



ARTICLE

Coastal and Marine Ecology

Long-term patterns in ecosystem phenology near Palmer Station, Antarctica, from the perspective of the Adélie penguin

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Abstract

Climate change is leading to phenological shifts across a wide range of species globally. Polar oceans are hotspots of rapid climate change where sea ice dynamics structure ecosystems and organismal life cycles are attuned to ice seasonality. To anticipate climate change impacts on populations and ecosystem services, it is critical to understand ecosystem phenology to determine species activity patterns, optimal environmental windows for processes like reproduction, and the ramifications of ecological mismatches. Since 1991, the

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Palmer Antarctica Long-Term Ecological Research (LTER) program has monitored seasonal dynamics near Palmer Station. Here, we review the species that occupy this region as year-round residents, seasonal breeders, or periodic visitors. We show that sea ice retreat and increasing photoperiod in the spring trigger a sequence of events from mid-November to mid-February, including Adélie penguin clutch initiation, snow melt, calm conditions (low winds and warm air/sea temperature), phytoplankton blooms, shallow mixed layer depths, particulate organic carbon flux, peak humpback whale abundances, nutrient drawdown, and bacterial accumulation. Subsequently, from May to June, snow accumulates, zooplankton indicator species appear, and sea ice advances. The standard deviation in the timing of most events ranged from ~20 to 45 days, which was striking compared with Adélie penguin clutch initiation that varied <1 week. In general, during late sea ice retreat years, events happened later (~5 to >30 days) than mean dates and the variability in timing was low (<20%) compared with early ice retreat years. Statistical models showed the timing of some events were informative predictors (but not sole drivers) of other events. From an Adélie penguin perspective, earlier sea ice retreat and shifts in the timing of suitable conditions or prey characteristics could lead to mismatches, or asynchronies, that ultimately influence chick survival via their mass at fledging. However, more work is needed to understand how phenological shifts affect chick thermoregulatory costs and the abundance, availability, and energy content of key prey species, which support chick growth and survival. While we did not detect many long-term phenological trends, we expect that when sea ice trends become significant within our LTER time series, phenological trends and negative effects from ecological mismatches will follow.

KEYWORDS

bacteria, climate change, match–mismatch hypothesis, penguins, phenology, phytoplankton, polar regions, sea ice, whales, zooplankton

INTRODUCTION

Globally, climate change has led to phenological shifts—changes in the timing of seasonal activities—in many plant and animal species (Cohen et al., 2018; Visser & Both, 2005). While some species are capable of responding rapidly to changing environmental conditions, others display little to no shifts, potentially because they rely on cues that are not affected by climate (i.e., photoperiod) or there is a small time window in which conditions are suitable for processes like reproduction or growth. It is expected that species will shift at different rates as ecological conditions for one species are often influenced by organisms at other trophic levels or different abiotic and biotic conditions (Cohen et al., 2018; Visser et al., 2004). Behavioral flexibility is often considered to be a trait that mitigates climate stressors (Beever et al., 2017), but phenological shifts are

not always beneficial as they can expose organisms to novel environments (Iler et al., 2021) and do not guarantee a synchrony or match in phenology between interacting species, which can lead to trophic decoupling and altered vital rates (Iler et al., 2021). To anticipate climate change impacts on population dynamics and persistence, it is critical to understand ecosystem phenology—including environmental drivers and multitrophic-level species responses—to determine whether species activities occur during periods of optimal conditions and to assess the ramifications of possible mismatches (Carter et al., 2018; Cushing, 1974; Iler et al., 2021).

Polar regions are experiencing the most rapid rates of air and sea temperature warming, as well as significant sea ice decline, and it is commonly assumed that species at high latitudes will shift phenology more than those at lower latitudes, reflecting the strong environmental

shifts. However, evidence for such shifts is mixed as latitude may not be a good proxy for local environmental conditions (Chmura et al., 2019; Pinsky et al., 2013), and many other factors such as trophic level, migratory life history, ecological specialization, timing of developmental stage, and generation time complicate determination of phenological patterns. These complexities emphasize more work is needed to understand the mechanisms underpinning species responses and subsequent species interactions (Chmura et al., 2019). Further, species in marine environments often exhibit more pronounced phenological shifts than those in terrestrial environments (Burrows et al., 2011; Chambers et al., 2013; Poloczanska et al., 2013), suggesting studies on polar ocean ecosystems could provide critical information to address phenological uncertainties.

To obtain an ecosystem view on phenology in a polar climate change hotspot, we conducted a case study using data from the Palmer Antarctica Long-Term Ecological Research (LTER) program, which has maintained routine monitoring at Palmer Station located along the West Antarctic Peninsula (WAP) since 1991 (Figure 1). This multidisciplinary program was established to study how sea ice structures the ecology of the region, and as with other LTER sites, shares the unifying ecological concept that physical factors drive the biology (Smith et al., 1995). Over the last 40–80 years, the WAP has experienced some of the highest rates of regional warming on Earth (Meredith & King, 2005; Turner et al., 2020; Vaughan et al., 2003), accompanied by some of the fastest sea ice

declines (Maksym, 2019; Stammerjohn et al., 2012), with the austral autumn–winter period showing the strongest seasonal trends in sea ice and warming, respectively (Figure 2). However, the WAP also experiences high interannual and decadal variability (Fogt et al., 2022; Hobbs et al., 2016; Stammerjohn & Scambos, 2020; Turner et al., 2020) as exemplified by a recent period (2009–2016) of cooler conditions (Turner et al., 2016) and sea ice increases (Schofield et al., 2018) that were then followed by resumed warming (Turner et al., 2020) and sea ice decreases (Figure 2). Due to the north–south orientation, the WAP is characterized by a latitudinal climatic gradient that has shifted south under the influence of climate change. Palmer Station sits at a hinge point between a cold, dry continental regime in the south (heavily ice covered) and a warm, moist maritime regime in the north (low ice coverage) (Ducklow et al., 2013; Henley et al., 2019; Montes-Hugo et al., 2009; Stammerjohn et al., 2008). Rapid and spatially variable rates of climate change make this a valuable model system to study biophysical interactions and how future changes may manifest through other polar environments (Schofield et al., 2010). In addition, the characteristically high variability allows for natural experiments on the impact of sea ice coverage on community structure, populations, and ecosystem dynamics.

The Palmer Station region is influenced by sea ice dynamics (e.g., extent and growth/retreat of sea ice) that play a major role in ecosystem structure and function, from primary and secondary producers to the survival of seabirds and presence of whales (reviewed in

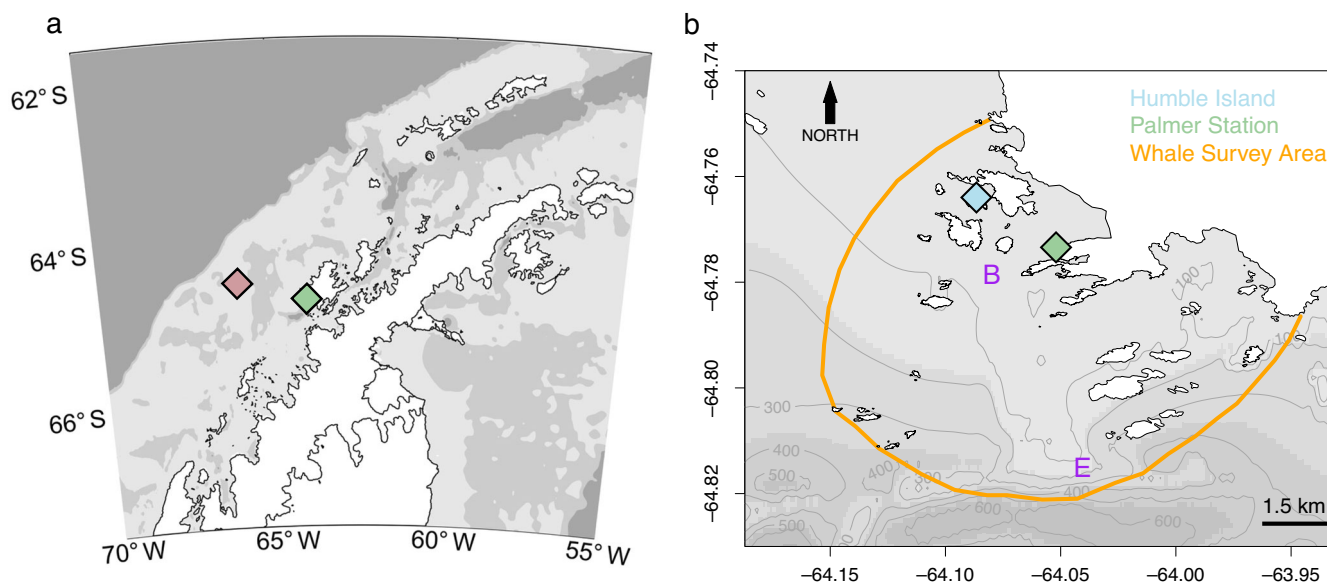


FIGURE 1 (a) Palmer Station (green diamond) is located on Anvers Island along the West Antarctic Peninsula. The sediment trap location is shown in pink. (b) Near Palmer Station, Station B and E water column sampling locations are shown in purple, the Adélie penguin breeding colony on Humble Island in blue and the whale survey region is defined by the Palmer Station small boating limits in orange. Seabirds and seals utilize many of the islands surrounding Palmer Station.

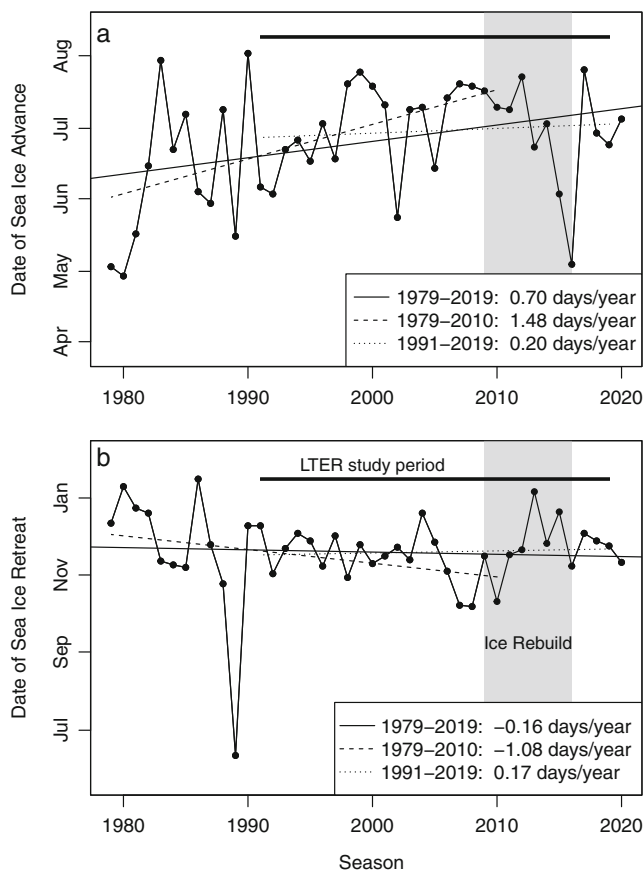


FIGURE 2 Trends in the date of sea ice advance (a) and retreat (b) for the 200-km region west and south of Anvers Island. Changes in trends and yearly variability for different time periods are highlighted: 1979–2019 (satellite era), 1979–2010 (warming most significant), and 1991–2019 (Long-Term Ecological Research [LTER] study period, horizontal line). There was a sea ice rebuild period from 2009 to 2016.

Appendix S1: Section S1; Figures 3 and 4). Within the diverse assemblage of marine and terrestrial species, some are considered to be polar with life histories tied to sea ice (e.g., Antarctic krill, Weddell seal, Adélie penguin, Antarctic minke whale) and others are subpolar or ice-avoiding (e.g., salps, southern elephant and Antarctic fur seals, gentoo and chinstrap penguins, humpback whales). Despite sea ice affinities, the life cycle of most organisms is attuned to ice seasonality where short-lived/planktonic species (e.g., bacteria, phytoplankton, and zooplankton) and long-lived/highly mobile species (e.g., whales) are hypothesized to respond rapidly to sea ice variability while migratory central place foragers (e.g., seals, seabirds) that are tied to breeding colonies have lower phenological flexibility (Appendix S1: Section S1).

