

## PROJECT SUMMARY

### Overview

Seasonal sea ice-influenced marine ecosystems at both poles are characterized by high productivity concentrated in space and time by local, regional, and remote physical forcing. These polar ecosystems are among the most rapidly changing on Earth. The PALmer (PAL) LTER seeks to build on three decades of long-term research along the western side of the Antarctic Peninsula (WAP) to gain new mechanistic and predictive understanding of ecosystem changes in response to disturbances spanning long-term, sub-decadal, and higher-frequency “pulses” driven by a range of processes, including long-term climate warming, natural climate variability, and storms. These disturbances alter food-web composition and ecological interactions across time and space scales that are not well understood. We will contribute fundamental understanding of how population dynamics and biogeochemical processes are responding within a polar marine ecosystem undergoing profound change.

### Intellectual Merit

Three multidisciplinary, interrelated research themes guide our proposed work:

**A. Drivers of disturbance across time/space scales: ecological and latitudinal response.** How does the near continuum of long-term “press” (climate warming), sub-decadal (interannual changes in sea-ice cover), and shorter-term “pulse” (storms) disturbance drive changes in the food web across the WAP?

**B. Vertical and alongshore connectivity as drivers of ecological change on local to regional scales.** How do vertical and alongshore transport and mixing dynamics along the WAP interact to modulate the distribution and variability of ocean physics, and in turn marine productivity, krill, and krill predators?

**C. Changing food webs and carbon cycling.** How will changes in the structure of the WAP food web affect cycling and export of carbon? Additionally, how will changes in primary producers, and their energy storage, affect higher trophic levels?

Within the newly proposed work we will continue to address the influence from natural climate modes (e.g., El Niño Southern Oscillation, Southern Annular Mode) on sea ice, weather, and oceanographic conditions that continue to drive change in ecosystem structure and function. Our sampling, analyses, and modeling cover multiple time scales—from diel, seasonal, interannual, to decadal intervals, and space scales—from hemispheric scale investigated by remote sensing, regional scale covered by a summer oceanographic cruise along the WAP, to local scale accessed by daily to biweekly small boat sampling at Palmer Station. Autonomous vehicles and moorings enable us to expand and bridge time and space scales not covered by vessel-based sampling, thus providing a seasonal to annual context. These observations are complemented with process studies that include manipulative experiments conducted during our research cruise and at Palmer Station. An extensive modeling effort with varying complexity allows us to improve mechanistic and dynamical understanding of the underlying processes driving change.

### Broader Impacts

PAL research on climate change and ecological transformation is harnessed through an education and outreach program promoting the global significance of Antarctic science and research. Using the recently-developed Polar Literacy Principles as a foundation, we will maintain and expand our virtual schoolyard program via virtual fieldtrips and dissemination of new polar instructional materials for K-12 educators to facilitate their professional development and curricula. We will leverage the development of Out of School Time materials for afterschool, 4-H, and summer camp programs; develop and implement an art and science exhibition designed for use in higher education focused on engaging lifelong learners; and produce high quality science communication resources to build awareness of PAL research directly to audiences in the cruise ship industry and indirectly through social media. We will broaden participation through a coordinated diversity, equity, and inclusion plan leveraging both virtual and traditional Research Experience for Undergraduates programs at our institutions aimed at underrepresented students.

This proposal requires fieldwork in the Antarctic.

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## PROJECT DESCRIPTION

**Introduction and PAL program evolution:** Polar marine ecosystems are regions of high seasonal biological productivity driven by local, regional, and remote physical forcing. Over the past 200 years, these ecosystems have provided society with food, fuel, and fiber (Chapin III et al. 2005, Ainley & Pauly 2013) and play a disproportionately large role, relative to their size, in global biogeochemical cycles (Hauck et al. 2015, Moore et al. 2018, Gruber et al. 2019). Indeed, the Southern Ocean alone is responsible for 40% of the annual global ocean uptake of anthropogenic CO<sub>2</sub> from the atmosphere (Gruber et al. 2019a,b). This is a unique marine ecosystem as it is structured by the expansion/retreat of a surface physical substrate in the ocean—sea ice—that results in extreme seasonality and interannual variability in food webs driven by associated changes in light, wind-ocean mixing, and global ocean-atmosphere circulation. Additionally, polar systems are among the most rapidly changing on Earth (Montes Hugo et al. 2009, Schofield et al. 2010, Brown & Arrigo 2012, Morley et al. 2020) and are sentinels of climate and ecosystem change, with charismatic species serving as global symbols of change. The PALmer (PAL) Long Term Ecological Research program is focused on understanding the seasonal sea ice-influenced marine ecosystem along the West Antarctic Peninsula (WAP) south of the Antarctic Polar Front (northernmost extent of the ice-influenced ocean). The central hypothesis of PAL is that seasonal, interannual, and long-term variability of sea ice structures the Antarctic marine ecosystem, from the timing and magnitude of primary production to the breeding success and survival of top predators. The WAP ecosystem is experiencing significant declines in sea ice since the 1970s and rapid warming since the 1950s (Schofield et al. 2010, Stammerjohn et al. 2012, Ducklow et al. 2013), making it a natural laboratory for studying ecosystem response to long-term warming. This proposal builds on three decades of research on gaining mechanistic and predictive understanding of ecosystem and biogeochemical responses to disturbances—spanning from long-term “presses” to higher frequency “pulses” driven by multiple processes (Collins et al. 2011). These include natural climate variability, long-term climate change, and feedbacks between physical and biogeochemical changes. In turn, these processes can alter species spatial distribution and food webs which affect carbon cycling/export, and compound effects of past/present harvest of marine living resources (industrial whaling, krill fishery). These characteristics make PAL a unique site for cross-site comparisons of LTER systems.

The major focus of all PAL proposals was how variations in climate forcing (Collins et al. 2011) modulate sea ice and ecosystem structure along the WAP (Smith et al. 2003). Initially PAL-1 and 2 (1990-2002) focused on studying a few key populations (diatoms, krill, penguins) in the context of high and low sea ice years. By PAL-3 (2002-2008), we recognized the WAP was one of the most rapidly warming regions on Earth and focused on documenting ecological responses to long-term directional climate change. For PAL-4 (2008-2014), we transitioned to a more comprehensive and process-oriented approach, with a re-designed PAL sampling grid to better span the WAP ‘climate gradient’ from the warmer northern to the colder southern regions with the aid of new ocean technologies and incorporating process-oriented experiments coupled to a range of system models. In PAL-5 (2014-2020), we emphasized adaptive sampling, process studies, and modeling embedded in our local and regional-scale program. During PAL-5 there was a significant recovery in sea ice (see ‘Results From Prior Support’) for which we expect the ecosystem response to ice recovery to be fully realized during this PAL-6 renewal. In 2017, sea ice began to decline once again. PAL-6A was put on LTER probation for two years; we are submitting this new proposal (PAL-6B) one year after the new award. The new science proposed herein also had to adapt to significant NSF U.S. Antarctic Program infrastructure shifts based on the current realities and capabilities of working in this remote, harsh location (see ‘Overview of PAL Sampling, Modeling, and Synthesis’). In PAL-6A, we expanded our understanding of physiological ecology and species-ecosystem resiliency in the face of multi-scaled disturbance and the inevitable fundamental alteration of this polar ecosystem due to global climate change. PAL-6B builds on the construct of PAL-6A (probationary period), but also includes an expanded phenological focus and further leverages an international consortium of research programs to expand our understanding of the climate gradient and the associated impacts on ecosystem structure along the WAP.

**Results From Prior Support:** Ducklow, **Schofield**, **Steinberg** (current PIs in bold), **Cimino**, **Doney**, Fraser, **Friedlaender**, Martinson, **McDonnell**, **Moffat**, Ohman, **Stammerjohn**, **van Mooy** “LTER Palmer, Antarctica: Land-Shelf-Ocean Connectivity, Ecosystem Resilience and Transformation in a Sea-Ice Influenced Pelagic Ecosystem” [includes a supplemental award, PLR-1344502, 09/2014–08/2021. \$7,754,664 (PAL-5)], “LTER: Ecological Response and Resilience to “Press-Pulse” Disturbances and a Recent Decadal Reversal in Sea Ice Trends Along the West Antarctic Peninsula” [PLR-2026045, 05/2021–04/2023. \$2,374,386 (PAL-6A)]

**Overview.** There has been significant progress during PAL-5 and in the first year of the probationary 2-year PAL-6A with 168 publications between 2014–present (italicized in reference section), many published in high profile journals (Nature, PNAS, Geophysical Research Letters, Philosophical Transactions of the Royal Society, Ecology & Evolution). We highlight ten significant publications in bold. A table summarizing available datasets is included as a supplementary document.

**Intellectual Merit.** *Long-term change and ecosystem transitions:* The WAP has changed significantly over at least the last fifty years (Henley et al. 2019) with change projected into the future (Boyd et al. 2016). The most rapid sea ice decreases in Antarctica have occurred along the WAP and Bellingshausen Sea (Stammerjohn & Maksym 2017). Seasonal sea-ice changes in the WAP are largely wind driven (Stammerjohn et al. 2011) forced by tropical Pacific and Atlantic Ocean teleconnections (El Niño Southern Oscillation–ENSO), and the Southern Annular Mode (SAM) (Stammerjohn et al. 2008b, Hobbs et al. 2016, Fig. 1A). The PAL sampling grid spans a climate gradient (Ducklow et al. 2013, **Steinberg et al. 2015**, Henley et al. 2019). While the number of sea-ice days per year has consistently been declining since the late 1970s, a reversal started in 2010 (**Schofield et al. 2018**; Fig. 1B). With this recent increase in sea-ice days, there was a weakening of warming trends, emphasizing the high variability of Antarctic climate (Hobbs et al. 2016). Nonetheless, long-term warming and sea-ice losses are statistically significant (Stammerjohn & Scambos 2020) and sea-ice decline resumed (Fig. 1B).

In the southern region of the PAL sampling grid, the summer upper-ocean mixed layer depth (MLD) has shallowed by a factor of two over the last 20 years (**Schofield et al. 2018**), with long-term observations showing concomitant increases in phytoplankton biomass (Montes Hugo et al. 2009, Brown et al. 2019, Fig. 1D). Biomass increases are positively correlated with phytoplankton species richness and evenness, driven by high diatom diversity (**Lin et al. 2021**). Interestingly, the second most dominant phytoplankton taxon, cryptophytes, shows low diversity (Brown et al. 2021). Increased phytoplankton biomass is consistent with observations/experiments suggesting continental shelf seasonal primary productivity is light-limited, which is alleviated with a shallower seasonal MLD (Schofield et al. 2017, Carvalho et al. 2019). The recent sea ice reversal resulted in increased annual phytoplankton biomass north of Palmer station (Kim et al. 2018), reversing long-term phytoplankton declines (Montes Hugo et al. 2009). To understand the light-driven changes in phytoplankton trends, PAL-6A incorporated the measurement of energy storage compounds reflecting physiological adaptations in an energy-constrained system. While the base of the WAP food web has changed significantly, long-term trends in zooplankton communities are mixed. The keystone species Antarctic krill (*Euphausia superba*) to date has no significant long-term directional change in the PAL study region (**Steinberg et al. 2015**) (Fig. 1E), although populations farther north have decreased (**Atkinson et al. 2019**). Other key macrozooplankton taxa show both increasing and decreasing trends in abundance, and some—such as ice krill (*E. crystallorophias*), salps, and pteropods—are correlated with ENSO or SAM climate cycles (**Steinberg et al. 2015**, Thibodeau et al. 2019). Climate also is driving long-term change in Antarctic Silverfish (*Pleuragramma antarctica*) larvae, with warmer sea surface temperature and decreased sea ice associated with reduced larval abundance (**Corso et al. 2022**).

Higher trophic levels show mixed responses to observed changes. Humpback whales (*Megaptera novaeangliae*) are increasing along the WAP, recovering from their near extirpation due to commercial whaling (Reilly et al. 2010, Pallin et al. 2018b). An increase in the population of ice-intolerant gentoo penguins (*Pygoscelis papua*) is coincident with a decrease in ice-obligate Adélie penguins (*P. adeliae*) by >90% near Palmer Station (Fig. 1F) while some colder southern colonies have only begun to show declines in recent years (Cimino et al. 2016a). Adélie breeding phenology at Palmer tracks regional trends in sea



ice over the last three decades (Cimino et al. 2019), and the population decline from 1974 to 2010 leveled-off during and after the sea ice trend reversal (Fig. 1B,F). In general, penguin populations are not only affected by shifts in sea ice in the ocean, but also storms (Fig. 1C) that can shift precipitation on land—impacting Adélie penguin breeding habitat quality, breeding success, and chick fledging mass (Fraser et al. 2013, Cimino et al. 2016a, 2014, 2019).

