic over the period 1976–2017, a result that aligns with Atkinson et al.'s (2019) findings that average krill length has increased, suggesting decreased recruitment. Based on these lines of evidence, we suggest strong krill recruitment events have become rarer, resulting in expanded intervals during which krill availability is very low. Our findings indicate that this low krill availability is associated with steep declines in the Adélie population around Palmer Station. Low krill availability may be the primary driver of Adélie decline; alternatively, unfavorable climatic conditions or loss of prey fish populations may be the primary driver of long-term decline, with low krill availability accelerating the rate and prompting the oscillations in Adélie rate of decline. Regardless, the Adélie population is not responding steadily to the mean size of the krill population, but instead is powerfully impacted by year-to-year fluctuations, with intervals of low krill availability driving precipitous and permanent population declines. This phenomenon may explain why our conclusions differ from those drawn from the bioenergetic model presented by Sailley et al. (2013), which assumes a quantity of krill biomass derived from measurements averaged across 12 years.

In this system, climate change has amplified the ecological impacts of natural oscillations by lengthening intervals of unfavorable conditions for primary productivity, resulting in episodic recruitment of a prey species, with prey shortages occurring for a predator between those recruitment events. Jackson et al. (2009) proposed that climate variability, in combination with climate change, will result in shifts to episodic recruitment in a number of species, suggesting that the dynamics observed here are likely to be replicated in other systems. Our findings indicate that the interplay between climate variability and anthropogenic climate change can cause ecosystem responses that depend on variability, and that are poorly summarized by long-term averages. Work on systems that experience fluctuating conditions should consider the ways that these oscillations can influence ecosystem functioning in the face of climate change, and the ways that climate change may amplify the ecological impacts of climate variability.

Data availability statement

All data collected by the Palmer LTER project are available through the Palmer LTER website at https://pallter.marine.rutgers.edu/data/ or through the Environmental Data Initiative (EDI) Data Portal at https://portal.edirepository.org/nis/home.jsp. KRILLBASE body length data are available from the British Antarctic Survey website at https://data.bas.ac.uk/metadata.php?id=GB/NERC/BAS/PDC/01319.

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Conflict of Interest

None declared.