Studying the impacts of climate change and variability across trophic levels has been a large focus of Palmer LTER work. While spring preconditioning, specifically the timing of sea ice retreat and its extent, is a dominant physical force governing biological processes at all trophic levels

(Saba et al., 2014), it is generally unclear how the winter and spring setup drives summer ecosystem shifts and how these shifts cascade from one trophic level to the next. A few studies have shown phenological shifts in phytoplankton (Schofield et al., 2017), zooplankton (Thibodeau, Steinberg, McBride, et al., 2020), and predators (Cimino et al., 2019), but in some instances, it is unclear whether these shifts are related to the timing of other biophysical processes. Further, past studies have used monthly or seasonal composites of variables to explain species phenological responses, which may not be ecologically relevant or sufficient to capture variability on sub-monthly scales (Kim et al., 2016). Smith et al. (1995) proposed a conceptual qualitative diagram of the annual timeline of key physical and biological components to understand ice–ocean–atmosphere and trophic interactions, which we update here using quantitative information from 1991 to 2019 to test relationships between biological responses and the seasonal progression of sea ice and other potential drivers. We examine ecosystem phenology from the perspective of Adélie penguins (*Pygoscelis adeliae*), which have life histories dependent on suitable sea ice, landscape, seascape, and preyscape conditions—making them a valuable case study species. We place our results in the context of past work and highlight future research directions to understand the mechanisms, patterns, and implications of climate-driven phenological shifts.

METHODS

Data

The Palmer LTER study region is located midway down the western side of the Antarctic Peninsula (Figure 1). Seasonal (October–March) observations are acquired annually in the vicinity of Palmer Station on Anvers Island (64.8° S, 64.1° W), while regional observations are acquired during annual January research cruises at a series of grid stations along the WAP. Many of the datasets used in this study (details provided below and as listed in Table 1) are available through the Environmental Data Initiative at: <https://pallter.marine.rutgers.edu/catalog/edi/index.php>. This long-term monitoring provides information on ecosystem-wide dynamics on intra-annual to multidecadal (~30 years) scales. The year represents the austral summer field season (e.g., 1991 includes October 1991 to September 1992).

Sea ice

Daily sea ice concentration were derived from the Scanning Multichannel Microwave Radiometer and Special Sensor

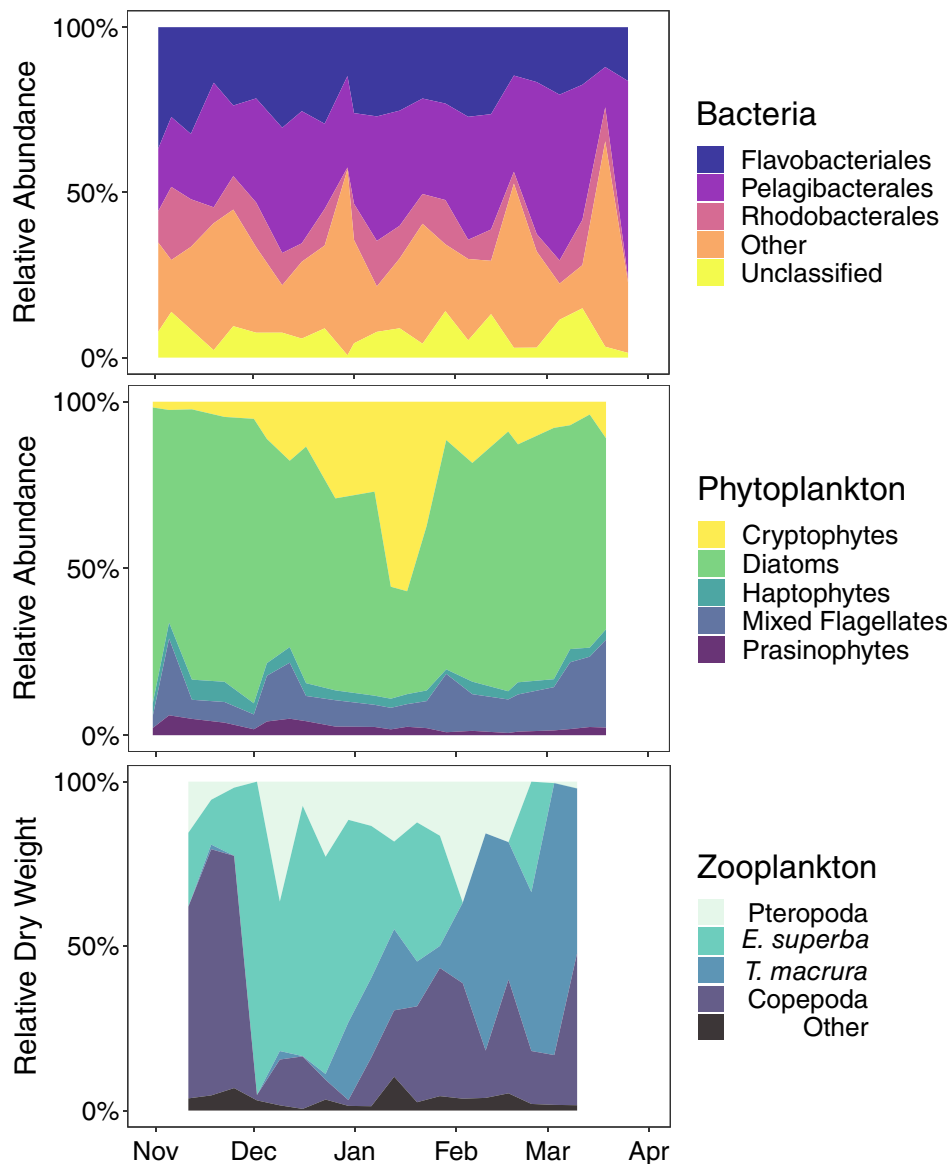


FIGURE 3 Overview of species abundance patterns in the Palmer Station region from microscopic heterotrophic marine bacteria and phytoplankton to zooplankton species. Bacteria (2015–2019), phytoplankton (1991–2014), and zooplankton (2017–2018) data are from weekly or biweekly sampling near Palmer Station. Time series of bacteria and zooplankton taxonomic identifications were added more recently to our sampling plan.

Microwave/Imager (SMMR-SSM/I) satellite data made available from the National Snow and Ice Data Center using the GSFC Bootstrap algorithm (version 3.1). Dates of autumn ice edge advance and spring ice retreat are extracted from the daily sea ice concentration data following methods described in Stammerjohn et al. (2008) and were determined for an $\sim 200 \times \sim 200$ km area in the vicinity of Anvers Island. In short, annual ice edge advance and retreat are defined as the day in which sea ice concentration first increases above, or last decreases below, the nominal “ice edge” threshold (here defined at 15% concentration) and remains above or below for at least five consecutive days, respectively. To understand long-term trends in sea

ice, we compared linear regressions over the entire satellite record (1979–2019), over a period of rapid warming (1979–2010), and over our study period (1991–2019) when there was a cooling period from 2009 to 2016.

Weather

Daily weather conditions (e.g., wind speed, air temperature, precipitation) were measured by both manual observations and the Palmer Station Automatic Weather Station and Meteorological Observing System. Data were quality controlled and erroneous values removed.

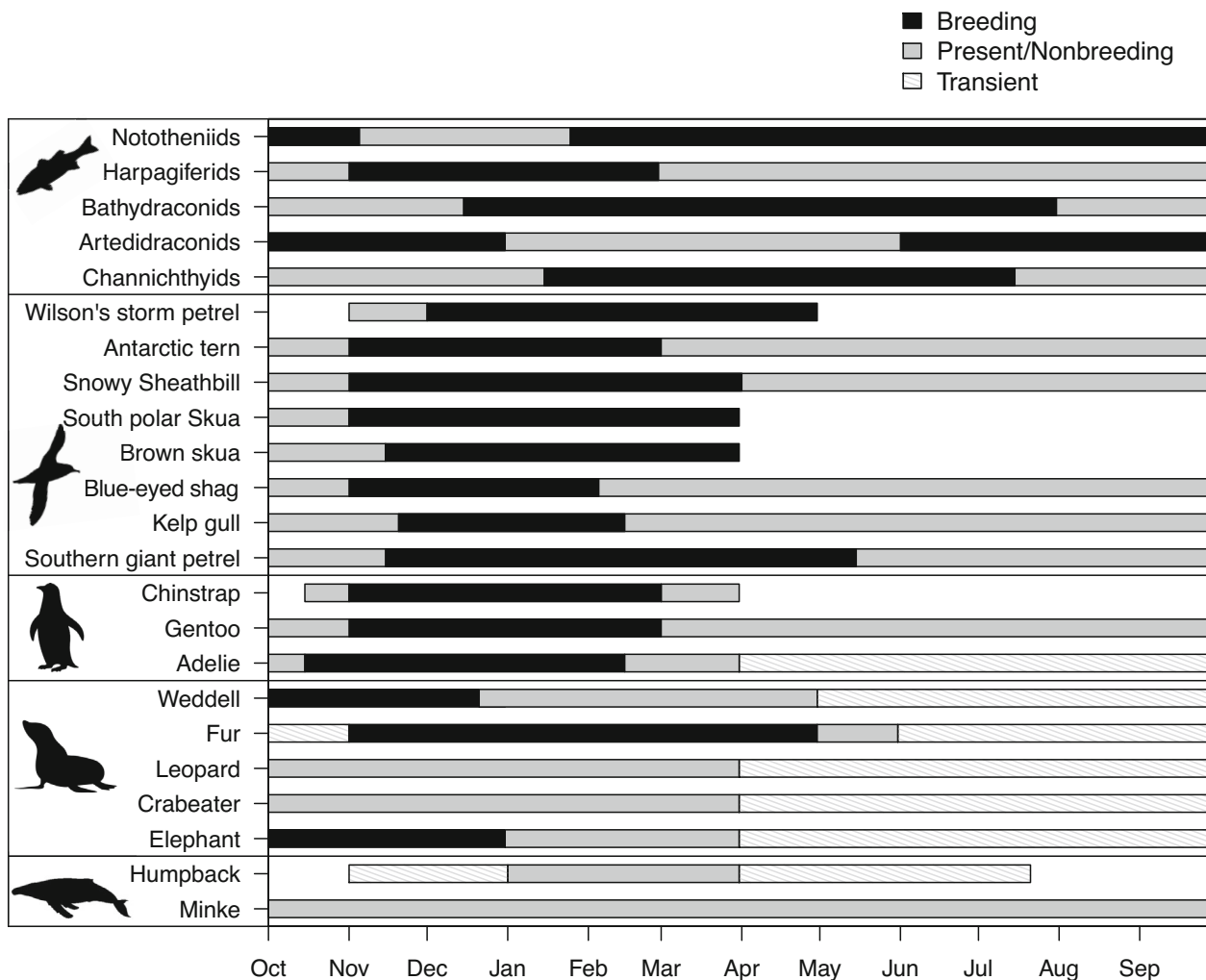


FIGURE 4 Overview of fish and top predator presence and activity patterns in the Palmer Station region. Top predator occupancy patterns are estimated from visual sightings, Palmer Station monthly reports, and literature reviews (caveats are discussed in the text).

Water samples

Chlorophyll *a* concentration was determined by extraction of samples collected sub-weekly to weekly throughout the year using a seawater intake system (at 6 m) at Palmer Station. Sea surface temperature (SST) average for the day was taken from the tide gauge at the end of Palmer Station pier.

Water column samples were also taken at inshore Station B (to ~75 m) and further offshore Station E (to ~200 m) on a twice-weekly basis from October to March, with sampling commencing as soon as sea ice and weather conditions permitted, but sampling gaps still occur due to inclement weather and ice cover. Data from Stations B and E show largely the same patterns (Saba et al., 2014). Seawater samples were collected at discrete depths using Niskin bottles for chlorophyll, phytoplankton pigments, nutrients, and bacteria species and abundance. The seawater was stored in dark amber Nalgene bottles and processed

immediately upon returning to the laboratory. Water column structure was determined using a conductivity, temperature, and depth (CTD) sensor. Mixed layer depth (MLD) was determined for each CTD profile using the maximum water column buoyancy frequency (for details, see Carvalho et al., 2017; Schofield et al., 2017). A quality index was used to quantify uncertainty in MLD determination, and profiles with a quality index <0.5 (i.e., MLD not resolved) were filtered out (Carvalho et al., 2017).

The protocol for filtering seawater, storing samples, HPLC pigment/phytoplankton composition analysis, and taxonomic composition of the phytoplankton assemblage via CHEMTAX is described in Schofield et al. (2017). Pigment data were integrated to 50-m depth. Diatoms and cryptophytes have defined marker pigments, while “mixed flagellates” represent taxa including dinoflagellates and unidentified phytoflagellates.