*Lateral connectivity and vertical stratification:* Along the WAP, cross-shore transports of freshwater, heat, and nutrients affect local stratification, thereby modulating biological productivity and the distribution of organisms. PAL focuses on both local- and large-scale ecological interactions (Kahl et al. 2010, Pickett et al. 2018, Cimino et al. 2016b) structured by WAP geography (Fig. 2 center panel), climate forcing and

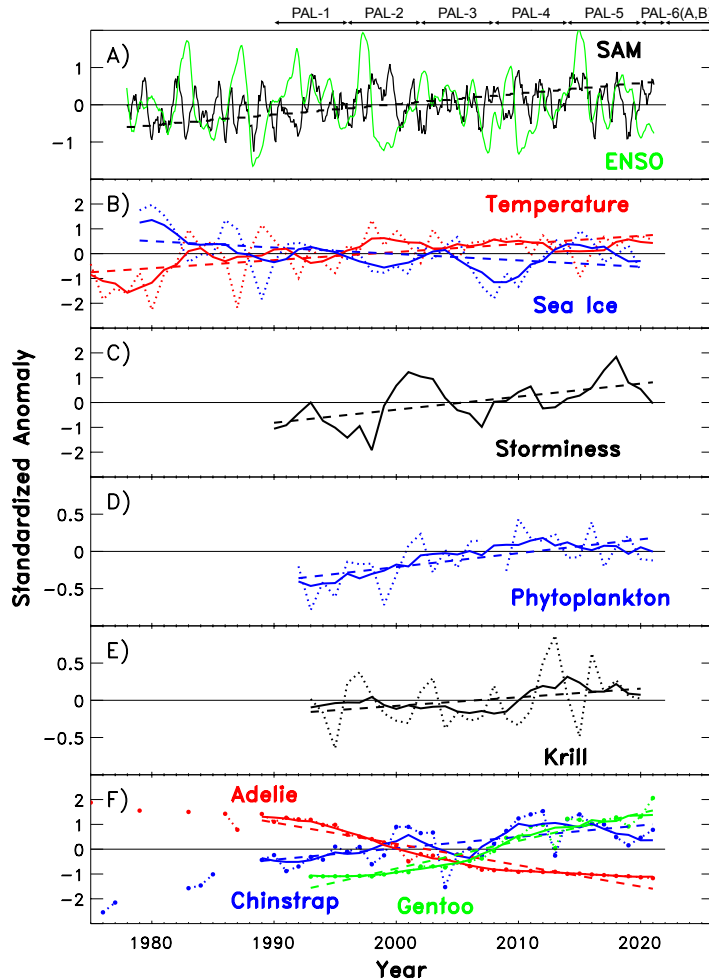


Figure 1. Long term trends in (A) climate cycles; (B) physical drivers: winter air temperature, sea ice duration, and (C) summer storminess from reanalysis; (D) seasonally/depth integrated summer phytoplankton; (E) January Antarctic krill abundance; and (F) penguin breeding pairs at Palmer. Data collected by PAL. Shown are standardized anomalies (dotted), smoothed multi-yearly variability (solid), and long-term trends (dashed).

limiting (Carvalho et al. 2016). Additionally, upwelling of mUCDW does not control Fe flux to the surface; instead, shallow sediment-sourced Fe inputs are transported horizontally from surrounding coastlines, within the upper 100 m, supplying a source of micronutrients to the coastal ecosystem (Sherrell et al. 2018). While coastal waters are nutrient replete, the same is not true for offshore shelf waters, where

ocean atmosphere ice connections. The warm (>1.5°C), nutrient-laden Upper Circumpolar Deep Water (UCDW) (Martinson & McKee 2012), transported by the Antarctic Circumpolar Current (ACC), abuts the continental shelf (Martinson et al. 2008, Clarke et al. 2012) and moves into coastal regions, principally through cross-shelf canyons (Klinck 1998, Dinniman & Klinck 2004, Couto et al. 2017a). UCDW enters the canyons as intrusions, forming small eddies (Moffat et al. 2009, McKee et al. 2019) and mixing with colder, fresher shelf water (Couto et al. 2017b) to form modified UCDW (mUCDW). The mUCDW transport, shapes the penguin biogeography, terminates in local coastal canyons that are hotspots for major Adélie penguin colonies (Schofield et al. 2013). These are hotspots for diatom blooms (Kavanaugh et al. 2015) that were hypothesized to result from either enhanced upwelling of nutrient rich mUCDW water or shoaling of the upper MLD, allowing phytoplankton to overcome light limitation. Incubation experiments from canyons showed macronutrients did not promote growth (Carvalho et al. 2019), consistent with observations that macro- and micronutrient concentrations do not seem to be

micronutrients—especially Fe, can be limiting (Annett et al. 2017, Sherman et al. 2020). PAL-6A built on this understanding by expanding the focus to include alongshore connectivity and circulation patterns, as existing conceptual models of the WAP heat and salt budgets did not account for the connectivity of Weddell cold polar water transported from the north (Moffat and Meredith, 2018; Wang et al., 2022).

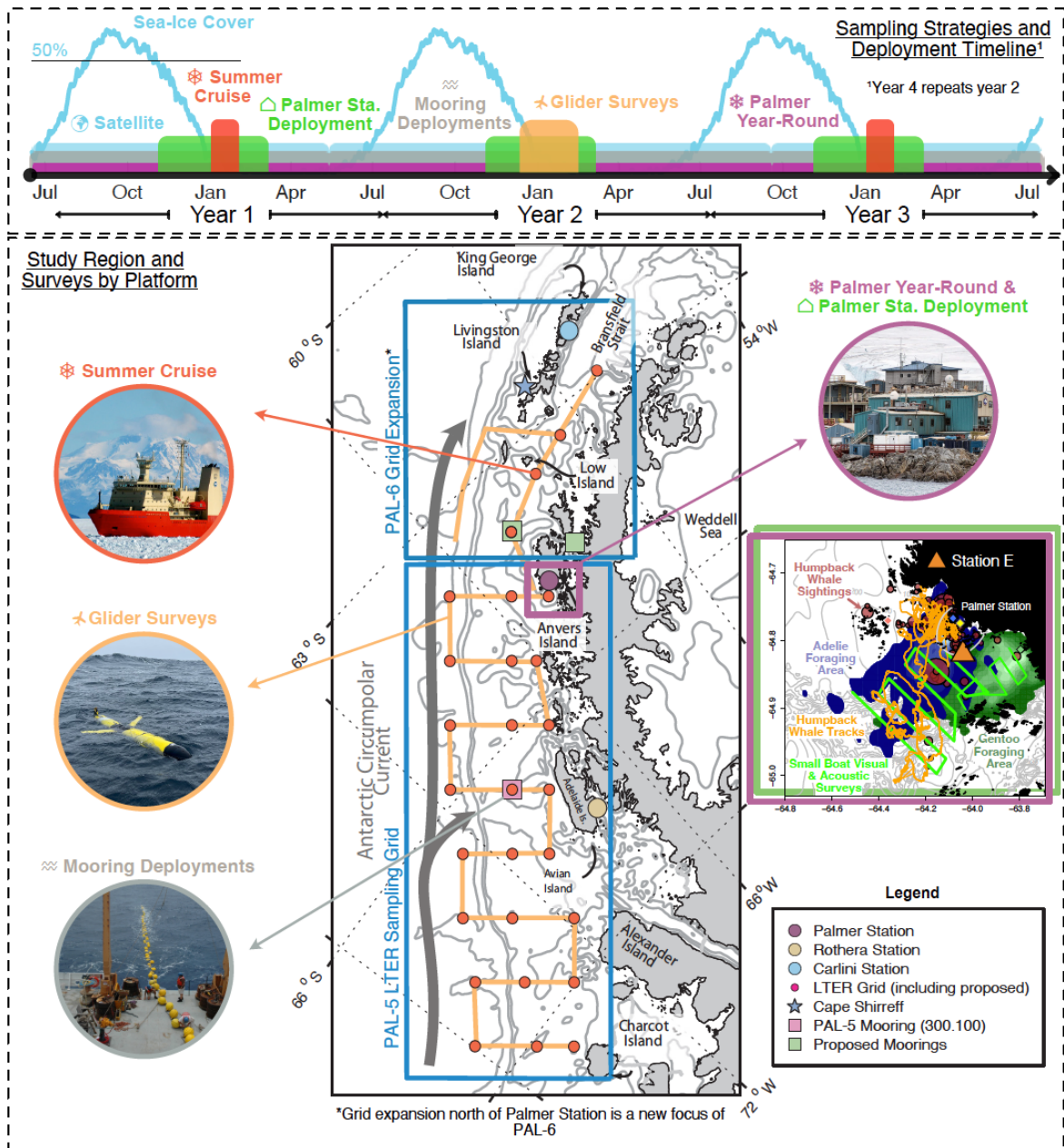


Figure 2: Study region and overview of sampling strategy. Top panel: timeline of sampling from Palmer Station and the regional survey platforms (cruise, gliders, moorings, satellites). Also shown is the climatological mean of sea ice cover near Palmer Station. Bottom Panel: Study region showing the PAL-5 grid and PAL-6 grid expansion, cruise and gliders, moorings, as well as sampling sites and key partner research stations. The map inset on the right shows typical local-scale presence/foraging of whales, penguin colonies, acoustic surveys and oceanographic sampling at Palmer Station.

Therefore, to capture variable Weddell Sea inputs the PAL sampling grid was extended northward in 2021 (see Fig. 2 box on “Grid Expansion”).

*Top-down controls and shifting baselines:* We focused on the re-emergence of whales in the WAP and potential impact on the demography of other krill-dependent predators through competition for resources (Laws & Fuchs 1977). Although not mutually exclusive, this top-down effect contrasts with a bottom-up perspective that climate-mediated changes in the physical environment regulates predator populations based on evolved life histories (Fraser et al. 1992). PAL focused on determining the demography and population dynamics of WAP whale populations and how their sympatric penguin competitors utilized the available prey-scape. Humpback whale recovery along the WAP (Bejder et al. 2016) is exemplified by high pregnancy rates (64%/yr) (Pallin et al. 2018a,b). Given the energetic demands of such high fecundity, it appears that krill are not a limiting resource for whales, despite revised estimates showing whale prey consumption is likely 3-6x higher than previously believed (Savoca et al. 2021). Acoustic surveys show high krill abundance near Palmer Station (Nardelli et al. 2021). Satellite telemetry demonstrates that whales utilize the entire PAL sampling region across the continental shelf in summer while moving to nearshore bays in fall (Curtice et al. 2015, Weinstein & Friedlaender 2017, Weinstein et al. 2017) where they encounter dense krill patches (Lascara et al. 1999, Nowacek et al. 2011, Friedlaender et al. 2013, Tyson et al. 2016, Nardelli et al. 2021) consistent with seasonal krill distributions. Along the WAP, Adélie and gentoo penguin breeding colonies are often sympatric (Lynch et al. 2012) and possibly compete for prey. In the Palmer region, while their diets and foraging areas can overlap horizontally, each have separate core spatial foraging regions and Adélie feed at shallower depths than gentoos (Cimino et al. 2016b, Kohut et al. 2018, Oliver et al. 2019). While penguin and whale foraging regions can overlap vertically and horizontally, penguins forage mainly during the day (Pickett et al. 2018), whereas whales forage nearly continuously and then transition to diurnal feeding in late summer as more night hours occur (Nichols et al. in press). This hyperphagic behavior by whales, foraging nearly twice as much in the early part of the season (Jan-Feb) than later (Mar-May), reflects a phenology of arrival to the Antarctic from breeding grounds far to the north. This timing coincides with the highest prey availability for efficient foraging across the broader region to replenish lost energy stores from months of fasting (Nichols et al. in press). That whales are not a constant presence around Palmer Station may reflect prey being episodically available in densities required for energetic needs relative to the penguins that can thrive on lower densities of krill. Interestingly, penguin demography is only marginally related to prey resources (Cimino et al. 2014), but prey availability or quality may become an important driver in the future to buffer the negative impacts of landscape nesting habitat quality on breeding success and chick mass (Cimino et al. 2019, 2014; Fraser et al. 2013).

*Food web structure and biogeochemical processes:* The seasonally sea ice-influenced ecosystem of the WAP is characterized by high primary productivity concentrated in space/time by local, regional and remote physical forcing (Li et al. 2016). Near-shore, coastal waters exhibit strong seasonal biological drawdown of inorganic nutrients (Kim et al. 2016, Kim et al. 2021) as well as pCO<sub>2</sub> and dissolved inorganic carbon, with concentrations modulated by sea ice, glacial freshwater input, and air-sea exchange (Hauri et al. 2015, Eveleth et al. 2017; Schultz et al. 2020, 2021). Mooring CO<sub>2</sub> data were used to construct the first full annual cycle of air-sea flux and net community production to constrain the annual mean CO<sub>2</sub> flux (Yang et al. 2021) and PAL data were combined to characterize time-evolving, spatial patterns of distinct ecological seascapes (Bowman et al. 2018). Additionally, Kim et al. (2022), using a newly developed biogeochemical data assimilation model, examined seasonal bacterial-food web temporal dynamics. In the southern WAP, increasing phytoplankton is associated with drawdown of atmospheric CO<sub>2</sub> (Brown et al. 2019) driven by a shallowing of the summer MLD (Schofield et al. 2018). On decadal time-scales, rising atmospheric CO<sub>2</sub> is projected to drive increasing pCO<sub>2</sub> and acidification of Southern Ocean surface waters (Boyd et al., 2016), but the acidification signal is difficult to detect, reflecting regionally-varying biological and physical factors (Hauri et al. 2015). Consequently, carbonate chemistry parameters, such as aragonite saturation, are not strong indicators of shelled pteropod abundance (Thibodeau et al. 2019), likely because the WAP is not yet significantly undersaturated with respect to aragonite (Hauri et al. 2015). Sea-ice seasonality plays an important role in dissolved inorganic carbon drawdown (Schulz et al. 2021). High seasonal net community production exceeds carbon export to depth via particle sinking, suggesting losses from the surface ocean

due to diapycnal mixing or other physical/biological mechanisms affect the efficiency of the biological pump (Stukel et al. 2015, Ducklow et al. 2018). Inverse modeling of the WAP marine food web clearly suggests that micro-heterotrophy represents a significant fraction of the carbon cycling (Garzio et al. 2013, Saille et al. 2013, Ducklow et al. 2015), supporting observations of significant viral activity (Brum et al. 2016). Growth seasons following low winter sea ice are associated with lower phytoplankton biomass (Saba et al. 2014) and shifts in phytoplankton community composition and size structure (Moline et al. 2004, Montes Hugo et al. 2009). The declines/shifts in phytoplankton affect pCO<sub>2</sub> as different phytoplankton taxa have disparate drawdown rates (Brown et al. 2019) and thus eukaryotic plankton diversity and carbon cycling are linked to sea-ice conditions (Lin et al. 2021, Schulz et al. 2021).

There is tight coupling between phytoplankton and zooplankton, and large summer phytoplankton blooms are associated with positive recruitment of *E. superba* krill (Saba et al. 2014). Strong *E. superba* recruitment since 2011 coincides with enhanced phytoplankton productivity and the recent sea ice reversal (Conroy et al. 2020a). A long-term increase in another krill species, *E. crystallorophias*, in the southern PAL region is attributed to increased phytoplankton production or more favorable timing of sea ice retreat leading to subsequent blooms (Steinberg et al. 2015). Zooplankton play a key role in the region's biological pump. Fecal pellets, mainly from krill, dominate sinking material captured by sediment traps (Gleiber et al. 2012), and shifts in zooplankton community composition between "krill years" and "salp years" lead to interannual variability in particulate organic carbon (POC) export. Furthermore, many taxa undergo diel vertical migration even in the summer (Conroy et al. 2020b), indicating active carbon transport to depth.

**Broader Impacts.** During PAL-5 and the first year of PAL-6, 22 PhD (10 graduated thus far) and 6 Masters (5 graduated) students, as well as 7 post docs were trained. The education-outreach team designed education programs focused on communicating PAL research to predominantly K-12 educator and student audiences with PAL graduate students being peer mentors. We matched these efforts with a companion NSF award from the Polar Science Division (grant#1525635) called *Polar Interdisciplinary Coordinated Education* (Polar ICE). PAL offered a range of development programs for K-12 educators, Video Teleconferences (VTCs) for K-12 students, and science communication media projects. To fulfill our Schoolyard LTER requirements, we offered 24 VTCs virtually connecting students and teachers to scientists at Palmer Station. We engaged 80 educators and ~1,152 students directly, and >3,300 indirectly (from video replay) from 10 states spanning 5-12th grade. We evaluated the VTC program by asking educators to assess/explain their students' engagement in, and identity with, science. The educators noted that VTC benefits included: 1) Ability to practice asking scientific questions— the importance of getting students to develop their own questions about PAL research and what it is like to be a scientist working in Antarctica, including how do you formulate research hypotheses, what scientific tools do you use, and how do you collect/analyze data? 2) Increased understanding and awareness of Polar Regions—students were especially interested to learn more about the Antarctic food web from the smallest microbes to the largest whales; and 3) Ability to meet a practicing scientist— it was important for students to have the opportunity to meet and talk to a real scientist. Since 2015, we engaged 75 K-12 educators in four, week-long professional development programs, reaching ~6,975 students. Our objectives were to contribute to the engagement of youth in science, especially grades 6-9, and increase student identity as a scientist through increased enthusiasm and personal engagement with scientists. Our aim was to make science personally relevant to students and influence their long-term interest in science through authentic science data experiences. Schofield participated in a broadcast on Public Radio (*You're the Expert*) with three comedians and host Chris Duffy, with ~300 Rutgers students and ~250,000 podcast downloads to date. Friedlaender's research was featured by news agencies including BBC and National Geographic reaching >70 million viewers. Fraser's seabird research will be featured in the BBC's *Frozen Planet II* fall 2022. Our work resulted in 7 peer-reviewed manuscripts in the *Journal of Marine Education*.

### Response to Proposal Reviews

The review panel summary of our 2020 PAL LTER submission highlighted concerns that we have addressed in this resubmission. An overall concern was the need for the *conceptual framework, clearly grounded in ecology, to be structured around testable hypotheses*. Our restructured conceptual model

provides a series of testable, predictive hypotheses that will be addressed with our observational/modeling strategy. Our proposal is focused on understanding how multi-scale disturbances drive the transition of a polar to a subpolar marine ecosystem across trophic levels. This is a critical as documenting ecosystem transitions in marine systems has been notoriously difficult (Gruber et al. 2020, Heinze et al. 2020, Pearson et al. 2021, Bahlai et al. 2021), due to the substantial passive and active connectivity in the ocean (Novi et al. 2021), combined with highly variable physical forcing (Morley et al. 2020). This proposal addresses multiple time and space scale disturbances (Levin 1992) as suggested by reviewers. Ecological disturbance theory underpins a significant portion of our research, and we will examine the impacts on the WAP pelagic ecosystem at multiple trophic levels across multiple scales of time (long-term “press” of warming, interannual-to-decadal climate oscillations such as ENSO-SAM, and wind or precipitation from short-term “pulse” storms) and space (spanning the WAP latitudinal climate gradient to local topography-driven predator foraging hot spots). We expanded a subtheme on phenology and potential future changes affecting food web energy transfer. We explicitly pose testable hypotheses for our research subthemes, and describe how field work, analyses, and modeling will be used to address them. Our research themes are explicitly mapped to our conceptual model (Fig. 3), and a new synthesis section shows how our work integrates across all research themes.

Other concerns raised in the panel summary included: ***Better 3-D modeling would improve the proposed work, including coupled physical-biogeochemical processes. The current 1-D model is not sufficient and the 3-D models are too coarse in resolution.*** We formulated a highly integrated approach for linking ocean bio-physical models across time-space scales and levels of complexity. In PAL-5 and 6A, the PAL team created a hierarchy of models, each tailored to address specific scientific questions and allowing for trade-offs between more computationally tractable 0-D box and 1-D column models versus full 3-D bio-physical simulations. We developed a 1-D column food-web model, with model physics forced from hydrographic observations and key biological parameters tuned to observed seasonal cycles via variational data assimilation (Kim et al., 2021, 2022). We also developed a fully dynamic 1-D sea-ice ocean physics model for the WAP shelf with/without assimilation of mooring and satellite observations (Saenz et al., under review). Our proposed new work will couple these 1-D models to test specific hypothesis and quantify model uncertainties on biological responses to environmental drivers of vertical mixing, freshwater, winds, and sea-ice cover. The 1-D model results feed into field experimental design and interpretation of a new, fully coupled 3-D bio-physical regional ocean-sea ice model for the WAP and adjacent Southern Ocean (Schultz et al. 2020, 2021). The 3-D model is built on the MIT-GCM and leverages collaboration with colleagues at the British Antarctic Survey (see letter of collaboration). Recently published multi-decade long simulations at *eddy resolution* (6-9 km on the WAP shelf) examine climatic controls on interannual and geographic variations across the WAP shelf/slope domain (north-south and onshore-offshore) in physics (ocean temperature and salinity, sea-ice extent, MLD, and freshwater inputs from the atmosphere and glaciers) and biogeochemistry (e.g., phytoplankton blooms and air-sea CO<sub>2</sub> flux) (Schultz et al. 2020, 2021). ***The justification for storms as a strong driver of the system was weak and didn't include alternative explanations to patterns in the data.*** We now include more references and present an initial analysis of trends in storminess (Fig. 1C) as well as alternative physical and biological processes that may lead to ecosystem impacts (see Theme A & B), highlighting alternative drivers (warming, increased melting) and species responses and physiological capacity that might mimic, counteract, or magnify storm ecological impacts (e.g., storm mixing causing dispersal of krill aggregations making predator foraging less efficient). ***Would be helpful to have a table with routine measurements on cruises and Palmer Station.*** We added Table 1 to address this concern. ***Some methods not well enough described or referenced and manipulative experiments described only in general terms, measurements could be more strongly connected to research questions.*** We include new information and references which provide details of our typical field sampling and experimental designs, and link experiments more closely to our hypotheses in the restructured description of our research activities. ***Lipidomics useful for energy as a currency for ecological modeling, but focused on phytoplankton, krill and other zooplankton, penguins and whales; does not include fish and bacteria. Other phenomena may be important besides lipid caloric content (e.g. balance of autotrophs vs heterotrophs) but not put forward as alternative***

**hypotheses.** We centered our biochemical focus on energy storage molecules, which include triacylglycerols and carbohydrates. Our own and other work strongly suggest heterotrophic bacteria are not significant sources of triacylglycerols. Instead, triacylglycerols may represent nearly half of daily primary production by phytoplankton (Becker et al., 2018), and triacylglycerols are extremely important in krill. The lipidomics method also yields polar lipids found in heterotrophic bacteria, thus we will have insights into how bacteria contribute to lipid transfer. Our method for carbohydrates is less sophisticated and does not resolve bacterial and phytoplankton sources. However, the microbial loop is relatively small in the WAP—only ~5% or less of primary production (Bowman et al. 2021, Ducklow et al. 2012, Kim et al. 2022). Thus, any contribution to carbohydrate (or lipid) synthesis is expected to be small. In addition to plankton and krill, we will analyze lipids of fish caught in net tows or found in penguin diet samples. The balance of heterotrophic and autotrophic processes is important, and we now incorporate variations in phytoplankton and zooplankton community structure into our hypothesis on variations in caloric content and energy flow. But again, as WAP bacteria production is low, by prioritizing the particulate carbon flow (vs. dissolved carbon) and heterotrophy by higher trophic levels (vs. bacteria) we focus our analyses on the most important terms in the system carbon and energy budget. **Relevant work not cited, e.g., Lynch’s penguin program.** We now include 5 citations including Lynch (see References).

We also address concerns raised in the panel summary for Broader Impacts which included: ***The Broader Impacts could benefit from programming targeting the graduate to post-doctoral level for diversity inclusion.*** Steinberg and Schofield have current under-represented minority graduate students conducting PAL research (Maya Thomas, MS student, African American; Claudia Moncado, MA student, Hispanic; Teemer Barry, PhD student, African American). Schofield has also been engaged with the LTER network DEI committee. McDonnell joined an NSF-sponsored teaching and learning project to improve recruitment and cultivate inclusive learning environments. We will offer an online “boot camp” using these techniques to expose undergraduates to PAL research and prepare them for future REU involvement. McDonnell will create a database of students from over 200 minority serving and primarily undergraduate institutions (related to NSF award #1831625). ***Assessments of outreach activities would enhance the program.*** We include an evaluation strategy in this proposal, based on lessons learned and resources developed through our NSF AISL (NSF award #1906897). These evaluation instruments will be used to collect youth data from our VTCs and educator professional development programs through existing pre- and post-survey techniques to evaluate our products/programs using formative and summative approaches.

### **Proposed Research**

**Conceptual framework.** Global change (warming, ocean acidification, increasing storminess) is predicted to restructure many ecological systems on the planet (Schimel et al. 1993, Running 2012), and a core challenge is to understand both the resilience to change and the potential trajectories of these ecological systems (Borer 2020). Understanding the resilience requires insight to both the capacity of the system to remain unaltered in the face of change and the potential for the system to recover to its pre-disturbed state (Holling 1996). Predicting potential ecological trajectories requires understanding ecological responses to, and variability resulting from, the interactions of multiple disturbances often operating over a wide range of temporal and spatial scales (Levin 1992, Holyoak & Wetzel 2020). Such studies are rare in marine ecosystems (Donohue et al. 2016). To this end, PAL-6B is focused on characterizing patterns, variability, and rates of change—and their relationships to external drivers—to understand disturbance responses, evaluate the consequences of the responses at the regional scale, and to predict into the future. This effort is encapsulated by our conceptual framework focused on how drivers of disturbance along the WAP (Fig. 3a) underly the ongoing system-wide ecological transition from a polar to a subpolar marine pelagic food web (Fig. 3c,d). The PAL LTER conceptual model (Fig. 3) is based on the fundamental concept that sea ice plays a central role in the population dynamics and life history strategies of organisms across all trophic levels of the polar food-web, spanning bacteria, phytoplankton, zooplankton, penguins and other seabirds, and marine mammals. PAL has the unique opportunity to study the rate of transition between two marine states, one represented by a fully polar system characterized by a productive, short, linear food web with high carbon export to a subpolar system with a more complex food web and lower rates of carbon export



(Fig. 3c). Understanding this transition is critical as the dynamics in the ocean-sea ice system underlies the biodiversity and productivity observed in polar ocean ecosystems (Convey et al. 2014).

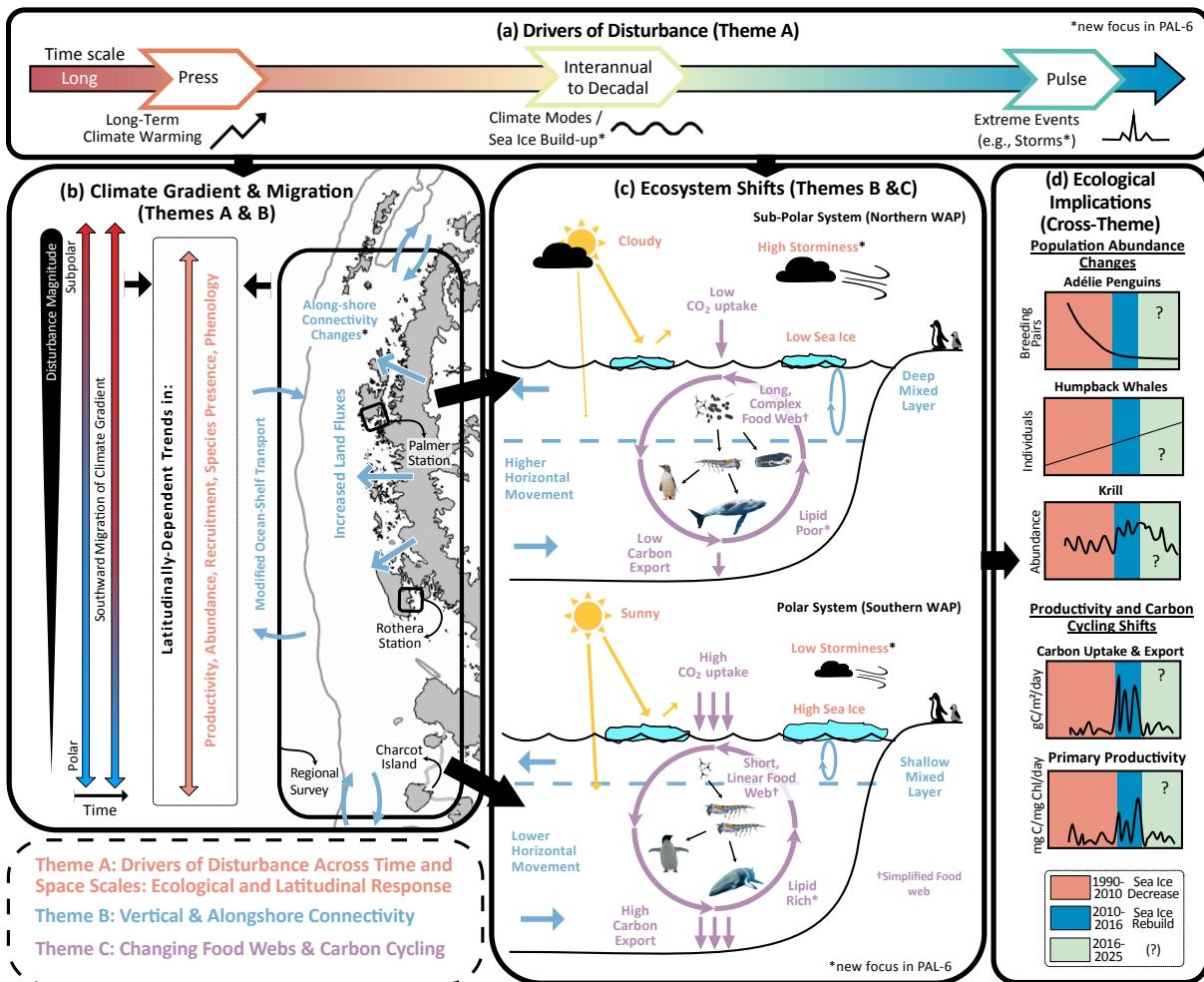


Figure 3: PAL Conceptual model and research themes: PAL spans a space and time climate-biogeographic gradient that has shifted due to local and atmospheric circulation changes affecting the ocean (3b). The shifting sea-ice structured polar system is affected by a range of disturbances spanning climate press (long-term warming), interannual to decadal variability (e.g., from ENSO, SAM) and pulses (storms) that affect both land and seascapes. A southern migration of the climate gradient and latitudinally-varying disturbances is predicted to result in continued change in ecosystem properties, across all trophic levels, at regional scales which has implications for food web structure and the cycling of carbon (3c). Combined, these responses result in significant system-wide ecological consequences for population abundance of key species, productivity and carbon cycling (3d). Note color coding of our three major research themes (bottom left) is also depicted to show where they play a specific role in the conceptual model (3b and 3c).