The dissolved inorganic nutrients analyzed were nitrate plus nitrite ($\text{NO}_3 + \text{NO}_2$, hereafter nitrate due to

TABLE 1 Overview of datasets and phenological patterns.

Variable (units)	Annual date and value at the:	Description and reference	Temporal resolution	Season range	Date	Value	Linear trend statistics
Weather at Palmer Station and regional sea ice							
Wind speed (m/s)	Minimum	Weather Station at Palmer Station	Daily; October to March, used a 10-day rolling mean	1991–2019	Dec-30 ± 25.3 days (Nov-5 to Feb-26)	1.9 ± 0.4 (1.29–3.04)	Date: slope = 0.57, $p = 0.31$; Value: slope = 0.006, $p = 0.42$
Snow depth (cm)	First and last day where depth = 0; Duration between first and last day	Snow depth measured at Palmer Station	Daily	1991–2019	Start: Dec-9 ± 21.8 days (Oct-21 to Jan-20); End: May-3 ± 21.8 days (Mar-12 to Jun-8)	Duration: 145.4 ± 34.8 (75–205)	Start: slope = 0.60, $p = 0.22$; End: slope = 0.090, $p = 0.86$; Duration: slope = -0.51, $p = 0.52$
Air temperature (°C)	Maximum	Weather Station at Palmer Station	Daily; used 10-day rolling mean	1991–2019	Jan-25 ± 20.8 days (Dec-19 to Mar-6)	3.3 ± 0.6 (1.85–4.31)	Date: slope = 0.73, $p = 0.11$; Value: slope = -0.02, $p = 0.07$
Sea ice advance and retreat date	Day when sea ice concentration first increases above 15% in autumn and decreases below 15% in the spring	Satellite sea ice concentration (Stammerjohn et al., 2008)	Daily	1991–2019	Advance: Jun-29 ± 20.5 days (May-3 to Jul-25); Retreat: Nov-18 ± 20.9 days (Oct-5 to Jan-5)		Advance Date: slope = 0.20, $p = 0.66$; Retreat Date: slope = 0.17, $p = 0.72$
Seawater sampling at Palmer Station							
Log ₁₀ chlorophyll (µg/L)	Maximum	Palmer seawater intake system	Generally, once a week but occasionally daily to multiple days a week	1991–2018 (missing or no data in 1992–1994, 2007–2009)	Dec-31 ± 31.7 days (Oct-26 to Feb-28)	1.2 ± 0.4 (0.35–1.69)	Date: slope = 0.52, $p = 0.55$; Value: slope = 0.017, $p = 0.10$
Sea surface temperature (°C)	Maximum	Palmer temperature gauge	Daily; used a 5-day rolling mean	1991–2019	Jan-24 ± 20.5 days (Dec-11 to Mar-8)	1.9 ± 0.5 (0.92–3)	Date: slope = -0.52, $p = 0.25$; Value: slope = 0.017, $p = 0.12$
Seawater sampling at Station B/E							
Bacterial biomass (mmol C m ⁻³)	Maximum	Station E water column sampling (Kim et al., 2016)	On average twice a week	2002–2018 (missing or no data 2006–2008, 2018)	Feb-16 ± 35.3 days (Nov-21 to Mar-31)	56 ± 37.9 (24.12–161.2)	Date: slope = -0.29, $p = 0.89$; Value: slope = 1.74, $p = 0.44$

(Continues)

TABLE 1 (Continued)

Variable (units)	Annual date and value at the:	Description and reference	Temporal resolution	Season range	Date	Value	Linear trend statistics
Nutrients: Phosphate (mmol m ⁻²)	Minimum	Station E water column sampling (Kim et al., 2016)	On average twice a week	1991–2018 (missing or no data in 1991–1995, 2000–2001)	Feb-8 ± 34.7 days (Nov-30 to Mar-28)	64 ± 10.7 (40.3–88.77)	Date: slope = 0.88, p = 0.52; Value: slope = -0.75, p = 0.06
Phytoplankton species		Station E water column sampling (Schofield et al., 2017)	On average twice a week	1992–2014 (no data in 2001, 2003, 2004, 2009, 2011)			
Mixed layer depth (m)	Minimum	Station E water column sampling (Carvalho et al., 2017)	On average twice a week	1991–2018 (missing or no data in 1991–1992, 1994–1995, 1998, 2002–2005, 2007–2009)	Jan-22 ± 33.4 days (Nov-16 to Mar-17)	-8.6 ± 4.4 (-19.8–3.96)	Date: slope = -0.91, p = 0.39; Value: slope = -0.13, p = 0.35
Bacteria species		Station B water column sampling at 10 m (Bowman et al., 2017; NCBI SRA at SRP091049, SUB2014638)	Once a week	2015–2019			
Zooplankton species		Station E, oblique net tows to 50 m	On average twice a week	2017–2018			
Sediment trap							
Pteropod presence in sediment trap	Day of first appearance	Sediment trap (Thibodeau, Steinberg, & Maas, 2020; Thibodeau, Steinberg, McBride, et al., 2020)	Time resolution of data varies across the year (see <i>Methods</i>).	2003–2017 (missing 2009)	May-26 ± 44.2 days (Mar-8 to Sept-16)		Date: slope = -2.63, p = 0.34
Particulate organic carbon flux (mg C m ⁻² d ⁻¹)	Maximum	Sediment trap (Trinh et al., 2023; Ducklow et al., 2008)	Time resolution of data varies across the year (see <i>Methods</i>).	1992–2015 (missing data in 2000, 2009 due to lost trap; Samples not processed from 2014 onwards; data gaps 2001, 2008, 2013)	Jan-30 ± 24.1 days (Dec-15 to Mar-16)	49 ± 32.8 (4.76–123.69)	Date: slope = 1.64, p = 0.07; Value: slope = -1.96, p = 0.12

(Continues)

TABLE 1 (Continued)

Variable (units)	Annual date and value at the:	Description and reference	Temporal resolution	Season range	Date	Value	Linear trend statistics
Predators							
Adélie penguin clutch initiation date	Mean date	Breeding chronology at Humble Island (Cimino et al., 2019)	Daily/near-daily penguin nest checks	1991–2016	Nov-13 ± 2.6 days (Nov-9 to Nov-19)		Date: slope = -0.072, $p = 0.29$
Humpback whale sightings (no. individuals/h of effort)	Maximum	Visual sightings of whales from boat-based surveys near Palmer Station	Daily to near-daily surveys but data are summarized by week	2014–2019	Feb-3 ± 32.5 days (Jan-3 to Apr-7)	3.2 ± 2.9 (1.13–8.48)	Date: slope = -8.29, $p = 0.34$; Value: slope = 1.08, $p = 0.13$

Note: Each variable description includes the temporal resolution and data availability, and statistics on phenological events include timing, magnitude, and trends. Statistics include the mean and standard deviation (SD) in dates and values at the minimum/maximum, and linear regression results to determine the trend in dates and/or values over time. Date and value data are given as means ± SD with ranges in parentheses.

the very low concentration of nitrite), phosphate (PO_4^{3-}), and silicate (SiOH^4). Samples were analyzed using standard protocols for nutrient autoanalyzers (i.e., continuous flow analyzers) (Parsons et al., 1984). For simplicity, we focused on phosphate concentrations that have similar seasonal patterns to nitrate concentrations (Kim et al., 2016) (Appendix S1: Figure S1) and are a higher quality dataset with respect to chemical analyses.

Bacterial biomass measurements via flow cytometry are described in Kim and Ducklow (2016) (Table 1). For bacterial *16S rRNA* gene sequencing, seawater was filtered through sterile 0.22- μm Sterivex filters (Millipore Sigma) from 2015 to 2017 and 0.2- μm Supor membrane disc filter (Pall Corporation, Port Washington, NY, USA) from 2018 to 2020, and stored at -80°C until extraction. Filters were extracted using the KingFisher Flex Purification System and MagMax Microbiome Ultra Nucleic Acid Extraction kit (ThermoFisher Scientific, Waltham, MA, USA). Extracted DNA was sent to Argonne National Laboratory for amplicon library preparation and sequencing using the Illumina MiSeq platform with the universal primers 515F and 806R (Walters et al., 2016), and a 2×151 bp library architecture. Reads were filtered, denoised, and merged with dada2 (Callahan et al., 2016) and then analyzed with paprica v0.7.0 (Bowman & Ducklow, 2015). Paprica utilizes phylogenetic placement with Gappa (Czech et al., 2020), EPA-ng (Barbera et al., 2019), and Infernal (Nawrocki & Eddy, 2013), and to place query reads on a reference tree constructed from the full-length *16S rRNA* genes from all completed genomes in GenBank (Haft et al., 2018). All unique reads were assigned to internal branches or terminal branches on the reference tree, and reads that were assigned as metazoan mitochondria or chloroplasts were omitted, as well as any reads that only appeared once (25% of all amplicon sequence variants). Sequences are available at NCBI SRA (Table 1).

Particle flux

A conical sediment trap (PARFLUX Mark 78H 21-sample trap, McLane Research Labs) was moored at 350-m depth with the trap suspended at 170 m on the northern WAP continental shelf ($64^\circ 30' \text{S}$, $66^\circ 00' \text{W}$; Figure 1) (Ducklow et al., 2008). The trap has 21 sample bottles that collect sequential samples throughout the year such that the sample bottles rotate weekly during peak particle flux in austral summer (November–April) and rotate monthly (bimonthly in July–August) during austral winter (May–October) (Ducklow et al., 2008).

Upon recovery each year, the trap samples were sealed and held at 5°C until return to the United States

for processing. Samples from heavy sediment flux periods were split up to 1/512 for subsequent analysis. Zooplankton swimmers were removed from each trap sample prior to being assayed. Total mass, dry mass, particulate organic carbon (POC), and particulate nitrogen were measured from each sample. Detailed methods for zooplankton removal are described in Ducklow et al. (2008) and sediment trap chemical analyses are described in the JGOFS Protocols (Knap et al., 1996). Briefly, after removal of zooplankton swimmers and splitting, samples were dried, homogenized, and fumed with dilute HCl to remove inorganic carbon. POC was measured on CHN Analyzers. Due to the multidecadal nature of the Palmer LTER, POC was measured at several institutions on several different CHN Analyzers: Perkin-Elmer 2400 (1992–May 1994), Europa Scientific SL (June 1994–1997), Exeter Analytical Elemental Analyzer (1997–2003), Carlo Erba EA 1108 (2003–2007), and Perkin-Elmer 2400 and Thermo Scientific Flash 2000 (2007–2013). Samples were all run against the same standard, acetanilide (C₈H₉NO) (Ducklow et al., 2008; Karl et al., 1991). Up to three replicate analyses of chemical properties were performed on each sample and the analytical replicates were averaged for each sample. When multiple traps were simultaneously deployed adjacent to each other during the same time frame, samples were averaged for corresponding intervals (Ducklow et al., 2008).

Zooplankton

Limacina rangii pteropods were also collected from the sediment trap from 2003–2004 to 2017–2018 and typically were present from April to December due to their ontogenetic vertical migration (see methods in Thibodeau, Steinberg, McBride, et al., 2020). Date of appearance was determined as the median date during the first sampling interval when more than 10 unbroken *L. rangii* shells were present in a sample cup for a given year (Thibodeau, Steinberg, McBride, et al., 2020).

Macro- and mesozooplankton were collected twice per week at Station E from December to March during the 2017–2018 and 2018–2019 field seasons. Zooplankton were collected using two net types: a 1 × 1 m, 700- μ m mesh square net and a 1-m diameter, 200- μ m mesh ring net, which were both towed obliquely to a target depth of 50 m. Sampling details and zooplankton abundance data are presented in Conroy et al. (Trinh et al., 2023).

Taxon-specific dry mass densities (in milligrams per cubic meter) were used to summarize zooplankton composition. For amphipods, larval fishes, and the krill species *Euphausia superba* and *Thysanoessa macrura*,

biovolume (measured by displacement) was converted to wet mass (1 g wet mass per 1 mL biovolume). Dry mass was calculated as 20% of wet mass for amphipods and larval fishes and as 25% of wet mass for euphausiids (M. Thomas and D. Steinberg, personal communication, 2022). For the pteropod *Limacina rangii* and gymnosome pteropods, respective individual dry masses of 8 and 20 mg were assumed (Thibodeau, Steinberg, & Maas, 2020). Individual dry masses were also used for chaetognaths (0.007 mg) (Mizdalski, 1988) and the copepods *Oithona* spp. (0.002 mg) (Metz, 1996), *Calanoides acutus* (0.8 mg) (Gleiber et al., 2016), *Calanus propinquus* (1.5 mg) (Gleiber et al., 2016), and *Rhincalanus gigas* (1.3 mg) (Gleiber et al., 2016). The mean individual body volume of small calanoid copepods (mostly 0.5–1 mm) was calculated as 0.025 μ L by assuming the body was a prolate spheroid with a length of 0.75 mm and width of 0.25 mm (Skjoldal et al., 2013). Individual dry mass of 0.005 mg was calculated from biovolume as described above for other taxa.