PAL-6B is taking a system-wide approach to determine how long-term press and shorter-term pulse disturbances (Fig. 3a) interact to drive ecosystem transitions. Seasonal sea-ice formation and retreat is a central driver of the WAP ecosystem. Superimposed on this are additional physical climate factors – storminess, glacial meltwater and precipitation, and lateral ocean circulation – that together control ocean surface mixing and vertical stratification (Fig. 3b,c). Global climate change and ocean/atmosphere warming are reducing the spatial extent and seasonal duration of sea ice cover along the WAP (Fig 1). Natural variability on interannual to decadal time-scales (Turner et al. 2016) overlays the long-term “press” of

climate change. In particular, changes in regional wind patterns associated with multi-year phasing of the SAM and ENSO (Fig. 1A, 3a) result in alternation between high or low sea-ice years (Stammerjohn et al. 2008a,b; Fig. 1B) and decadal climate cycles can result in temporary reversals in sea ice loss (Schofield et al. 2018; Fig. 1B) providing PAL with a natural experiment to assess the potential recovery across different trophic levels. For example, during the first two decades of PAL, the WAP exhibited a large decline in the seasonal duration of sea-ice (Fig. 1B) reflecting a trend to a more positive SAM phase (Stammerjohn et al. 2008a,b; Fig. 1A) with changes in winds, heat input from the deep ocean, and air/ocean temperatures (Martinson et al. 2008, Couto et al. 2017a). When PAL-5 was proposed, the loss of sea ice from the northern region in the PAL study area was so pronounced that we hypothesized that the ice-dependent ecosystem was approaching a tipping point (Bestelmeyer et al. 2011) to a new, ice-intolerant or ice-independent ecosystem (Sailley et al. 2013). However, a subsequent cool period and sea-ice recovery (Fig. 1B), provides an opportunity to assess the potential of the ecosystem to recover, and preliminary analysis suggests differential recovery across trophic levels. The sea-ice trend has again reversed, returning to the predicted decline given global warming. Indeed, in 2022 we are observing the lowest Antarctic sea ice levels on record (Raphael & Handcock 2022). Despite the cooling period, there remains a significant long-term warming trend (Stammerjohn & Scambos 2020) that is differentially expressed on the WAP. It is also predicted that long-term warming in polar regions will continue and accelerate (IPCC 2021).

In addition to the long-term press changes and the decadal climate cycles are short time-scale “pulse” disturbances, such as storms. Antarctica shows strong regional variability in storm intensity, with the Bellingshausen Sea and the WAP being a hotspot for storm genesis and decay (Hoskins & Hodges, 2005), with storm intensity (measured by wind, ocean waves, and snow accumulation). During summer, storm frequency varies quasi-weekly over local to regional spatial scales, and stormy conditions range from high winds (sustained winds >30 mph) with no precipitation, to calm winds with high rain/snow, to blizzard conditions. Southern Ocean winds, wave height, and ocean power over the last decade have been increasing (Young et al. 2011, 2017; Young & Ribal 2019; Reguero et al. 2019) and migrating southwards, including along the WAP (Fig. 1C). We have documented ecological impacts of these storm pulse events (Chappell et al. 1989, Cimino et al. 2019, Fraser et al 2013). For example, storminess directly impacts ocean vertical mixing altering phytoplankton productivity and community composition (Saba et al. 2014, Schofield et al. 2017; Fig. 3c) and affects breeding success in seabirds (Cimino et al 2019, Fraser et al 2013). Characterizing the ecological responses to pulse landscape disturbance drivers is a focus of our research Theme A (Fig 3a) while Theme B addresses seascape responses.

In PAL, we exploit the near-continuum of “press-to-pulse” temporal drivers which is differentially expressed along the WAP, providing us with a climate gradient over our study domain (Fig 3b,c). The northern regions are characterized by subpolar climate (shorter ice season, warmer moist atmosphere) and the southern regions by a polar climate (longer ice season, cooler dry atmosphere). The transition between the two appears to be shifting from north to south along the WAP and currently the “hinge point” of the transition is located at our long-term study site at Palmer Station (Montes Hugo et al. 2009, Kavanuagh et al. 2015). We predict this hinge point will continue to move southward, a process we term *climate migration*, reflecting the long-term press of planetary warming, providing us with an opportunity to study the ecosystem transition (Fig. 3b). For example, following the sea-ice reversal in the 2010s, the WAP ecosystem responded with increased phytoplankton productivity (Kim et al. 2018) and krill recruitment (Conroy et al. 2021a; Fig 1E); however, increases in other trophic levels are not yet evident. This could reflect time lags associated with life history strategies. For example, Adélie penguin fledglings do not return to natal breeding colonies for 3-6 years (LeResche & Sladen 1970), and several more years will definitively determine if there was any resilient recovery in Adélie penguins associated with the return of sea ice. Similarly, longer time series are needed to link variability in pregnancy rates and population growth of humpback whales (that favor ice-free conditions) to changing ice conditions.

Additionally, we use the variability associated with the relatively wide continental shelf (100-200 km) that has an on-to-offshore gradient—from the land-influenced nearshore region driven in part by melting glaciers and an along-shore coastal current—to open ocean conditions on the continental slope more influenced by the Antarctic Circumpolar Current and deep-water upwelling (Fig 3b). On local scales (10’s



of km in the horizontal, 10-100s meters in the vertical), physical dynamics influence key ecosystem processes like rates of marine productivity and the breeding success of near-shore penguin colonies (Fig. 3c). Critically, we understand these drivers to be partially interdependent: SAM is influenced by human-driven climate change, and the pulse-like forcing of individual storms shows a long-term southward migration along the WAP (Fig. 1A,C). Our conceptual model, hypotheses, and observational, modeling, and synthesis strategy explicitly recognizes this complexity and Theme B in particular focuses on how ecological variability is influenced by external inputs (heat, nutrients, organisms) to the WAP (Fig. 3b,c).

Sea ice plays a critical role, directly or indirectly, in the population dynamics and life history strategies of organisms across all trophic levels in the WAP (Fig. 3). The strong north-south climate and sea-ice gradients provide a biogeographic trend along the WAP, from a polar ecosystem in the south to a transitioning sub-polar ecosystem in the north (Fig. 3b,c). Polar ecosystems are typically characterized by a relatively short, linear food webs, with diatoms, abundant krill and ice fish, and sea-ice obligate species such as Adélie penguins. Longer, more complex food webs with higher regenerated productivity with sea-ice avoiding species tend to define sub-polar ecosystems (Fig. 3c). On interannual timescales, years with high sea-ice extent are followed by higher primary productivity, krill recruitment, and penguin breeding success (Ducklow et al. 2006, Saba et al. 2014, Steinberg et al. 2015, Schofield et al. 2017, Cimino et al. 2019, Fig 1). Conversely, krill recruitment is poor following low sea-ice years (Saba et al. 2014, Fountain et al. 2016) with conditions favoring gelatinous salp blooms (Steinberg et al 2015). The cumulative impacts of sea-ice decline and climate migration result in shifts in species composition, changes in species' distributions, phenological adjustments, and mis-matches in trophic coupling (Smith et al. 1998a,b, 2003; Ducklow et al. 2007, 2012, 2013). These changes impact biogeochemical cycling and is the focus of Theme C (Fig. 3c,d). *We use a holistic approach to understand the importance of short-term processes and feedbacks between local (snow cover, landscape geomorphology, storms), regional (wind, sea ice), and basin scale processes (climate change, teleconnections) that interactively underlie food web dynamics and biogeochemistry.*

## MAJOR RESEARCH THEMES AND PROPOSED RESEARCH

Our proposal addresses LTER network's five areas of core research through three multidisciplinary, interrelated PAL research themes based on our conceptual model, which guides our proposed work, and integrates with our strong education/outreach program.

**A. Drivers of disturbance across time/space scales: ecological and latitudinal response.** *How does the near continuum of long-term "press" (climate warming), sub-decadal (interannual changes in sea ice cover), and shorter-term "pulse"(storms) disturbance drive changes in the food web across the WAP?*

**B. Vertical and alongshore connectivity as drivers of ecological change on local to regional scales.** *How do vertical and alongshore transport and mixing dynamics along the WAP interact to modulate the distribution and variability of ocean physics, and in turn marine productivity, krill, and krill predators?*

**C. Changing food webs and carbon cycling.** *How will changes in the structure of the WAP food web affect cycling and export of carbon? Additionally, how will changes in primary producers, and their energy storage, affect higher trophic levels?*

**D. Broader Impacts.** *How do we engage and excite broad audiences, while building a lasting knowledge of the issues facing our polar regions, without physically transporting individuals to the poles? To what extent can we create virtual/cost-effective experiences to help the public connect to these habitats?*

A detailed overview of our integrated sampling/modeling/methods strategy is provided after this 'Major Research Themes and Proposed Research' section. Our approach is a multi-faceted program combining spatial sampling from regional annual-monthly datasets collected by satellites-ships-autonomous gliders with daily-weekly temporal data collected at Palmer Station and by ocean moorings (Fig. 2). The seasonal sampling at Palmer is complemented with similar decadal time series collected in the subpolar north and polar south by U.S. federal and international partners (see below). Core time series sampling is complemented with experimental manipulations designed to measure responses in and across trophic levels to changes environmental drivers (e.g., temperature, light, nutrients, food concentration/quality, pH). The observed variability in space/time combined with the experimental response functions is used to inform a

suite of statistical, diagnostic, and prognostic models allowing us to simulate and predict ecological trajectories to the prevailing or expected changes for polar systems.

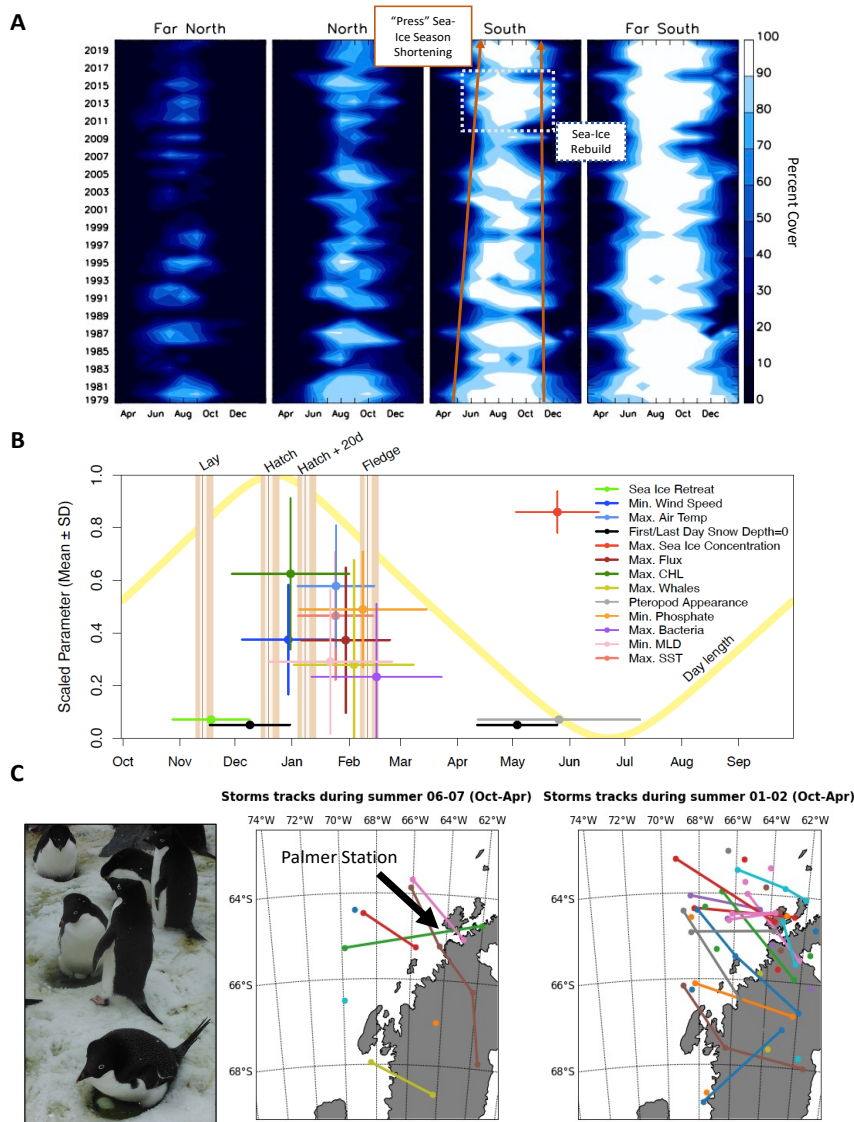
#### **A. DRIVERS OF DISTURBANCE ACROSS TIME/SPACE SCALES: ECOLOGICAL AND LATITUDINAL RESPONSE**

*Motivation:* Compared to temperate ecosystems, the WAP experiences high levels of natural climate variability intrinsic to polar seasonal sea-ice zones. This variability can disrupt long-term press trends—such as the recent decade of cooling that briefly reversed the decreasing trend in sea ice. The ecosystem response to these disturbances is filtered through the relevant biological time scales for organisms that vary widely from days for bacteria, phytoplankton and some microzooplankton, to years for krill, to nearly decades for seabirds and whales. Thus, the impact of a given disturbance is taxon- and life-history dependent: a pulse event is multi-generational for most plankton but transient noise for longer-lived taxa. Thus, in an environment with high natural variability, we need to determine how long-term “press” and short-term “pulse” disturbances interact to drive observed changes in the WAP food web, the response of individuals over time (reflecting resilience), and/or if there is evidence of legacy (long-lasting) effects.

**Subtheme A1. Long- and short-term spatial shifts in ecosystem productivity.** The WAP region is a natural laboratory for studying press-to-pulse forcing, with its long-term warming trend (Vaughan et al. 2001, Schneider et al. 2012) along with the recent cooling (Henley et al. 2019) and a series of short-term extreme pulse events (Fountain et al. 2016, Clem et al. 2020) (Fig. 4). The “press” of climate change, reflecting increased atmospheric/ocean temperatures and altered circulation patterns, is changing the seasonal growth and retreat of sea ice (Fig. 4A) modulated by interannual to decadal climate cycles and shorter-term synoptic “pulse” events (Figs. 1C, 4C). Climate cycles and extreme disturbance events (which we define as extreme outliers as falling outside the 10th to 90th percentile of a probability density function), can amplify or dampen the ongoing press of climate change as observed in other ecosystems (Boucek & Rehage 2014, Smale & Wernberg 2013). We define pulse events as synoptic storms ranging from a few hours to weeks and the ecological response to them can be short-lived (resiliency), long-lasting, or even irreversible (legacy effect or tipping point) (Thibault & Brown 2008, Wernberg et al. 2016, Hughes et al. 2017). The frequency of pulse storm events is also expected to increase over decadal time scales (Smith 2011, Poloczanska et al. 2013, Harris et al. 2018, Fig. 1C); however, documenting the impacts, transitions, and potential tipping points in ocean ecosystems has been difficult (Gruber et al. 2021, Hienze et al. 2021). PAL is well positioned to study the ecosystem responses to the changing forcing across subpolar systems in the north, polar systems in the south, and systems in transition at Palmer Station.

**A1 Hypotheses & Approaches. A1a.** *While the interactions of tropical Pacific and Atlantic Ocean teleconnections and Southern Annular Mode (SAM) underlie the interannual variability in sea ice, the long-term “press” of warming will continue to migrate subpolar conditions southward along the WAP. A1b.* *Earlier spring ice-free waters initially result in increased primary and secondary productivity, but over time, late ice advance and early ice-free springs will result in a decrease in ecosystem productivity due to deep vertical mixing driven by ocean exposure to strong Antarctic winds.* The high physical variability is differentially expressed across the WAP, thus climate-related impacts have affected the northern WAP for a longer period compared to the southern WAP (Fig. 1A, 4A). These include changes in cloud cover, air/ocean temperatures, winds, sea-ice cover, and ocean mixing and circulation, all of which exert strong impacts on the ecosystem from nutrients and phytoplankton (Kim et al. 2016, 2018) to zooplankton (Steinberg et al. 2015, Thibodeau et al. 2019) to predators (Cimino et al. 2014, 2019). The recent decade of cooling reflects these climate cycle interactions as well (Meehl et al. 2019, Stammerjohn & Scambos 2020). PAL’s 30 years of data enable new explorations of interannual to decadal variability.

To study long-term shifts in the WAP ecosystem due to the press of climate change, we will analyze how the dominant modes of spatial/temporal variability of key environmental, biological, and biogeochemical variables have changed over the last 3 decades, including contrasting the relation to earlier studies that documented the first decade of change (Ducklow et al. 2008, Martinson et al. 2008, Ross et al. 2008, Smith et al. 2008, Stammerjohn et al. 2008, Vernet et al. 2008). We will use seasonal WAP time series collected by Carlini-Palmer-Rothera spanning subpolar-transitional-polar systems with long term records of phytoplankton productivity, communities and biogeochemistry. Cruise data will provide the



*Figure 4. Theme A: Ecological response across a range of time/space scales. (A) Seasonal sea ice changes (% cover) centered on winter (x-axis) and over time (y-axis, 1979-2021) along the climate gradient of the WAP (left to right panels) (Subtheme A1). (B) Patterns in the mean and standard deviation in seasonal phenological interactions (centered on summer) of important biological and physical properties in relation to key events in the Adélie penguin breeding cycle (Subtheme A2). (C) Storm tracks along the WAP during the austral spring/summer seasons (Oct-Apr) with low (2006-07, middle) and high (2001-02, right) storm intensity (see also Fig. 1C); extremes in storm-driven precipitation can have a devastating impact on Adélie penguin nesting habitat (left) and egg survival (Subtheme A3).*

shorter storm events. The PAL modeling team is also collaborating with the Northern Gulf of Alaska LTER on similar ocean biogeochemical variability simulations (Hauri et al. 2021). Our modeling strategy will involve: a combination of hindcast simulations to characterize ecosystem response to historical press

horizontal and vertical gradients along/across the WAP for the physics, chemistry, bacteria, algae, zooplankton and higher trophic levels. In addition to traditional techniques using empirical orthogonal functions and reduced space optimal analysis (Martinson et al. 2008), we will use the PAL multivariate statistical “self-organizing maps” (Bowman et al. 2018) to define and track, over time unique biophysical seascapes, or geographical units, along the WAP and how they change in space and time. The rate of change in physical and chemical components will be compared to the biological responses and demographic rates accounting for the lifespans of major trophic levels (Bestmeyer et al. 2011). The marine ecosystem and biogeochemical models, developed during PAL-5 (Schultz et al. 2021, Kim et al. 2021), will be used to simulate ecological responses to both long-term change, decadal variability, and

trends and interannual to decadal variability in the context of the PAL data synthesis described above, idealized simulations with specified changes in future climate, disturbance frequency/magnitude, and climate projections using realistic future forcing output from global Earth System Models. The hindcast simulations will allow us to refine estimates of model predictive skill, quantify sources of model uncertainty, and characterize the degree of predictability of different ecosystem components using emerging ecological forecasting concepts (Dietze 2017, Bonan & Doney 2018). The WAP physical climate patterns and ecosystem responses will be assessed relative to simulated Southern Ocean basin-wide change under different future climate scenarios (Boyd et al. 2015, 2016; Moore et al. 2018). A key focus will be to resolve the rates of transition in ecosystem productivity and structure between sea-ice and oceanic ecosystem states along the WAP climate gradient. Taken together, these synthesis efforts will allow us to test the climate migration and hypothesized ecosystem transitions across trophic levels in our conceptual model.

**Subtheme A2. Trophic responses to temporal shifts in seasonal phenology.** Climate change and variability is known to shift the distribution and phenology of animal populations (Lyon et al. 2008), and PAL-5 described phenological shifts for animals ranging from invertebrate pteropods (Thibodeau et al. 2020a) to Adélie penguins (Cimino et al. 2019). While this is central to our conceptual model, it remains unclear what combination of environmental drivers affects other animals (e.g., krill and marine mammals) and if they respond similarly by shifting their phenology. WAP biota are adapted to high climate variability but the underlying press of climate change can lead to unexpected, amplified pulses in seasonal forcing. This is particularly true in nutrient-constrained, energy-limited (light) polar environments, where seasonal variability is occurring near a physio-ecological threshold and shifts can have long legacy effects (Fountain et al. 2016). It is well documented that the advance and retreat of winter sea ice has changed, effectively altering the start and length of the open water summer season (Fig. 4A). The ecosystem impact from such decadal and interannual variability will depend on the spatial scale, frequency, magnitude, seasonal timing, duration, as well as the underlying state of the ongoing press of climate change (Harris et al. 2018). Additionally, when presses and interannual/decadal variability are exerted simultaneously, the potential for effecting a species shift or reaching a tipping point is enhanced (Scheffer et al. 2001). The long-term shifts in phenology will be studied using the seasonal time series collected at land-based research stations spanning the WAP latitudinal climate gradient (Fig. 2).

**A2 Hypotheses & Approaches. A2a.** *Shifts in the timing of sea ice advance and retreat is reflected in the seasonal phenology of phytoplankton and zooplankton, which in turn drive match-mismatch dynamics at higher trophic levels—with potential fitness consequences.* **A2b.** *Early retreat favors subpolar life histories or warm water species, late retreat favors ice obligate polar species or cold water species.*

Spring preconditioning expressed in the timing of sea ice retreat is a dominant physical force governing biological processes across trophic levels (Saba et al. 2014). To assess the seasonal phenology, we will compare years with early versus late spring sea-ice retreat and the effects on the marine ecosystem. We will focus on determining if ongoing climate press alters the ecosystem responses over time. We will assess the difference in the sign or nature of the biological response to changes in sea-ice seasonality, and whether the trophic level response can be scaled to these seasonal changes to identify possible match-mismatch dynamics. For example, our recent analyses suggest the following changes occurred during the recent cold period (2009-2016, more ice): (1) enhanced phytoplankton productivity in the south (Schofield et al. 2018); and (2) increased frequency of krill (*E. superba*) recruitment (Conroy et al. 2020a), but it is unclear if the timing or abundance shifted.

Early and late sea ice retreat years will be compared to determine how shifted baselines (we define as the subpolar north versus the polar south ecosystem structure) may alter seasonally-integrated ecosystem responses, and which life history traits (life span, foraging behavior, reproductive frequency/flexibility/timing) are sensitive to changing sea ice seasonality. To identify trophic mismatches, our observational studies of the timing, presence or abundance of biophysical properties around Palmer Station will be linked to population trajectories and reproductive success of krill predators (focused on penguins and whales) (Fig. 4B). This will be enhanced by new bio-acoustic approaches (see methods below) initiated during PAL-5 that allows for prey mapping. For penguins, phenotypic plasticity in egg laying

exists (Cimino et al. 2019), but it is unclear how this relates to shifts in the timing of local primary productivity and krill availability to sustain chick rearing, and what is the optimum environmental window for breeding success. We will compare penguin clutch initiation dates and breeding success with the timing of: phytoplankton/zooplankton peaks in abundance, optimal weather windows (spring snowmelt and calm weather), and peaks in whale abundance (a possible krill competitor). For whales, we will quantify the timing of arrival and departure from the waters surrounding Palmer Station, their behavior, and the relationship with environmental properties. Recent studies suggest that humpback whales are extending their stay at their lower latitude breeding grounds (Avila et al. 2019), which may manifest as a shorter residence time at WAP feeding grounds, indicating that whales satisfy their energetic demands more quickly, influencing recent accelerated reproductive rates (Pallin et al. 2018b). Whales arrive when prey densities are high, allowing for nearly continuous feeding (Nichols et al. in press). We predict this may be accentuated as the earlier retreat of winter sea ice will open foraging areas earlier in the summer. Long-term WAP model simulations will provide a longer-term context to assess food web trajectories that might be predicted with increased warming, seasonally open water, and flow of carbon through the food web.

**Subtheme A3. Storm forcing plays a disproportionate role in structuring the variability in land-based elements of the WAP ecosystem.** Similar to sea ice, Antarctic wind patterns and storm intensity are linked to global climate change and synoptic-scale variability through tropical teleconnections and other climate modes (Yuan et al. 2018, Holland et al. 2019). A long-term southward shift in storminess (understood as the frequency, intensity, and seasonality of storm events) driven by the intensification of SAM is changing the seascape and landscape in ways not well documented nor understood. The increase in SAM is driven by both climate warming (which is expected to continue), and the decrease in ozone over Antarctica (which is reversing). Thus, storm forcing will likely change in magnitude and/or seasonal timing in the near future (Thompson et al. 2011), with poorly understood consequences for Antarctic ecosystems (Goyal et al. 2021). While these long-term consequences are not well understood, ecological impacts from storm events have been well documented (Chappell et al. 1989, Cimino et al. 2019, Fraser et al. 2013, Chapman et al. 2011, Massom et al. 2008, McClintock et al. 2008, Patterson et al. 2003). For example, for seabirds nesting on land, snow accumulation patterns drive nest microclimate conditions, breeding phenology, and reproductive success (Patterson et al. 2003, Fraser et al. 2013, Cimino et al. 2019), where snow or meltwater can bury or flood nests, drown eggs or small chicks, or lead to the wetting of chick down that is not waterproof (Chapman et al. 2011, Massom et al. 2008, McClintock et al. 2008, Boersma et al. 2014). Summer storms can be catastrophic, for example 2001-2002, an extreme weather year, had massive penguin breeding failures due to multiple storms hitting Palmer Station (Fig. 4C) (Massom et al. 2008).