Penguins

Adélie penguin breeding phenology has been studied at Palmer Station since 1991 (Cimino et al., 2019). Briefly, each year nest sites were monitored daily or near daily by recording the date of egg lay/loss and egg hatch/loss. For the colony on Humble Island, we used mean clutch initiation dates (CIDs, the day the first egg was laid) and hatch dates for each year (from Cimino et al., 2019). The guard phase is the date of hatching to the date of crèche (~20 days of age) when chicks are guarded and brooded at all times by at least one parent (Sladen, 1958). We highlight this period as time from hatch to 20 days afterward (Chapman et al., 2011). Chicks then enter their phase of most rapid growth, the crèche phase, when chicks form independent groups outside of the nest (Taylor & Roberts, 1962).

Adélie penguin chick fledging mass (CFM) was measured at Humble Island as chicks gathered on beaches and occur approximately 54 days after eggs hatch (for methods and drivers, see Chapman et al., 2011; Cimino et al., 2014; Salihoglu et al., 2001). We used 54 days after hatch to highlight fledge dates. In Adélie and other penguin species, CFM is an important indicator of chick overwinter survival and subsequent recruitment into the breeding population (Cappello & Boersma, 2021; Chapman et al., 2010). Protocols were carried out in accordance with the approved guidelines of the Columbia University Institutional Animal Care and Use Committee (Assurance number AAAH8959).

Whales

Visual observations of whales were recorded during boat-based surveys within the Palmer Station boating limits (Figure 1). The number of observations was standardized by effort and summarized weekly. Our results focus on the total number of humpback whale sightings for all ages. Minke whales were not included due to low sample size. All whale observations were conducted under scientific research permits issued by the National Marine Fisheries Service (NMFS) under the authority of the Marine Mammal Protection Act of 1972 (permit numbers: 14809 and 23095) and National Science Foundation (NSF) Antarctic Conservation Act (ACA) permits (2015-011 and 2020-016).

Predator sightings from Palmer Station reports

To obtain additional information on predator species (penguins, seals, and whales) presence in the Palmer region from March to October when we do not usually have personnel in the field, we reviewed monthly reports produced by the on-station research associate from 2010 to 2021 (<https://pal.lternet.edu/publications/station-cruise-reports>). These reports often document animal observations as interesting anecdotal information. We used these reports as presence-only information and pooled records across months to ascertain the likelihood of species presence in the Palmer region during the austral winter along with information from literature reviews.

Statistical analyses

To identify when important phenological events occur for most variables of interest (summarized in Table 1), we determined the day of the year with either the minimum or maximum value and the corresponding value at that minimum/maximum. In addition, we focused on the day of sea ice retreat and advance, the first and last day with snow on the ground, the day of pteropod appearance, and penguin CIDs. For parameters with high daily variability (i.e., air temperature, wind speed, SST), we smoothed the data using a 5- or 10-day rolling mean (see Table 1) because the period with sustained minimum/maximum values is more informative than a one-day peak. Datasets with daily to near-daily measurements allow for higher certainty in determining the true day of the minimum/maximum value. We show the annual and climatological seasonal progression of these variables and report the mean, range, standard deviation, linear trend, and coefficient of variation in the day and value at

the minimum/maximum for each parameter. For the coefficient of variation, temperature measures were converted to Kelvin, which is appropriate for this statistic. We investigated variability in the mean conditions across years, and the anomaly from the mean in the five earliest (1992, 1998, 2007, 2008, and 2010) and latest (1991, 1994, 2004, 2013, and 2015) sea ice retreat years. To calculate these anomalies, the mean of the conditions in all years was subtracted from the mean of early and late retreat years. We compared the coefficient of variation in the date and/or value at the day of the minimum/maximum in early and late sea ice retreat years. When visually comparing the values at the minimum/maximum across variables, we scaled values between 0 and 1.

We computed linear regressions between the day of sea ice retreat and day of the minimum/maximum value for each variable to determine which parameters were significantly related to the timing of sea ice retreat. We also used generalized additive models (GAMs) to test hypotheses that the phenology of certain events drives the phenology of other events or species demographics. GAMs are capable of fitting complex nonlinear relationships, and a smoothness parameter(s) was estimated by generalized cross-validation using the R “mgcv” package (R Core Team, 2019, version 4.0.5). Models were run with a Gaussian error distribution. Using a stringent Pearson’s correlation coefficient threshold of 0.5, we eliminated correlated independent variables that had a less direct influence on the response variable.

We tested for four different candidate models that represent our hypotheses on ecosystem phenology near Palmer Station: (1) if the day of the chlorophyll maximum was related to the timing of maximum SST, minimum wind speed and sea ice retreat; (2) if the day of the phosphate minimum was related to the timing of maximum chlorophyll and SST, sea ice retreat, and minimum wind speed; (3) if the day of the bacterial biomass maximum was related to the timing of maximum chlorophyll and SST, and sea ice retreat; and (4) if Adélie penguin CFM was related to the timing of the maximum SST, chlorophyll, and air temperature, minimum wind speed, sea ice retreat, and the first day with no snow on the ground. Our models were limited to variables with sufficient sample sizes. For example, MLD was likely an important driver of many of these processes but was not used due to a low sample size as it was often the case that the MLD could not be resolved, and similarly, a change in the timing of whale presence could result in greater competition for krill and impact CFM but the sample size was low (Table 1). For each candidate model representing our hypotheses, all possible combinations of predictors were fit using the dredge function within the R package MuMIn (Barton & Barton, 2015). The best fit models

were determined by the corrected Akaike information criterion for small sample size (AIC_c) (Burnham & Anderson, 2002). We report models with a $\Delta AIC_c < 2$, which were considered to have substantial support. We also report the percent contribution of each variable to each model, the adjusted R^2 , the percentage of deviance explained, log-likelihood, Akaike weight, and Pearson's correlation between observations and fitted values.

To view the system from a penguin perspective, we subtracted Adélie penguin CIDs from each phenological variable and determined the mean and standard deviation in the number of days before/after clutch initiation that each event occurred. Using the predictor variables in the supported GAMs for Adélie penguin CFM, we show the mean dates for these key parameters in the three highest and lowest CFM years to demonstrate the potential optimal environmental timing.

RESULTS

Mean phenological patterns

There are strong seasonal cycles in the physical environment, phytoplankton blooms, bacterial accumulation, species presence, and breeding patterns (Appendix S1:

Figure S1) that mainly relate to changes in photoperiod and corresponding temperature changes driving spring sea ice retreat and its subsequent advance in autumn. The mean sequence of seasonal events in relation to the Adélie penguin breeding cycle is as follows (Figure 5). Adélie penguins arrive to their breeding colonies in mid- to late October and lay eggs in mid-November as sea ice is typically retreating and snow is nearly melted (on average, by early December), with chicks subsequently hatching in mid- to late December as day length reaches its maximum (Figure 5). Shortly after, during the chick guard phase in early January, chlorophyll concentrations peak and wind speeds are at a minimum. MLDs reached a minimum as air and sea temperatures peak in mid- to late January. This is followed by maximum POC flux and whale sightings, and minimum phosphate concentrations as Adélie penguin chicks fledge in early February. Bacterial biomass reaches a maximum near the end of our sampling period in mid-February (Appendix S1: Figure S1) but may continue to increase beyond this time. It is not until early May that snow begins to accumulate on the ground again, which is near the time that a new cohort of pteropods begins to appear in the sediment trap. A few weeks later, at the end of June, sea ice begins advancing in our study domain and day length is at its minimum (Figure 5).

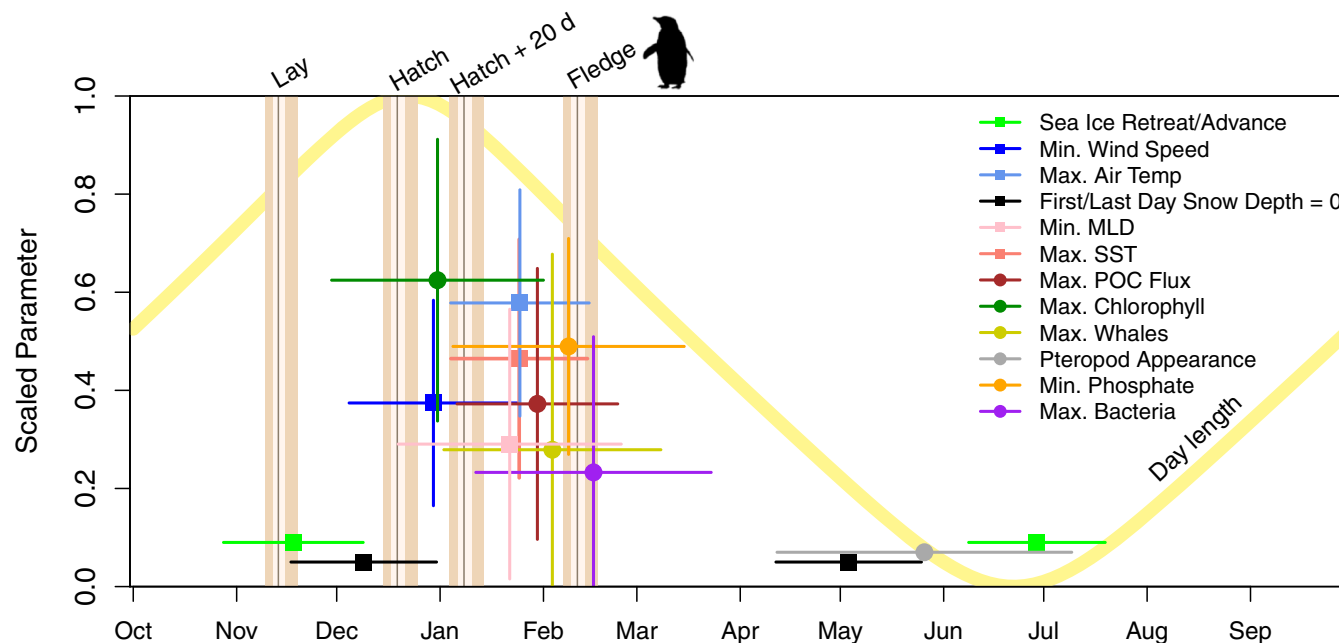


FIGURE 5 Phenological patterns in key parameters measured near Palmer Station. The phenological timeline highlights the mean and standard deviation in the timing and magnitude of events in relation to the Adélie penguin breeding cycle with the brown vertical line representing the mean, the beige inner bar is the 25%–75% quantile, and tan outer bar is the range. The chick incubation phase is from the time eggs are laid until hatch; the guard phase is from hatch until crèche (hatch + 20 days) when chicks are guarded full time by parents; and the crèche phase is from approximately 20 days of age until chicks fledge. All parameters were standardized between 0 and 1. Squares indicate ice–ocean–atmosphere physical drivers. MLD, mixed layer depth; SST, sea surface temperature; POC, particulate organic carbon.

Interannual variability and trends in phenological patterns

Superimposed on this mean sequence of seasonal events is high interannual variability in the timing of these events (Figure 4; Appendix S1: Figure S1). The timing of many weather (wind, snow, and air temperatures) and ocean (SST and sea ice) conditions as well as POC flux had standard deviations ranging from 20 to 25 days, while other parameters (nutrients and MLD) and biological properties (chlorophyll, bacterial biomass, and whale sightings) had standard deviations ranging from 31 to 35 days (Table 1). Pteropod appearance had the highest standard deviation at 44 days, but was also the parameter with lowest sampling resolution (bimonthly to monthly), and thus, least certainty in defining its phenology (Table 1). Thus, these standard deviations should be interpreted in relation to sampling frequency, such as daily (weather, sea ice, and SST), biweekly (nutrients, MLD, chlorophyll, and bacteria), versus weekly (whales and POC flux), where datasets with biweekly to weekly sampling should have greater uncertainty in determining the day of the minimum/maximum, and thus, potentially a higher standard deviation as a result. Overall, this variability was still striking in comparison to the interannual variability in mean Adélie penguin CIDs at ~3 days and intra-annual variability that was generally within 1 week (Cimino et al., 2019). There was also notable variability in the maximum or minimum value for all properties (Figure 5; Table 1).