The above has led to the development of a storm-intensity focus in PAL-6A&B, that a significant increase in the frequency or duration of storms will affect both landscape and seascape environments, which in turn critically impact survivorship, recruitment success, and the health of seabird populations. These episodic or compound extremes could have worse effects than the slow decadal-scale progression of the mean state (Gruber et al. 2021). We will focus on how long-term storminess patterns have changed along the WAP, and their impact on landscape processes that are critical to seabirds. These landscape storm effects may be related to changes in surface air temperature, clouds, precipitation, and snow accumulation. This complements our research in Theme B, where we focus on the seascape and how storminess contributes to vertical mixing and physical transport, impacting upper ocean ecosystem dynamics. Other LTER sites have already reported changes how storm frequency and magnitude can be key factors structuring foodwebs (Gaiser et al. 2020) and our new focus offers a rich opportunity for cross-site synthesis.

**A3 Hypotheses & Approaches. A3a.** *The long-term southern migration of the climate gradient has led to a relative increase in storm activity (storm frequency, wind intensity, snow and precipitation) in the northern WAP compared to the southern WAP. A3b.* *Intensifying storm events will initially, and disproportionately, increase the level of disturbance to land-based features and species with life histories tied to land in the northern WAP compared to the southern WAP.*

Few studies in the WAP have examined the effect of storm disturbances over local (10s kms) and synoptic (2-15 days) scales, including the potentially distinct effects on seascape versus landscape

processes. Towards this end, we will develop WAP-wide storm metrics using model reanalysis that can then be validated with Palmer Station and other weather station data, and these metrics will also be appropriate for distinguishing seascape (see Theme B) versus landscape effects (subtheme A3, here). These metrics may include precipitation (rate, frequency, and duration), wind speed and direction, cloud cover, and storm intensity (magnitude of low-pressure center). We will use these metrics to calculate mean storm characteristics and test for decadal trends, where the interpretation of decadal trends will rely on understanding of longer-term changes outlined in subtheme A1. Using WAP penguin breeding colony locations and available population trajectories (Humphries et al. 2017), we can test if different colony locations and species experience different storm impacts that ultimately impact population trends. Multidecadal reanalysis datasets for the Southern Hemisphere (ERA-5, Dee et al. 2011) will be used to calculate storm timing and location. Algorithms will be used to identify storms based on changes in direction and speed using a threshold level for ‘cyclone vorticity units’ (Grise et al. 2013). These regional-scale storm metrics will be compared to Palmer Station meteorological data to both ground-truth our metrics and understand how regional-scale processes influence local weather. Daily observations of precipitation and snow depth are recorded at Palmer Station and snow depth is recorded at other focal penguin colonies (e.g., Avian Island). We will test for shifts in the timing of snowmelt in spring and snow accumulation at the end of austral fall (complementary to subtheme A2), the proportion of days with rain versus snow precipitation, and how this relates to press and decadal forcing. We will also determine periods of snow presence during the penguin breeding season to understand how the magnitude/timing of snowfall impacts penguin reproductive success, and at what ages chicks are most vulnerable to landscape storm effects.

## **B. VERTICAL AND ALONGSHORE CONNECTIVITY AS DRIVERS OF ECOLOGICAL CHANGE ON LOCAL TO REGIONAL SCALES**

*Motivation.* Our conceptual model (Fig. 3) suggests that disturbances on press-to-pulse timescales are impacting upper ocean structure (e.g., MLD and stratification) and biological processes spanning marine productivity (Schofield et al. 2017), zooplankton distribution (Steinberg et al. 2015), the behavior and diets of top predators (Fraser and Hoffman 2003), and carbon export (Ducklow et al. 2008). While our focus has been on warming, sea ice retreat, and increased melting from land as drivers of these changes, recent research has revealed that storminess (introduced in subtheme A3) is also a critical source of water column disturbance for the WAP ecosystem. Previously PAL focused on exchange between the shelf and the open ocean as it is a driver of change in the ecosystem structure, but wind forcing has recently been linked to vigorous exchange between the WAP and the colder Weddell Sea from the north (Wang et al. 2022), highlighting the importance of along-shore movement of water, nutrients, and organisms for understanding ecosystem change along the WAP. We will use our decadal time series and new process studies to understand how upper-ocean ecosystem function/structure is shaped by the sometimes competing effects of shifts in wind forcing and along-shore exchange. This will be coordinated with efforts to understand press-scale impacts of drivers (Theme A) that then fuel impacts on food webs and carbon cycling (Theme C) (Fig. 3).

**Subtheme B1. Shifts in Upper Ocean Dynamics and Links to System Productivity.** Marine primary productivity along the WAP is strongly influenced by light, rather than the supply of deep nutrients, and therefore understanding the variability of MLD is of critical importance (Vernet et al. 2008, Carvalho et al. 2019). Winter sea ice preconditions the early spring mixed layer and influences summer productivity by modulating the upper layer stratification (Venables et al. 2013). Freshwater discharge from melting sea ice and land glaciers during spring and summer result in shallower mixed layers. Long-term change in these processes has decreased by half the MLD in the southern PAL (Fig. 5A), with an accompanying increase in productivity (Schofield et al. 2018; Fig. 1). Changes in storminess (see subtheme A3), however, will either compete with or contribute to the upper ocean changes driven by the above. Apart from direct impacts on MLD (Fig. 5B), storm-driven vertical mixing reduces phytoplankton concentrations (Moline & Prezelin 1996, Saba et al. 2014), while increased cloudiness lowers the light energy available for photosynthesis.

**B1 Hypotheses & Approaches. B1a.** *The competition between ice melt (from glaciers and sea-ice) and storm intensity (wind, precipitation) is a main driver of the synoptic-to-interannual variability in upper ocean structure (deep water ventilation, mixed layer depth, upper ocean stratification) along the WAP.*

**B1b.** By modulating upper ocean properties (B1a) and atmospheric forcing (cloudiness, air-sea fluxes), a climate-driven southward shift in storm activity is having a significant impact on variability of marine productivity along the WAP.

To understand the relative role of storms, freshwater discharge, and sea ice conditions on the upper ocean structure of the WAP (B1a), we will augment our observational efforts to resolve upper ocean variability in synoptic (2-15 days) scales. Moorings equipped with sensors to measure physical (temperature, salinity, pressure, radiation) and biological (chlorophyll concentration, acoustic backscatter for zooplankton concentrations) responses in the surface mixed layer will be deployed for 60-90 days off Palmer Station during the late spring-to-summer (Fig. 2). Bi-weekly sampling at Palmer Station provides seasonal time series of upper water column physical properties, chemistry, and biology (Table 1) from Oct–Mar (Fig. 2A). This is complemented with month-long glider missions in Jan-Feb that provide high-resolution measurements of optical properties, chlorophyll, and acoustic characterization of zooplankton throughout the water column even during storms. The Palmer weather station provides data to characterize atmospheric forcing, and this will be augmented by an additional station on Hugo Island (Fig. 2) to capture atmospheric conditions on the open shelf. This integrated observational strategy resolves the temporal (synoptic to seasonal) and spatial (10-100 m in the vertical, 10-100 km in the horizontal) scales necessary to understand the response to strong storm events. Sustaining these measurements year-over-year will allow us to quantify the impact of interannual variability and infer how changes in storminess impact ecosystem structure.

Addressing B1a requires understanding how storm activity contributes to upper ocean variability relative to other forcing, including winter sea ice concentrations (Brearley et al. 2017) and glacier meltwater discharge (Moffat et al 2008, Meredith et al. 2013). By integrating satellite sea-ice concentration

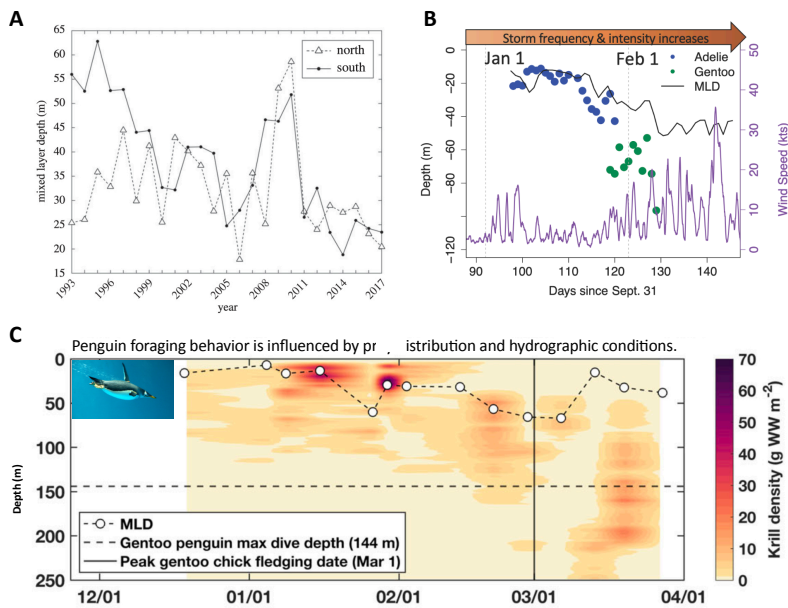


Figure 5: (A) Observations show strong oceanographic (MLD) variability since the start of PAL (Schofield et al. 2018; Subtheme B1). In seasonal time-scales, penguin foraging depths (B) and krill density (C) are modulated by these physical changes (Subtheme B3), but a mechanistic understanding of how storm and other disturbances (i.e., sea ice) compete to impact ecosystem processes in relevant timescales is lacking.

observations and *in situ* observations from Palmer Station, moorings, gliders, and the biannual summer cruise, we can construct budgets for key upper ocean properties (salinity, temperature, MLD) and quantify the competition between these processes in determining the evolution of the mixed layer and other upper ocean characteristics. For example, we expect low winter sea ice followed by spring/summer storm activity to lead to deep summer mixed layers, but for these changes to be blunted by high meltwater discharge (i.e., low surface salinities) from land. This approach to understanding the synoptic-scale response to storms will inform the development of biologically-relevant storm metrics that are part of subtheme A3.



Addressing B1b will require using the same observational approach but focusing on how storms compete with or contribute to other drivers of disturbance. We want to understand how marine productivity is impacted because of single storms and changes in both seasonal to interannual storm frequency. How changes in stratification and mixed layer properties impact primary productivity will be examined using mooring- and glider-based chlorophyll validated with measurements collected during the summer cruise or Palmer Station sampling (Fig. 2). This will be complemented with incubation experiments measuring microbial responses to variable light conditions that simulate variable mixing systems. Our extensive datasets of seasonal primary productivity and net community productivity (see below) will be re-analyzed in the context of newly acquired understanding of storm effects from the multi-year observational effort proposed here.

**Subtheme B2. Along-shore variability and connectivity.** PAL-5 focused on the key role that cross-shelf lateral transport of heat, freshwater, and nutrients plays on the distribution of organisms and biological productivity on the WAP as warm, nutrient-rich Circumpolar Deep Water is carried across the shelf. While those findings address critical questions about the impact of lateral transport from the open ocean to the WAP shelf, this region also exhibits significant physical and biological variability along the coast (Fig. 6A). Along-shore WAP physical gradients strongly modulate glacier retreat (Cook et al. 2016) and primary productivity (Fig. 6B, Montes-Hugo et al., 2009). Modeling (Wang et al. 2022) and observational (Aguilar-Gonzalez, *in prep*) studies show that this along-shore variability is driven by intrusions of cold water of Weddell Sea towards the southern WAP. This process is wind-forced and strongly seasonal with substantial interannual variability modulated by SAM. The ecological implications of this exchange have not yet been explored but are a new and potentially a significant driver of observed environmental and biological variability in the PAL study region. The transport of cold-water masses provides an input of polar species to the northern PAL region which has been transitioning to a subpolar state (Ducklow et al. 2013). This connectivity with a polar system may play a fundamental role in stabilizing and determining the resilience of the WAP in the face of long-term press of global warming (Pearson et al. 2021).

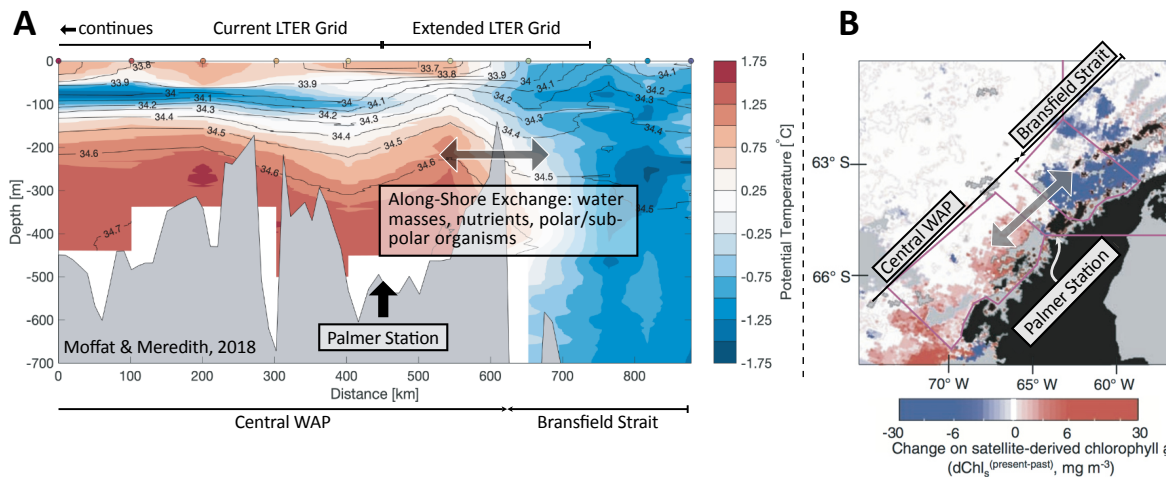


Figure 6: Hydrographic properties (ocean temperature) significant gradients, with larger long-term warming in the southern region (A; Moffat & Meredith 2018) which are co-located with strong long-term changes in Chlorophyll concentrations (B; Montes-Hugo et al. 2009). The exchange between these regions is poorly understood (Subtheme B2).

**B2 Hypothesis & Approach.** Along-shore exchange between the WAP and the Weddell Sea is a significant contributor to heat, salt, and nutrient budgets, and modulates food web productivity and structure by potentially transporting polar species (of phytoplankton, zooplankton, fish) into the northern, transitioned subpolar region.