During the LTER study period, there were only a few marginally significant trends. The maximum air temperature decreased over time ($-0.02^{\circ}\text{C year}^{-1}$, $p = 0.07$), potentially because the day of peak temperature was slightly later over time ($0.73 \text{ days year}^{-1}$, $p = 0.11$; Table 1). There was also a marginally significant trend toward higher chlorophyll concentrations ($0.017 \text{ mg L}^{-1} \text{ year}^{-1}$, $p = 0.10$) but no significant trend in the timing of peak concentrations. Similarly, the value of minimum phosphate concentrations decreased over time ($0.75 \text{ mmol m}^{-2} \text{ year}^{-1}$, $p = 0.06$), also with no significant trend in timing, suggesting larger phytoplankton blooms resulted in greater nutrient drawdown. Given that the timing of the spring sea ice retreat is considered to be a major ecosystem driver (at least initially in spring), the absence of many linear trends in phenological events follows the absence of a significant trend in the spring sea ice retreat, at least as observed during our study period (1991–2019), which notably stands in contrast to the 1979–2010 time period when a stronger trend toward an earlier spring ice retreat was observed (Figure 2). In comparison, the autumn sea ice advance was more variable but significantly trended toward a later advance during 1979–2019 ($0.70 \text{ days year}^{-1}$, $p = 0.03$) and 1979–2010

($1.48 \text{ days year}^{-1}$, $p = 0.002$; Figure 2). The high interannual and decadal variability in the day of sea ice retreat and advance resulted in different rates of change over different time periods, which is necessary to consider when examining trends since the late 1970s (beginning of satellite era) versus during the LTER study period (1991 onwards) (Figure 2).

Sea ice as a driver of phenology

Given the high interannual variability in both spring sea ice retreat and ecosystem variables just noted, it is not surprising that only a few ecosystem parameters showed significant linear relationships with the timing of spring sea ice retreat. In these few cases, nearly all linear relationships were positive, for example, a later/earlier spring ice retreat coincided with later/earlier Adélie penguin CIDs ($p = 0.004$), later/earlier first day with no snow on the ground ($p = 0.06$), later/earlier peak whale sighting ($p = 0.02$), and later/earlier pteropod appearance ($p = 0.06$). In comparison, a later/earlier sea ice retreat led to an earlier/later sea ice advance ($p = 0.001$).

Another way to test sea ice as a driver of phenology, especially when interannual variability is particularly high and/or there is an asymmetric phenological response to late versus early spring sea ice retreat, is to investigate the phenological anomalies associated with the five latest (1991, 1994, 2004, 2013, and 2015) versus five earliest (1992, 1998, 2007, 2008, and 2010) sea ice retreat years (Figure 6a; Appendix S1: Figure S1). In late sea ice retreat years, the following events happened later (upper panel of Figure 6a): penguin CIDs, snow melt, chlorophyll and bacterial peaks, minimum MLDs, minimum phosphate, maximum whale abundance, and pteropod appearance; while the following events happened earlier: minimum wind speed, maximum SST, maximum POC flux, snow accumulation, and ice advance. Notably, many of these phenological anomalies ranged between 10 and 20 days (i.e., were 10–20 days later or earlier than their respective means). Further, in late retreat years, the magnitude of the anomalies (i.e., the value of each variable at the maximum/minimum; lower panel of Figure 6a) showed lower wind speeds, deeper MLDs, colder air/sea temperatures, short-lived summer POC flux, and lower whale abundances. While late retreat years had near-average chlorophyll, phosphate, and bacterial biomass concentrations, earlier retreat years showed large negative anomalies. A few of these datasets had low sample sizes (e.g., whales, MLD, and POC flux), thus relationships should be treated with caution. However, these relationships generally follow known connections between each parameter and sea ice

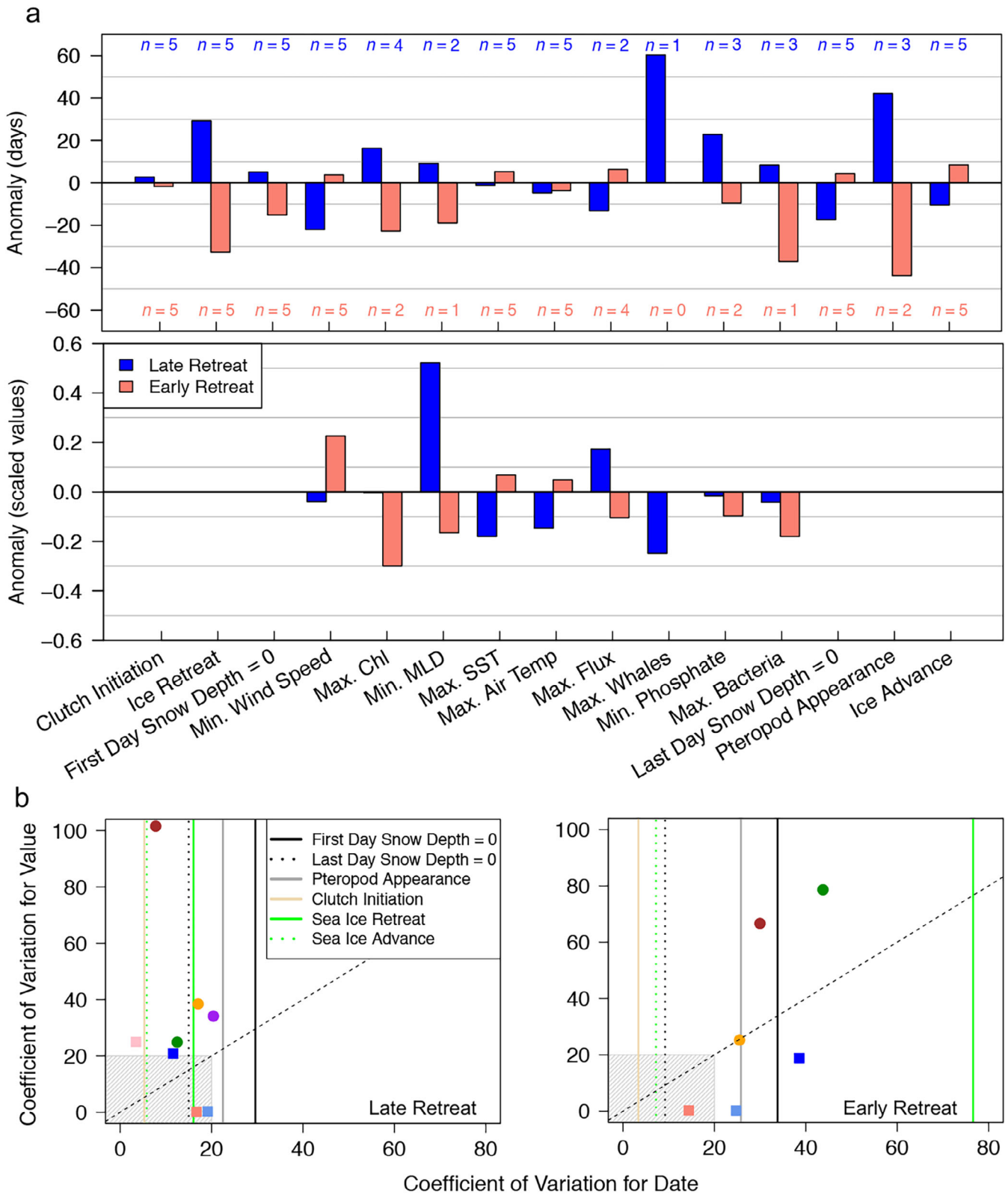


FIGURE 6 Phenological anomalies and variability in key parameters measured near Palmer Station. (a) Phenological anomalies in the mean top five late and early sea ice retreat years in the timing (top) and magnitude (bottom) of key events. *N* represents the sample size for each variable. To calculate the anomalies, the climatological means were subtracted from the mean of early or late years. (b) Phenological variability in the timing and magnitude of key events is represented by the coefficient of variation in years with late and early sea ice retreat. Colors are identified in Figure 5. Years with late retreat were 1991, 1994, 2004, 2013, and 2015 and years with early retreat were 1992, 1998, 2007, 2008, and 2010. Vertical lines are datasets where only the date was recorded (i.e., there is no corresponding value at that date). The gray box highlights a low coefficient of variation and the diagonal line is a 1:1 relationship. chl, chlorophyll; MLD, mixed layer depth; SST, sea surface temperature.

preconditioning except for the case of deeper MLDs with later sea ice retreat.

There were also different patterns in coefficient of variation in late versus early sea ice retreat years (Figure 6b). Late sea ice retreat years had a lower coefficient of variation, with the date of the minimum/maximum value often within ~20% (with exception of snow melt and pteropod appearance) and the magnitude of the value at the minimum/maximum generally <25% (with exception of phosphate, POC flux, and bacterial biomass). Early retreat years often had a higher coefficient of variation with only the SST maximum, penguin CID, the last day with no snow, and sea ice advance within the 20% coefficient of variation. Interestingly, the day of sea ice retreat had the highest coefficient of variation of ~80%. These results suggest under late ice retreat the system is more “predictable”—especially from the perspective of Adélie penguins that established life history patterns over evolutionary time based on dependable environmental conditions.

Additional drivers of phenological variability

GAMs were used to relate the timing of the chlorophyll maximum, phosphate minimum, bacterial biomass maximum, and Adélie penguin CFM to the timing of hypothesized important phenological events (Table 2). For the chlorophyll maximum models, two separate models containing the day of sea ice retreat and minimum wind speed were the only models with a $\Delta AIC_c < 2$ (deviance explained = 6.8% and 13%; Appendix S1: Figure S2) where a later retreat or minimum wind speed led to a later chlorophyll maximum. The date of the phosphate minimum was positively linearly related to the day of the chlorophyll maximum, explaining 31.5% of deviance (Figure 7a; Appendix S1: Figure S3), and on average the phosphate minimum was 40 days after the chlorophyll maximum. The day of the bacterial biomass maximum was related to the day of sea ice retreat and SST peak with SST being the stronger predictor (variable importance = 67%). These two

TABLE 2 Models describing phenological events and species demographics.

Model no.	Formula (percent contribution)	R^2	Deviance explained (%)	Log-likelihood	AIC_c	ΔAIC_c	Akaike weight	R (observed vs. fitted)
Day of maximum chlorophyll ($n = 22$)								
1	1	0	0	-106.8	218.18	0	0.49	NA
2	Day of sea ice retreat (100)	0	6.81	-106	219.33	1.15	0.28	0.26
3	s(Day of min. wind) (100)	0.1	13.49	-105.2	219.64	1.46	0.24	0.38
Day of minimum phosphate ($n = 16$)								
4	Day of max. chl. (100)	0.3	31.65	-76.3	160.59	0	1	0.56
Day of maximum bacteria biomass ($n = 16$)								
5	Day of sea ice retreat (32.95) + Day of max. SST (67.05)	0.6	69.86	-52.54	118.79	0	0.6	0.84
6	Day of max. SST (100)	0.5	52.35	-55.29	119.57	0.78	0.4	0.72
Adélie penguin chick fledging mass ($n = 21$)								
7	Day of min. wind (100)	0.3	29.26	-121	249.49	0	0.39	0.54
8	First day without snow (43.51) + Day of sea ice retreat (27.84) + s(Day of max. SST) (28.65)	0.4	46.57	-118.1	250.19	0.69	0.27	0.68
9	First day without snow (26.63) + Day of min. wind (73.37)	0.3	34.6	-120.2	250.93	1.44	0.19	0.59
10	Day of max. air temperature (11.33) + First day without snow (37.69) + Day of sea ice retreat (23.32) + s(Day of max. SST) (27.65)	0.4	53.66	-116.6	251.36	1.87	0.15	0.73

Note: Generalized additive models relating phenological events or species demographics to the timing (e.g., day of minimum or maximum value) of other important events from 1991 to 2019. The models are described by the R^2 , deviance explained, log-likelihood, corrected Akaike information criterion for small sample size (AIC_c), ΔAIC_c (difference from the lowest AIC_c ; the amount of information lost), Akaike weight revealing relative model support, and the Pearson's correlation (R) between observed and predicted values. Variable importance is shown by the percent contribution to the model. Only models with substantial support ($\Delta AIC_c < 2$) are shown. Each dataset has different data gaps (sample sizes [n] are shown).

Abbreviation: SST, sea surface temperature.

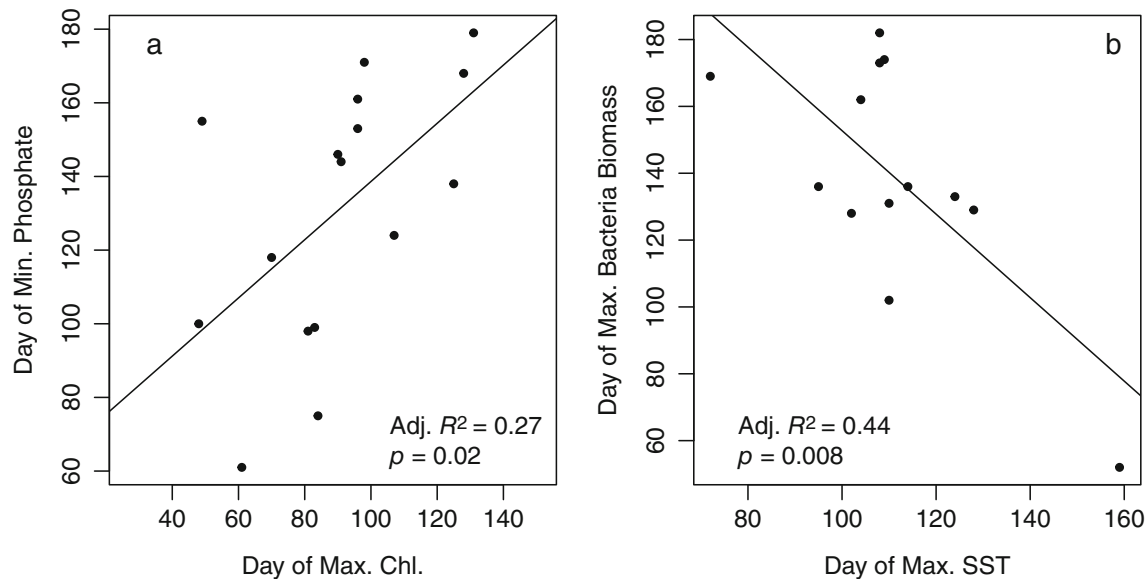


FIGURE 7 Relationships between (a) the day of minimum phosphate and maximum chlorophyll (chl) and (b) the day of maximum bacterial biomass and maximum sea surface temperature (SST).

best performing models explained 52%–70% of the deviance. A later sea ice retreat led to a later bacterial biomass maximum, while a later SST peak led to an earlier maximum (Figure 7b; Appendix S1: Figure S4).

The seasonal progression of phenological events from a penguin perspective showed sea ice retreat occurred around the time that penguins lay eggs, snow melted during the middle of the incubation phase, the wind minimum and chlorophyll maximum occurred shortly after chicks hatched, followed by a suite of events occurring during the crèche phase—including minimum MLD, maximum air/sea temperature, maximum POC flux, and minimum phosphate (Figure 8a). The maximum bacterial biomass and whale abundance occurred near the time of chick fledging. Months after Adélie penguins left their colonies, snow began to accumulate, pteropods appeared at depth, and sea ice advanced.

CFM is an integrated measure of parental investment from incubation to chick fledging given food resources and environmental constraints. For CFM, there were four models that performed well and explained ~30%–53% of the deviance (Table 2). These models contained different combinations of five variables: the day of the wind speed minimum, sea ice retreat, SST and air temperature maximum, and the first day with no snow on the ground. A later wind minimum, SST peak, and first day with zero snow were related to lower CFM, while a later air temperature maximum and sea ice retreat were related to higher CFM (Appendix S1: Figure S5). The three highest and lowest CFM years demonstrated these relationships (Figure 8a). In most models, the effect of wind, SST, and snow on CFM was more than a 200 g decrease, while the effect of sea ice

and air temperature on CFM was an ~140 g increase (Figure 8b). A 100–200 g change in CFM could influence chick overwinter survival in the Antarctic Peninsula and Ross Sea (Ainley et al., 2018; Chapman et al., 2010).

DISCUSSION

Using multidecadal records from a long-term monitoring program, we summarized a diverse assemblage of species and their occupancy patterns, and determined the mean, variability, trends, and relationships between phenological events near Palmer Station. We found high interannual variability but few significant phenological trends. We acknowledge some uncertainty in our results due to the temporal resolution of measurements, which varied across datasets from daily to over a week, and the length of each time series ranging from a few years to multiple decades (Table 1). We also did not focus on how underlying decadal variability may affect relationships based on the various lengths of different time series. However, by merging these datasets and focusing on the highly productive spring–summer season, we tested and confirmed the long-standing hypothesis that a main driver of ecosystem dynamics is the timing of the spring sea ice retreat. We created a conceptual illustration to visualize the main patterns (Figure 9). Our results suggest the ecosystem is more “predictable” during years of late sea ice retreat when the timing of phenological events is more similar (i.e., lower variability) than during years of early sea ice retreat. This is notable for species with inflexible life history strategies that are dependent on the consistent timing of key events

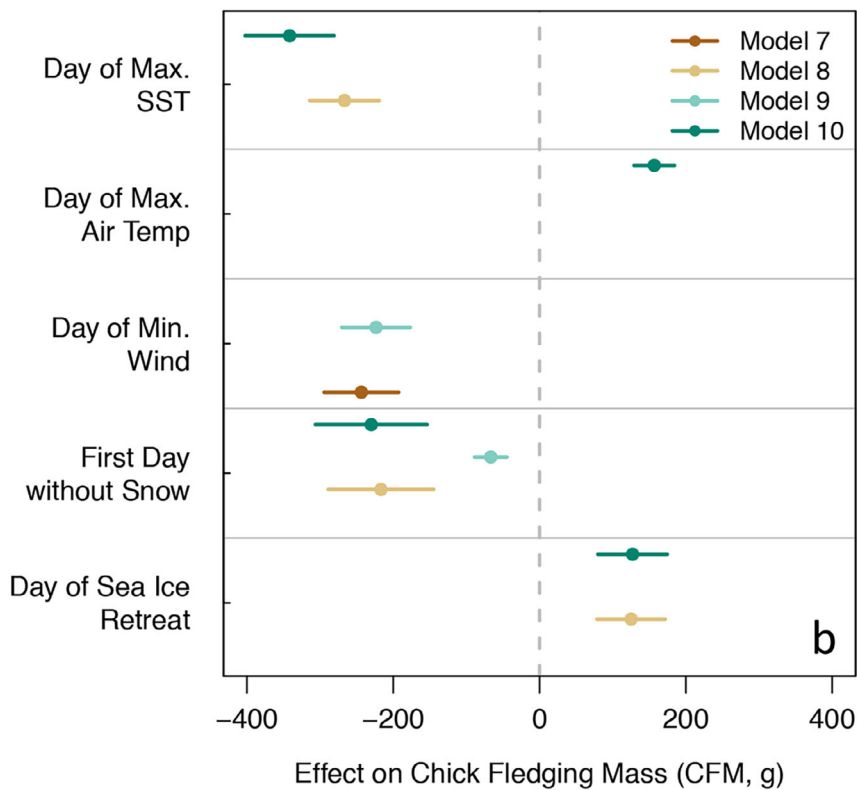
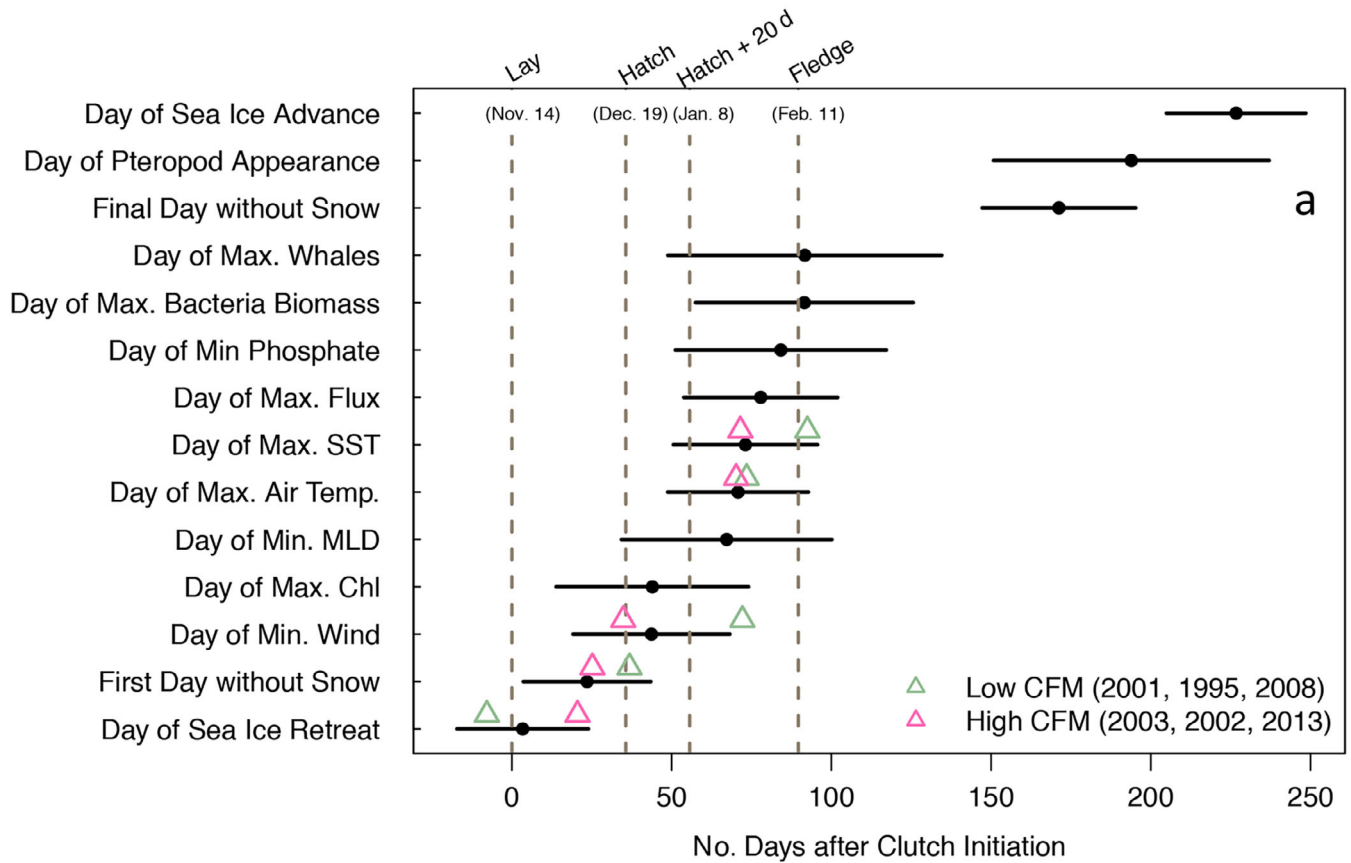


FIGURE 8 Legend on next page.

for survival or reproduction. For example, the Adélie penguin can shift its phenology (days to a week) in response to the environment (Cimino et al., 2019), but this likely is not enough to match the larger shifts in the environment (weeks to over a month), making them susceptible to mismatches in optimal environmental windows or prey characteristics (Cury & Roy, 1989). The long-term nature of this research program provided a unique opportunity to investigate patterns in ecosystem phenology in a warming region, while simultaneously filling and revealing gaps in our understanding; this study provides context for how we might expect ecosystem shifts to manifest under continued climate change.

Phenological patterns in the physical environment

We provide the first ecosystem-wide quantitative timeline of important phenological events in the Palmer Station vicinity, including sea ice, weather, oceanography, and biological responses. In Antarctica, there is a strong seasonal cycle in solar irradiance and weather conditions with day length varying from <4 h in winter to >21 h in summer at Palmer Station. The weather is generally mild, compared with the interior of Antarctica, but strong seasonal cycles can be punctuated by high daily to weekly variability due to periodic storms and atmospheric anomalies. Increasing day length and the timing of sea ice retreat in the spring trigger a sequence of events near Palmer Station during the austral summer when critical biological activities occur. During years of early sea ice retreat, the ocean is exposed to atmospheric forcing for a longer period of time compared with years of later sea ice retreats (Figure 9). Depending on storm characteristics during spring/early summer, this can lead to different ecosystem conditions and, thus, high variability in phenological events. In general, during years of early retreat, events happened earlier and conditions were warmer, windier, and snow melted earlier.