To address B2, we have extended the PAL grid northwards to span the southern edge of Bransfield Strait (Fig. 2). This new grid was successfully sampled for the first time during our 2021 cruise (Fig. 2), and included the full suite of shipboard bio-physical observations (Table 1). Subsurface moorings were deployed during austral fall 2022 to capture the year-round variability in along-shore exchanges between the warm southern WAP and the cold Bransfield Strait (Fig. 2). Ocean gliders, such as the one successfully deployed during Nov-Dec 2021, fill the gaps of mooring and shipboard surveys (Fig. 2). Analyses on the impact on the coastal WAP ecosystem by this exchange will focus on whether physical properties (heat, salt), summer nutrient budgets, food web structure, and productivity change along the coast consistently with the intensity of intrusions of cold water from the Weddell Sea. Because the exchange appears to show high interannual variability (Wang et al. 2022), multi-year datasets will allow us to understand whether species affiliated with high sea ice and cold-water such as large centric diatoms, Antarctic Silverfish, or ice krill, play a role in the food web structure of the northern WAP during “high exchange” years—which would run counter to current conceptualization of the climate gradient, where polar species are only more abundant towards the south. These results will inform our efforts to understand changes to food webs and carbon export (Theme C) by incorporating the horizontal along-shore movement of organic and inorganic material into our models of ecosystem evolution. This effort will benefit from the partnership with the time series at Carlini Station and NOAA at Cape Shirreff (Fig. 2).

**Subtheme B3. Response of krill and predators to vertical and alongshore changes driven by storms.**

The characteristics of krill aggregations are critical determinants of predator demographics and foraging behavior, and carbon cycling. Storms and other oceanographic dynamics discussed above may affect krill through passive advection and dispersion, or cue active vertical migrations below the turbulent mixed layer (Croll et al. 2009, Warren et al. 2009). Along the WAP, a mechanistic understanding of storm impact on krill distribution and abundance is missing. Storms might cause vertical redistribution of krill through an increase in turbulence or trigger active avoidance of the surface turbulent layer via vertical migration. In turn, krill predators may target deeper prey patches away from the influence of the wind, or krill aggregations could drop below threshold densities required for successful foraging. Storms not only affect krill predators in the water (Fig. 5D), but also have consequences for those breeding on land (Subtheme A3). For example, in summer whales forage during all hours of the day predominantly in the upper 20 m of the water column but when krill begin active (or storm driven) vertical migration, whales often cease foraging (Nichols et al. in press). How the frequency of these events affects body condition and inter-annual variability in female humpback whale pregnancy rates (~35-70%) (Pallin et al. 2018b) is of great interest.

**B3 Hypotheses & Approaches. B3a.** *Storm-induced ocean currents and turbulence change krill distribution, abundance, and aggregation structure, leading to smaller, diffuse, and deeper patches. This in turn alters krill predator foraging dynamics (deeper dives, decreased foraging efficiency) and demographics (reduced penguin chick fledging mass and whale pregnancy rates).* **B3b.** *Despite the positive and near immediate impacts of sea ice rebuild on lower trophic levels, negative storm effects dominate over any positive sea ice effects, hindering Adélie penguin population increase.*

To address B3a, acoustic surveys using RHIBs and gliders will measure the seasonal and interannual variability in krill patch structure (e.g., location, depth, density, size, and biomass; Bernard and Steinberg 2013, Bernard et al. 2017, Nardelli et al. 2021) within penguin/whale foraging regions near Palmer Station (Fig 5C, Nardelli et al. 2021). While these surveys are limited during storms, mooring/glider observations (Subtheme B1) will provide data throughout storm events. It is critical to better understand vertical shifts in krill biomass resulting from diel vertical migration, as there is a seasonal shift in krill (*E. superba*) depth range distribution, from shallow in midsummer to deeper later in early fall (Nardelli et al. 2021). This process is likely related to changes in light and a progressive behavioral shift toward diel vertical migration (Fielding et al. 2014, Siegel 2012, Taki et al. 2005). This change can reduce prey availability and therefore foraging behavior for predators that have evolved life histories around this movement (Friedlaender et al. 2013, 2016). For example, the chick rearing period in penguins and the hyperphagic period of baleen whales to recover lost energy stores occur during periods when krill are ubiquitously available and whales target

dense krill patches (Cade et al. 2021, 2022; Savoca et al. 2021). We will test how the frequency and strength of storms impact krill behavior and aggregation characteristics that in turn impact predator behavior.

Penguins and whales have different energetic demands, foraging modes, and spatial foraging ranges. Preliminary data collected during PAL-5 revealed an apparent relationship between increased wind speeds and deeper mixed layer depths, and predator dive depths (Fig 5C). Baleen whales are bulk-feeders and require high-density prey patches to make feeding energetically profitable while penguins can utilize smaller or lower-density patches as they target single prey, suggesting contrasting responses of predators to storm-driven alterations in prey. Near Palmer Station, satellite-linked, motion-sensing and time-depth recorders deployed on penguins and whales provide information on foraging effort and locations at fine spatial-temporal scales (Pickett et al. 2018, Cade et al. 2022, Nichols et al. in press). Whale relative abundance will be determined throughout the season using moored passive acoustic hydrophones. Merging behavior and abundance time series provides a seasonal view of biological activity. Statistical models (e.g., generalized linear and/or additive models) will be used study whale foraging responses to prey, storm properties, and oceanographic conditions. Further we will investigate whale presence (visual sightings, vocalizations from passive acoustics, and satellite tags) to disturbances assessing if whales shift distribution and alter foraging behavior during and after storms.

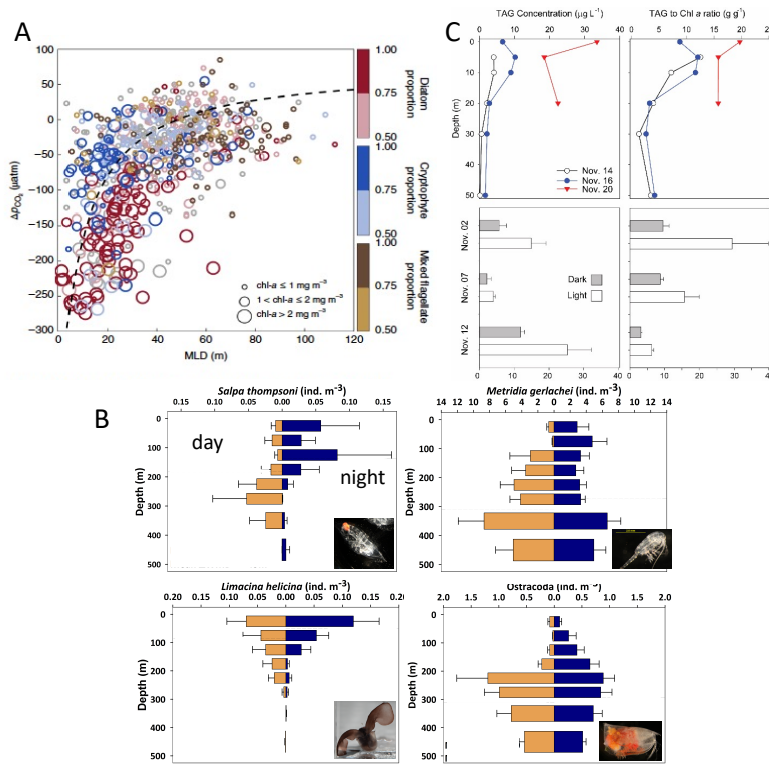
We will use the Population Consequences of Disturbance conceptual framework (how exposure to a stressor can affect ecological drivers on an individual's vital rates with the integrated effects on population dynamics) to assess how storms affect the behavior and physiology of penguin and whale population dynamics (Pirotta et al. 2018, New et al. 2015). We seek to determine the differential effects of disturbance and resilience on krill predators with different life histories, foraging behaviors, and demographic patterns. Specifically, changes in foraging behavior can affect adult fitness, body condition, and reproductive rates, as well as offspring survival. Preliminary analyses suggest mean chick fledging mass decreases later in the austral summer as storm disturbances increase. If storms are not a factor influencing chick mass, parental effects or ecosystem phenology (see Subtheme A2) may play a larger role. For whales, changes in foraging effort and increases in body condition should correlate with increased pregnancy rates. We will test for linkages between whale foraging efficiency related to storms with female pregnancy rates the following year. Our prediction is that in seasons with more storms and poorer foraging conditions, fewer whales will become pregnant. However, as whales are long-lived, we predict this will not have a major effect on the long-term positive population trend (Fig. 3 bottom right panel).

Consistent with our conceptual model, the recent ice rebuild period resulting in an increase of phytoplankton production and krill recruitment, we predicted that the ice-dependent Adélie penguin population would increase in response—but this has yet to be seen. Even with the recent increase, sea ice was still lower than in the 1990s when Adélie populations were already declining. Negative effects from more frequent and/or intense storms may dominate over positive sea ice effects, or the short-term sea ice increase might not have surpassed the threshold needed to result in higher Adélie recruitment and a subsequent population increase. Therefore, to address B3b, we will conduct statistical analyses that include sea ice conditions (Subtheme A1), landscape storm metrics (Subtheme A3), and seascape and prey response to storms (Subtheme B1) to determine how these variables differ during the sea ice rebuild phase and within the following years, as penguins do not recruit for 3-6 years. The combination of these metrics will help decipher the relative magnitude of landscape versus seascape storm effects on penguin demography and long-term resilience to sea ice decline.

**C. CHANGING FOOD WEBS AND CARBON CYCLING** *Motivation.* Central to our conceptual model, the structure of the pelagic food web plays a fundamental role in regulating net community production, air-sea exchange of carbon dioxide (CO<sub>2</sub>), and the export of organic carbon to the deep ocean (the biological pump, Ducklow et al. 2001, 2015; Salliey et al. 2013; Steinberg & Landry 2017; Lin et al 2019, 2021). Furthermore, food web interactions affect assimilation and trophic transfer efficiency of energy and carbon throughout the food web. Our previous synthesis efforts provided constraints on carbon flow through the food web and indicated the critical importance of the size structure and composition of phytoplankton and the fraction of primary production routed through microzooplankton versus directly to

larger zooplankton and krill (Sailley et al. 2013, Ducklow et al. 2015). Climate-driven changes in the planktonic food webs will force changes in productivity, carbon exchange, and energy storage, only discernible in a long-term program. In PAL-6B we will build upon decades of plankton and biogeochemical measurements to quantify these changes.

**Subtheme C1. Phytoplankton primary productivity, diversity, and carbon dynamics.** The structure of the pelagic food web varies across the WAP shelf, with distinct differences between nutrient replete productive coastal waters (Serebrennikova & Fanning 2004, Kim et al. 2016, Sherrell et al. 2018) and outer continental shelf waters



**Figure 7. Theme C: Food webs and carbon cycling.** (A) Relationship between PAL summer grid-wide averages of mixed layer depth (MLD) and the air-sea pCO<sub>2</sub> difference where negative values indicate undersaturation that drives the transfer of CO<sub>2</sub> from the atmosphere to the ocean; phytoplankton community structure marked by symbol color and chlorophyll concentration by symbol size (Brown et al. 2019) (relevant to Subtheme C1). (B) Diel vertical migration of common zooplankton along the WAP continental shelf (Conroy et al. 2021). Note the higher abundance in surface waters at night. Diel vertical migrators ‘actively transport’ carbon to depth by feeding in productive surface waters at night and metabolizing their food at mesopelagic depths during day (seeking refuge from visual predators) (Subtheme C2). (C) Top panels: Triacylglycerol (TAG) concentrations and TAG:chl a ratios in the water column at Palmer Station E showing increased caloric content as the spring bloom progresses. Bottom panels: influence of light on TAGs in dawn-to-dusk incubations, illustrating the production of TAGs in sunlight and consumption in the dark (Subtheme C3).

characterized by low biomass and micronutrient limitation (Annett et al. 2017). Coastal waters are characterized by early spring centric diatom blooms (Hart 1942, Nelson & Smith 1991, Prézelin et al. 2000), regulated by water column stability and light limitation (Moline et al. 1998; Vernet et al. 2008, Carvalho et al. 2016, 2019). Offshore WAP waters are characterized by seasonal spring blooms associated with the retreat of sea ice (Smith & Nelson 1985) that decline as micronutrients become limiting (Sherman et al. 2020). Cryptophytes, mixed flagellates, and small pennate diatoms are associated with lower salinity coastal waters and dominate in the later summer (Schofield et al. 2017, Rozema et al. 2017, Nardelli et al. submitted) leading to the hypothesis that they will thrive under conditions of increased warming and sea-ice melt (Moline et al. 2004). As highlighted in our conceptual model, the relative abundance of these phytoplankton taxa affects seawater CO<sub>2</sub> saturation, atmospheric CO<sub>2</sub> uptake, and carbon flow through the food web (Brown et al. 2019, Fig. 7A). Phytoplankton composition and size distribution affects the flow of carbon through the food web, with krill and other macrozooplankton grazing on large phytoplankton cells, and smaller cells consumed by microzooplankton (Garzio et al.

2013). Therefore PAL-6B will study the environmental drivers of not only phytoplankton biomass but also expand our focus on the role of phytoplankton physiological ecology and diversity on carbon cycling.