While we did not detect major phenological trends, there were strong physical and biological responses to variability in sea ice retreat. In general, long time series are needed to detect meaningful trends because short-term studies can produce spurious, misleading results (Cusser

et al., 2020). Cusser et al. (2020) suggest that the impact of research can be maximized at any time scale by understanding how patterns emerge as studies become longer. Further, the length of the time series needed to detect a consistent trend likely varies by location, the process under investigation, and the stability of the system studied. With the high variability at our study site and possible increased variability in the future (Bracegirdle et al., 2019; Rintoul et al., 2018), it appears that a time series longer than three decades is needed to produce statistically significant trends for many biological responses under study in the context of longer term (40–80+ years) warming trends that are not present in our shorter LTER time series (Henson et al., 2010). As previously discussed, many of our variables under study span the full LTER time series but some do not (e.g., whales), and the certainty of the phenological trend may also depend on the temporal resolution of the measurement (e.g., daily vs. weekly). Therefore, continued monitoring and more frequent measurements would benefit phenological trend detection. Similarly, the variables analyzed in this study were observed at one location (the Palmer Station area), a location characterized by strong coastal dynamics and thus higher variability relative to the broader WAP region. Indeed, studies of satellite-derived phytoplankton phenology over 1997–2022 show spatial trends including a later start to the growing season over the offshore area defined by the outer marginal ice zone (J. Turner, personal communication). While high-latitude regions are expected to have strong phenological trends (Poloczanska et al., 2013), we emphasize that it is important to consider the underlying environment during the period of study regardless of time series length to avoid incorrect ecological interpretations (e.g., concluding no phenology trend amid climate change when one would not be expected based on stable physical drivers). Our results suggest that when sea ice trends become significant within our LTER time series, we will detect significant trends in phenological events.

Phenological patterns at low- to mid-trophic levels

Phytoplankton, bacteria, and zooplankton species usually show predictable patterns of species occurrence. Each

FIGURE 8 Ecosystem phenology from an Adélie penguin perspective and the associated effects of variation in phenology on chick fledging mass (CFM). (a) The mean and standard deviation in the number of days after clutch initiation (first egg laid) that each phenological event occurred. Vertical lines are the average date of egg lay, chick hatch, 20 days after hatch, and chick fledging. For the three lowest and highest CFM years, the mean day of phenological events for variables that were predictive of CFM are shown in green and pink (Table 2). (b) The mean and standard deviation in the predicted effect of each independent variable on CFM when individual variables were increased from the four best performing generalized additive models (Table 2). chl, chlorophyll; MLD, mixed layer depth; SST, sea surface temperature; temp, temperature.

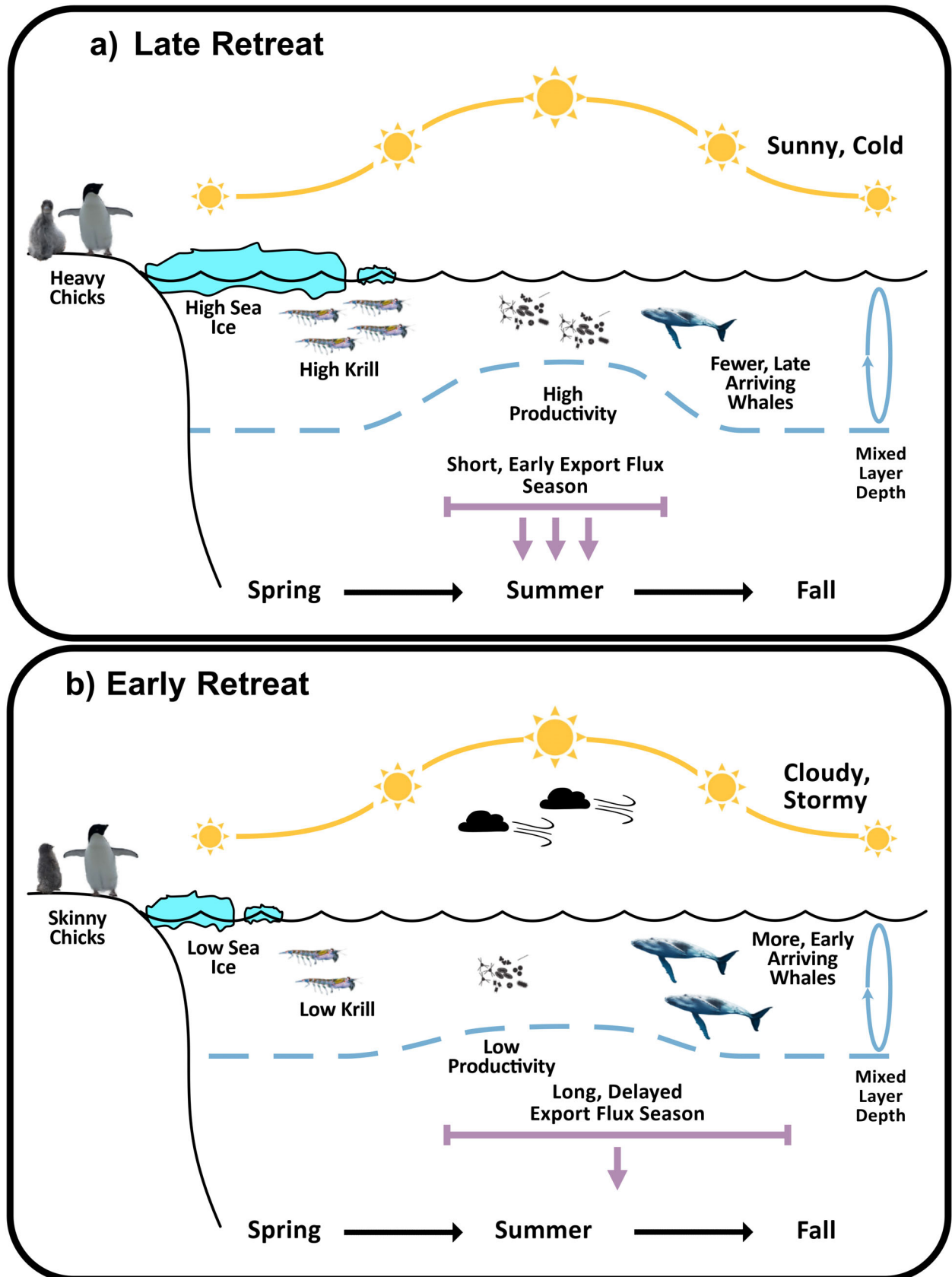


FIGURE 9 Legend on next page.

group has about five taxa that dominate the community composition each year. The chlorophyll maximum occurred on average in early January, but there was high variability in both the timing and magnitude of the bloom. Models for the chlorophyll maximum showed later sea ice retreat and wind minimum caused a later chlorophyll maximum, which explained ~10% of the deviance, suggesting that a seasonal maximum/minimum alone does not capture the dynamics of organisms with high turnover rates (~weekly). Sea ice and wind influence water column stratification where shallow MLDs and exposure to sufficient light levels lead to phytoplankton blooms (Lin et al., 2021; Saba et al., 2014; Schofield et al., 2010; Van Leeuwe et al., 2020). Ephemeral storms can cause a variable light environment through cloudiness and wind-driven water column mixing that likely influence the timing and magnitude of blooms and may play a larger role in bloom phenology in years of early sea ice retreat. While nutrients did not have a dominant role in bloom dynamics, the timing of the chlorophyll maximum was the only leading indicator of the timing of the phosphate minimum, emphasizing the predictable nature of phytoplankton nutrient utilization.

Bacterial biomass peaks were on average in the middle of February, one of the latest biological events in our timeline (except the appearance of whales and pteropods), but the bacterial biomass climatology (Appendix S1: Figure S1) suggests bacteria continue accumulating at the end of our sampling period, likely taking advantage of the period with warm water. The steady increase in bacterial biomass throughout the summer is not due to growth rates that peak in mid-summer but likely due to decreasing loss rates (e.g., viruses, bacterivores). This pattern was different from phytoplankton dynamics, with a mid-season peak and then a decline driven by day length and irradiance (Tortell et al., 2014). In most polar studies, bacterial peaks lag phytoplankton blooms by about 2–4 weeks (Billen & Becquevort, 1991; Ducklow et al., 2001), but here differences range 11–108 days but on average are 58 ± 32 days, and may be even greater if bacteria biomass reaches its true maximum outside of our study period. Models for the bacterial biomass maximum showed later sea ice retreat led to a later bacterial biomass maximum, whereas a later

SST peak led to an earlier maximum, which explained ~50%–70% of the deviance. The timing of the SST maximum was the strongest predictor. Warm water causes high bacterial production (Ducklow et al., 2012; Kim & Ducklow, 2016), and therefore, when the SST peak occurs earlier, there is an extended period of warm water favoring bacterial growth and leading to a later bacterial biomass maximum. Increasing bacterial production may have large implications for POC export attenuation, as more organic carbon is recycled through the microbial loop in the euphotic zone.

Taxa-specific life history traits and multiple environmental cues drive seasonal shifts in Antarctic zooplankton composition. Recruitment and seasonal migrations (vertical and horizontal) are fundamental processes underlying zooplankton changes throughout the annual cycle in the Southern Ocean (Dietrich et al., 2021; Ward et al., 2012). As a result, zooplankton taxonomic and size composition change from spring to late summer as SST increases after sea ice retreat near Palmer Station (Figure 3; Conroy et al., n.d., unpublished manuscript). The seasonal ascent of Antarctic zooplankton is coupled to sea ice retreat and the onset of increased phytoplankton productivity (Atkinson & Shreeve, 1995; La et al., 2019). Earlier phytoplankton blooms as a result of earlier sea ice retreat likely result in earlier accumulation of zooplankton biomass in surface waters. There is a risk of mismatch in the timing of phytoplankton blooms and zooplankton consumption, but the generalist diets of zooplankton likely limit population-level consequences, which rarely have been demonstrated in nature (Atkinson et al., 2015; Kharouba & Wolkovich, 2020). However, changes in zooplankton diet composition due to seasonal mismatches may impact their physiology, affecting their quality as prey for higher predators.

The ecological ramifications of phenological shifts at lower trophic levels are complex, and further study is needed to understand the consequences. With climate change, the expectation is for warmer waters, reduced phytoplankton biomass (smaller cell sizes), and more frequent salp blooms (Bracegirdle et al., 2008; Brown et al., 2019; Moline et al., 2004). High phytoplankton productivity leads to high krill and copepod abundances

FIGURE 9 Conceptual diagram illustrating the effect of late (a) and early (b) sea ice retreat on ecosystem structure and function from the austral spring to fall. (a) During years of late sea ice retreat, the weather is sunny, but air and water temperatures are colder. There is a higher density of krill recruits, and there is a shorter duration export flux season with a higher peak in flux occurring earlier. There is higher productivity and a shallower, more stable ocean mixed layer. Ice-intolerant humpback whales arrive later and are less abundant. Adélie penguins lay eggs later and raise chicks that have a higher mass at fledging. (b) During years of early sea ice retreat, the weather can be stormier and warmer. There is a lower density of krill recruits and a longer export flux season with a later and lower peak. There is lower productivity that peaks earlier and deeper mixed layer depths. Humpback whales arrive earlier and are more abundant. Adélie penguins lay eggs earlier, but chicks are of lower mass at fledging.

(Gleiber, 2014; Steinberg et al., 2015), whereas warmer waters favor salps and pteropods (Groeneveld et al., 2020; Thibodeau et al., 2019) where the latter two species can graze down phytoplankton stocks (Bernard et al., 2012), potentially leading to interspecific competition for phytoplankton prey (Loeb et al., 1997; Stukel et al., 2021). Although salps and pteropods are important prey themselves (Henschke et al., 2016; Hunt et al., 2008), they may route carbon and energy away from Antarctic krill, the dominant diet of many vertebrate predators (Trathan & Hill, 2016).

Peak POC flux lagged behind most of the other seasonal variables, which is likely due to the complex interplay of factors that regulate exports—from physical changes in the water column to biomass production and trophic interactions of organisms. Vertical particle export is regulated by the growth and sinking of phytoplankton, as well as repackaging of particles by zooplankton into fecal pellets, the fragmentation of POC by zooplankton grazing, and remineralization by bacteria (Briggs et al., 2020; Henson et al., 2019; Moreau et al., 2020; Steinberg et al., 2008). Delayed peak POC flux relative to phytoplankton biomass is thus likely due to the lag of zooplankton seasonal ascents, recruitment, and growth, which then result in increased fecal pellet production in late summer. Interannual differences in cumulative POC flux oscillate on a 5-year cycle, matching the life cycle of krill, where maximum POC export occurs when krill abundance is low but body size is large, as the production of large, longer fecal pellets have higher sinking rates (Trinh et al., 2023).

Match–mismatch dynamics in the case of the Adélie penguin

Adélie penguins have a short temporal window in which to breed and have a life history that is not tuned to the high interannual variability associated with a subpolar system where sea ice retreat occurs earlier (Fraser & Trivelpiece, 1996; Fraser et al., 1992). This suggests they could be more vulnerable to ecological mismatches during years of early ice retreat. Penguins are dependent on optimal weather and landscape conditions to raise chicks, and also optimal at-sea foraging environments to deliver energy-rich foods to their growing chicks with increasing food demands. Previous work both near Palmer Station and in other regions of Antarctica showed that penguin CID was related to sea ice, snow, and other local weather variables, with variable consequences for breeding success (e.g., Emmerson et al., 2011; Youngflesh et al., 2017). At Humble Island, CFM was not related to CID (Cimino et al., 2019), so to further understand the drivers of CFM,

we tested whether CFM was related to phenological events and found that a later wind minimum, SST peak, and snow melt were related to lower CFM, whereas a later air temperature maximum and sea ice retreat were related to higher CFM. These variables also appeared in the best performing CFM models in Cimino et al. (2014) that used mean conditions during the chick-rearing period at the same location. This previous work showed local weather (e.g., wind, temperature) was an important driver of CFM as inclement weather could hypothetically increase thermoregulative costs for chicks without waterproof feathers, or wind-driven transport of krill could affect chick feeding frequency or food quality/quantity. Both modeling efforts showed that these weather variables could have an ~100–200 g effect on CFM, possibly providing a buffer after fledging that could aid in survival (Chapman et al., 2010). Yet, it remains unclear how these variables are influencing the mass of a chick (i.e., through landscape or seascape effects).

The mean timing of phenological events in years with high and low CFM provides an indication of what might be optimal for the Adélie penguin breeding cycle. For example, while sea ice retreat typically occurred at the time of clutch initiation, a later retreat occurring halfway through the incubation phase was favorable. This later retreat could lead to more abundant and available prey because krill recruits overwinter underneath sea ice. In years when small krill made up a high proportion of penguin diets, foraging trips were shorter and chick mass was higher (Cimino et al., 2014; Fraser & Hofmann, 2003). Such ecosystem conditions would also be in accordance with a polar system to which their life cycle is attuned. CFM was also higher when snow melted in the middle of the incubation phase, before chicks hatch, which follows the negative impacts that snow melt or puddles of water can have on egg or chick survival and growth (Boersma & Rebstock, 2014; Thyen & Becker, 2006; Wilson et al., 2004).

Chicks were heavier in years when the day of the minimum wind speed was at the time of chick hatching, which could influence chick mass through landscape or seascape effects. The guard phase is a critical period when it is particularly important for chicks to be fed adequate food, as they have little to no fat reserves. The timing of low wind speeds and shoaling of MLDs influence the formation of phytoplankton blooms that on average occurred slightly after hatch. Phytoplankton energy storage lipids increase with higher light levels, which may influence the energy density of krill that consume them (Becker et al., 2018). Considering the maximum photoperiod occurs near the time of chick hatch, krill may be energy rich at this time. High wind speeds during this period can also alter water column properties

and prey distributions that could in turn affect adult foraging behavior and chick feeding schedules (Warren et al., 2009). In the Ross Sea and East Antarctica, meal mass, prey type, provisioning frequency, and colony size/competition were important drivers of chick mass (Ainley et al., 2018; Clarke et al., 2002; Whitehead et al., 2015). Additionally, young chicks are subject to metabolic costs due to wetting, which can be amplified directly by wind (Chapman et al., 2011) or indirectly by influencing where snowfall accumulates and subsequently melts (Fraser et al., 2013). Chicks benefit from guarding parents up to day 14 when the chick becomes too large to be fully insulated by an adult. It is not until after the guard stage that total metabolic costs caused by wetting decrease as the chick's down grows deeper (Chapman et al., 2011), highlighting the potential importance of low wind speed and no precipitation on chick growth during this time.

Finally, higher CFM was associated with the maximum SST and air temperature occurring in the middle of the crèche phase roughly at the mean. Warmer weather during the crèche phase may counteract the negative impacts of wetting or thermoregulatory costs due to being cold. Chicks are vulnerable to wetting when unguarded and before they develop waterproof fledging plumage (at an age of ~40 days) (Chapman et al., 2011). The wetting effect is not a prominent driver in southerly breeding sites, where temperatures are colder and precipitation is lower and can remain in a solid state.

While our CFM models were supported by the data, a model with only phenological events is likely not fully explanatory, as many other factors are involved in parental care and chick growth (e.g., discussed in Cimino et al., 2014). Short-term extreme events (e.g., storms, giant icebergs) can also have catastrophic effects that could outweigh optimal spring preconditioning and summer phenological events (Dugger et al., 2014). For example, 2001–2002 was an extreme weather year that had massive penguin breeding failures and the lowest CFM in our time series (Massom et al., 2006) with multiple storms hitting the Palmer region. As the Palmer region shifts to a more subpolar system, the weather has been more maritime with increases in the frequency of rain or snow events (Kirchgäßner, 2011; Turner et al., 2005). The timing of these events may be important to consider in terms of chick age, and subsequent growth or survival rates. Further, as Adélie penguins have not shifted their phenology significantly over the last few decades, it draws into question whether meteorological conditions have changed. For example, the duration of both the Adélie penguin breeding period from courtship (October) to chick fledging (February) and the generally snow-free period from snow melt (December) to accumulation (May) are about five months. If the Adélie penguin

breeding schedule was historically aligned with the snow-free period, this suggests that snow is either melting later, or the frequency or intensity of fall–winter snow events has increased such that it takes longer for the snow to melt in the spring (Ding et al., 2020; Medley & Thomas, 2019).

Climate-driven shifts in phenology are widely demonstrated across trophic levels (Thackeray et al., 2016), but the underlying mechanisms or the impacts on consumer fitness are rarely documented (Chmura et al., 2019; Kharouba & Wolkovich, 2020). Food sources tend to shift phenology at faster rates than their consumers (Both et al., 2009; Visser et al., 2012; Zhemchuzhnikov et al., 2021) where phytoplankton shift faster than zooplankton and zooplankton faster than their predators (Poloczanska et al., 2013). Although the phenological and trophic flexibility of zooplankton may limit the population-level consequences of mismatches (Atkinson et al., 2015), the Adélie penguin may be at more risk due to its fixed breeding timing and specialization on Antarctic krill at this breeding location. Altered species interactions during reproduction may be more impactful than abiotic effects (Ockendon et al., 2014). While it remains contested if trophic mismatches can have population-level consequences (Both et al., 2006; Franks et al., 2018; Johansson et al., 2015; Miller-Rushing et al., 2010; Reed et al., 2013; Saino et al., 2011), inadequate food resources can cause reduced growth rates and may lead to reduced survival or fitness (Gaston et al., 2009; Lameris et al., 2018, 2022; Ross et al., 2018; Sedinger et al., 1995). A greater mechanistic understanding is needed as well as identification of baselines for defining optimal food resource characteristics. For example, asynchronies with food peaks may not have consequences if food is abundant (Corkery et al., 2019; Dunn et al., 2011) or alternatively, synchronization with food peaks could have negative consequences if food abundance is low (Vatka et al., 2014). Time-series analyses relating seasonal krill availability (e.g., Nardelli et al., 2021) to foraging penguins and their reproductive performance will be critical for testing whether phenological mismatches between krill and Adélie penguins impact penguin population dynamics. Finally, episodic extreme events or compound effects of suboptimal environmental conditions and low food quality/availability could have more harmful effects than slow decadal change or high interannual variability (Gruber et al., 2021).

CONCLUSIONS

The Palmer LTER is uniquely positioned to study climate effects on ecological processes, especially given its location and geography, which provide a natural laboratory

for studying the ecosystem response along a regionally intensified climate gradient. This analysis underscores how critical LTER programs are for multitrophic-level responses to environmental variability. As climate change continues to cause an increase in high-frequency variability (e.g., storms and other extreme events), only with long-term observations can we distinguish and quantify, and thus better predict, how ecosystems respond to both increased variability and long-term change (e.g., Orgeret et al., 2022).

Phenology is a key topic in global climate change research and our study indicates that species responses vary across trophic levels, life histories, and predator–prey–competitor dynamics. Further, species responses cannot be understood in isolation, therefore making it critical to consider many factors—from optimal environmental windows, matches in prey availability/characteristics to predator or competitor dynamics—to obtain a holistic understanding of how phenological shifts affect a species (Durant et al., 2007). By studying phenological effects from an ecosystem view, we can begin to understand how these multiple pressures may interact to influence a single species as well as the fitness of their offspring. As this is a multifaceted problem, we acknowledge we have only begun to disentangle how phenological shifts may shape our study system moving forward. Future work should also consider the width of optimal windows, in addition to the timing of key events that were focused in this study, which could be more important as a narrow window may not be sufficient for processes like reproduction (Visser & Both, 2005). Further, it may be important to examine how phenological shifts propagate across an annual cycle where phenological compression or stretching can impact demographics (Cappello & Boersma, 2021). Studies rarely document phenological shifts in relation to food resource quality (Visser & Both, 2005), which is a near-term objective of our monitoring program. An important goal of the Palmer LTER is to determine mechanistic processes, and as climate changes are projected to intensify, we suspect phenological shifts will become a more important driving mechanism for desynchronizing species interactions within our ecological network.

AUTHOR CONTRIBUTIONS

Megan A. Cimino and Sharon Stammerjohn conceived of the study. Megan A. Cimino, John A. Conroy, Andrew Corso, Hugh Ducklow, William Fraser, Ari Friedlaender, Ross Nichols, Logan Pallin, Darren Roberts, Megan Roberts, Donna Patterson-Fraser, Deborah K. Steinberg, Patricia Thibodeau, Rebecca Trinh, and Oscar Schofield contributed to data collection. Megan A. Cimino, John A. Conroy, Elizabeth Connors, Heather Hyewon Kim, Ross Nichols, Patricia Thibodeau, Rebecca Trinh, and

Sharon Stammerjohn contributed to data analysis. Megan A. Cimino wrote the first manuscript draft with subject contributions from John A. Conroy, Elizabeth Connors, Jeff Bowman, Andrew Corso, Hugh Ducklow, Heather Hyewon Kim, Gregory D. Larsen, Ross Nichols, Logan Pallin, Rebecca Trinh, Sharon Stammerjohn, and all authors contributed to the final draft.

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CONFLICT OF INTEREST STATEMENT

There are no conflicts of interest.


DATA AVAILABILITY STATEMENT

Data are available from the Environmental Data Initiative (EDI) at: <https://pallter.marine.rutgers.edu/catalog/edi/index.php>. Weather and SST data (Palmer Station Antarctica LTER & P. Information Manager, 2019) are available from EDI: <https://doi.org/10.6073/pasta/cddd3985350334b876cd7d6d1a5bc7bf>. Sea ice data (Palmer Station Antarctica LTER & Stammerjohn, 2022) are available from EDI: <https://doi.org/10.6073/pasta/Od7bc478d0b40cddf6ae faaab21a545c>. Chlorophyll data (Palmer Station Antarctica LTER & Schofield, 2022) are available from EDI: <https://doi.org/10.6073/pasta/8026c74d03e29a7fb16f0f191007e267>. Discrete water column data (Palmer Station Antarctica LTER & Waite, 2022) are available from EDI: <https://doi.org/10.6073/pasta/7358be99bd7ec1c73293893defb289d3>. Pteropod length data (Palmer Station Antarctica LTER & Thibodeau, 2020) are available from EDI: <https://doi.org/10.6073/pasta/c6374c28a1352cf31cb947ef1bcb8366>. Penguin phenology (Palmer Station Antarctica LTER et al., 2022a) is available from EDI: <https://doi.org/10.6073/pasta/cb20f29bb1113e986bfcff8873f7de97>. Penguin chick fledging mass data (Palmer Station Antarctica LTER et al., 2022b) are available from EDI: <https://doi.org/10.6073/pasta/>

875086ecf38755f29f7aa8209e839e7f. Sequences (Bowman et al., 2017) are available at NCBI SRA at SRP091049 and SUB2014638. Code and associated data (Cimino, 2023) are available from Zenodo: <https://doi.org/10.5281/zenodo.7520769>.

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SUPPORTING INFORMATION

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

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