**C1 Hypotheses & Approaches. C1a.** *Phytoplankton diversity and taxonomic structure will change with declining sea ice, driving changes in atmospheric CO<sub>2</sub> uptake and carbon export. C1b.* *Variations in phytoplankton community structure will lead to variations in the total ratio of high energy lipids to lower energy carbohydrates not captured in bulk measurements of primary and/or community production.*

Understanding the dynamics of physical forcing of phytoplankton biomass in Subthemes A1 and B1 will provide critical insights that will inform Subtheme C1 where we focus on phytoplankton community structure within the context of measurements of physical (MLD, incident irradiance) and bulk biogeochemical properties, including: patterns of seasonal nutrient drawdown (Kim et al. 2016), oxygen, dissolved inorganic carbon and alkalinity (Hauri et al. 2015; Shadwick et al. 2021a,b), surface pCO<sub>2</sub>, POC, and total chlorophyll as well as rate measurements from 14C-uptake, and net community production (Eveleth et al. 2017, Ducklow et al. 2018), and instantaneous carbon export from short-term sediment trap deployments. These rate measurements will be complemented with detailed measurements of phytoplankton diversity, via automated microscopy. Assessment of the energy flow through the food web will be added as a new core measurement program, by establishing estimates of the upper limit of available chemical energy from photosynthesis, and then traced through the food web with microcalorimetry. Because the energy content of different biochemicals that contribute to biomass and detritus can vary by a factor of at least two, drivers of variations in the energy content will be assessed through lipidomic and carbohydrate analyses of primary chemical energy storage biochemicals (see below).

The total chemical energy capture estimated by Picosecond Lifetime Fluorescence (Kuzminov & Gorbunov 2016, Lin et al. 2016) and fast repetition rate fluorometry will provide estimates of photosynthetic electron transport (Lin et al. 2016, Park et al. 2017, Falkowski et al. 2017) combined with microcalorimetry to estimate the conversion efficiency to cellular constituents. This will be combined with detailed time/space measurements of phytoplankton species diversity at species level through automated microscopy (Sosik & Olson 2007), particle size distribution (Karp-Boss & Boss 2007), phytoplankton and bacterial community diversity/activity via DNA/RNA profiling (Luria et al. 2017, Djurhuus et al. 2018, Brown et al. 2021, Lin et al. 2022; see Bowman letter of support). Spatial/temporal maps will be complemented with controlled manipulative incubations to access the response of natural microbial communities to dynamic environmental conditions. For example, light regimes in experiments will be designed to simulate differences in mixed layer depth over time and characterize how phytoplankton respond by altering their reservoirs of energy storage biochemicals and/or how community composition shifts. These experiments will be similar in detail to the previously-published studies from our group (e.g. Collins et al. 2018) and complement similar efforts at other marine pelagic LTER sites (Northeast US Shelf, Northern Gulf of Alaska, California Current, Beaufort Lagoons). The biogeochemical ramifications of altered phytoplankton community structure will be examined in regional food-web (Sailley et al. 2013), 1-D PZND-biogeochemical (Kim et al. 2021 and 2022), and 3-D bio-physics (Schultz et al. 2021) models.

**Subtheme C2. Food webs, carbon cycling, and export processes.** Vertical export of POC is a key process in the WAP biological pump though on local scales lateral transport may be significant (Stukel et al. 2015). POC export over the northern WAP shelf is dominated by krill fecal pellets (Gleiber et al. 2012), and a recent modeling effort shows that krill fecal pellet production in the Southern Ocean marginal ice zone is equivalent to 17-61% of annual POC export in this zone (Belcher et al. 2019). Interestingly, mean krill size within a cohort in a given year is the best predictor of export as measured by the PAL long-term sediment trap (Trinh et al. submitted). Krill size thus may be a ‘master trait’ for predicting WAP POC flux, as shown for copepod fecal pellet POC flux (Stamieszkin et al. 2015). Zooplankton vertical structure and behavior play key roles in mediating carbon export (Steinberg & Landry 2017, Cavan et al. 2019, Archibald et al. 2019). Many zooplankton feed in surface waters at night, migrating to the mesopelagic zone to metabolize their food during the day, resulting in the ‘active transport’ of carbon to depth. Light is the proximate cue for zooplankton diel vertical migration (DVM), although Becker et al. (2018) speculated that diel variations in energy-rich lipids by phytoplankton, and, thus, food quality, may also play a role. Analysis of WAP

zooplankton diel vertical distribution patterns collected during PAL-5 indicates strong DVM by a number of key taxa (salps, ostracods, copepods, pteropods), controlled by photoperiod and MLD (Conroy et al. 2020; Fig. 7B). This runs contrary to the presumption that near continuous summer daylight would dampen DVM. Zooplankton DVM through summer could result in substantial active carbon transport out of the euphotic zone, which may help resolve controversial low particle export to primary production ratios observed for the WAP (Buesselar et al. 2010, Stukel et al. 2015, Ducklow et al. 2018, Stukel et al. in press).

**C2 Hypotheses & Approaches. C2a.** *Export of zooplankton fecal pellet carbon will vary between major zooplankton taxa, and positively scale with animal size, leading to regional, interannual, and longer-term changes in carbon export. C2b.* *Zooplankton active carbon transport by diel and seasonal vertical migration is a substantial export term compared to passive sinking of POC (fecal pellets, phytoplankton aggregates) in the WAP.*

To test these hypotheses, we will continue our ongoing measurements of zooplankton abundance and diversity across the PAL grid. Relative contribution of sinking zooplankton fecal pellets, phytoplankton aggregates, or other particulate matter will be quantified to examine the role of phyto- and zooplankton community composition to export (Gleiber et al. 2012, Wilson et al. 2013) using polyacrylamide gel traps on our new sediment trap array (Durkin et al. 2022) and a new high-sensitivity lipid biomarker method (Hunter et al., 2021). We will combine ongoing experiments of zooplankton fecal pellet production with zooplankton abundance and size data to develop size-based algorithms of fecal pellet production and export. We will examine assimilation efficiencies of key lipids and carbohydrates by krill and copepods (see below), in parallel with spatially resolved surveys of lipidomes and carbohydrates in sinking particulate organic matter (POM), collected in drifting sediment traps (Collins et al. 2016, Fulton et al. 2017) deployed at Process Study stations across the WAP latitudinal and coastal-shelf-slope gradients. To obtain measurements of zooplankton DVM active flux, we will build upon our completed analysis of zooplankton DVM patterns during austral summer along latitudinal and offshore gradients of the WAP, by applying taxon-specific metabolic data from the literature and our own ship-board metabolic experiments (Thibodeau et al. 2020a) using an automated respirometer that we designed (Collins et al., 2018). Preliminary estimates suggest active transport is a substantial, unaccounted, export term in the WAP C budget, with mean active C transport below 150m by summed DVM taxa equivalent, or exceeding, passive POC export measured by sediment traps in summer. We will add active transport by seasonal vertical migrants such as hibernating copepods (*Calanus acutus*) that build up C-rich lipid stores in summer and migrate to the mesopelagic zone in fall; this “lipid pump” (Jónasdóttir et al. 2015) has yet to be quantified anywhere in the Southern Ocean.

These export process measurements will be tied to PAL data to make predictions of the role of zooplankton-mediated carbon export in the WAP that will be compared with geochemical estimates of net community production (from surface O<sub>2</sub>/Ar and seasonal nutrient drawdown) and export via <sup>234</sup>Th deficit (Stukel et al. 2015, see letter of support) and particle flux measured by drifting sediment traps. Active zooplankton carbon export will be included in our regional food web and biogeochemical models using a new zooplankton DVM parameterization (Archibald et al. 2019) adapted to polar summer conditions.

**Subtheme C3. Energy storage and food web interactions.** Light availability is a fundamental feature structuring productive coastal systems and export of carbon, but a more detailed and nuanced understanding of how light energy is stored chemically by phytoplankton and ultimately flows through the ecosystem is a critical core issue for the WAP. Phytoplankton have evolved methods of storing chemical energy (e.g., lipids, carbohydrates), chief among these, particularly for eukaryotic phytoplankton, is the synthesis of energy storage lipids, such as triacylglycerols (TAGs; Becker et al. 2018). Preliminary findings show this phenomenon is significant across the WAP: 1) the concentration of TAGs in phytoplankton are 90% higher in light incubations vs. those in the dark; 2) TAG concentrations in the water column were 6X higher at 5 m depth than at 30 m; and 3) euphotic zone TAG inventories doubled between mid- and late-November, coincident with the onset of the bloom (Fig. 7C). We posit that temporal and spatial gradients in TAGs and other energy storage molecules in phytoplankton can influence the abundance, behavior, and energy density of krill, and thereby, other organisms in the food web. For example, zooplankton exhibiting DVM begin feeding at sunset when TAG and concomitant caloric content of their phytoplankton prey peak at the surface

(Becker et al., 2018). Similarly, near Palmer Station in summer, humpback whales forage in the surface most intensively at night (Nichols et al. in press). Since TAG synthesis is related to sunlight, these and other energy storage molecules may compose a critical link between summer light history and the ultimate energetic poise of the WAP ecosystem. The Palmer Station time series provides a unique framework to examine this question.

Finally, despite our prior results suggesting krill are not a limiting resource for predators, differences in prey quality (i.e., lipid, carbohydrate, and caloric content) affect the ability of predators to meet their energetic demands, and have implications for penguin demography, such as penguin chick mass and breeding success (Chapman et al. 2010, 2011). Quality of penguin and whale prey also differs by taxa, with fish (myctophids) having the highest prey quality in terms of lipid content and energy density, followed by different krill species (Ruck et al. 2014). Krill (*E. superba*) in the south PAL region had 20% higher total lipid content than those in the north, a difference explained, in part, by gradients in nutrients and phytoplankton stocks (Ruck et al. 2014). Further, Adelie penguin chicks in the south had enriched carbon and nitrogen stable isotope signatures indicating a diet associated with sea ice food webs (e.g., crystal krill, Antarctic silverfish) (Gorman et al 2021). Lipid-rich and sea ice associated prey species may provide a buffer to environmental variability or unfavorable conditions and without these high-quality prey penguin demographics may suffer (Fig. 8). These observations, along with the clear linkages between lipid biosynthesis and light (Fig. 7B), suggest that prey quality may also be affected by climate migration, which we will examine in PAL-6B using new lipidomic approaches (Becker et al. 2018, 2022; Collins et al. 2016, 2018; Bowman et al., 2021).

**C3 Hypotheses & Approaches. C3a.** Temporal and spatial gradients in lipids, carbohydrates, and caloric content (i.e., prey quality) in phytoplankton influence the abundance, behavior, and energy density of krill and higher trophic levels. **C3b.** Prey quality cascades through the food web, affecting absorption of chemical energy in predators.

Lipids have a long history as tools for understanding trophic interactions in Antarctic marine

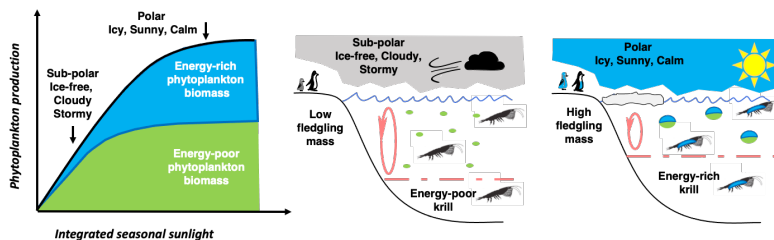


Figure 8. A model of the potential connections between sunlight, primary production, energy-content of phytoplankton biomass, krill energy-content, and penguin chick fledging mass (Subtheme C3). We hypothesize that while seasonally integrated sunlight affects phytoplankton community structure, it also fundamentally affects the food-quality of the food web. Thus, changes on physical conditions (depicted for simplicity as sub-polar and polar endmembers) will alter how energy flows through the WAP ecosystem, and ultimately affects higher trophic levels. Left: a hypothesized relationship between sunlight and chemical energy content of phytoplankton where seasonally-integrated sunlight affects not only primary production, but also the energy-richness of phytoplankton biomass. Middle: in the subpolar end-member scenario, deep mixed layers and clouds lead to low seasonal sunlight, low energy phytoplankton and krill, and low chick fledging mass. Right: in the polar end-member scenario, shallow mixed layers and clear skies lead to high seasonal sunlight, high energy phytoplankton and krill, and high chick fledging mass.

communities (Bottino 1974, Hagen et al. 1996, Kattner et al. 2012, Nichols et al. 1989, Skerratt et al. 1995, Ruck et al. 2014, Bowman et al. 2021), and state-of-the-art lipidomics allow us to obtain nearly complete lipidomes (1,000 + molecules) from the samples we will collect each season (Becker et al. 2018, Collins et al. 2016, 2018). Our carbohydrate method (Engel and Händel, 2020) does not resolve specific polysaccharides (e.g., laminarin; Becker et al., 2020), but captures their monosaccharide composition and provides the information necessary to determine caloric contributions from carbohydrates. We will examine how the molecular diversity (lipids) and energy

content (lipids and carbohydrates) of energy-storage molecules vary between key functional groups along the latitudinal and cross-shelf gradients of the WAP, and from time scales diel to interannual, considering the implications for energy transfer through food web. We posit that storage molecules may not only mitigate temporal (seasonal) variations in prey availability for consumers, but also spatial (patchiness/dilution) variations in prey availability. We will conduct lipidomic analyses of the bulk planktonic community (filtered samples; Collins et al. 2016, 2018; Becker et al. 2019) and key phytoplankton taxa via flow sorting (Popendorf et al. 2011) across the regional sampling grid and at Palmer Station. We will analyze sea-ice algal communities in ice cores, as our data suggest that seasonal sea-ice contains as much energy storage lipid as the entire water column below. Finally, we will analyze krill, other major zooplankton taxa, and small fish (net tows), thus tracing chemical energy through the food web of this sunlight constrained system.

We will also examine how well fish, penguins and marine mammals absorb energy-rich biochemicals during digestion. We propose to develop an index of lipid and carbohydrate absorption efficiency through comparative analysis of diet samples and excreta. In penguins, we will collect paired samples of diet (via lavage) and excreta of individuals. We will use data from local krill populations as proxies for whale diets and collect feces when opportunities arise during whale operations. Bomb microcalorimetry will be used on representative subsamples to determine total energy content and determine the relative contribution of TAGs, wax esters, and other lipids (e.g., phospholipids, Harvey et al., 2012; Ju et al., 2004, 2009) along with carbohydrates. These biochemical and caloric data will provide a framework for developing hypotheses connecting spatial and temporal distributions of chemical energy in phytoplankton, zooplankton, and representative krill predators.

Complementary lipid and energy contents data will provide novel insights on whether prey energy content influences predator behavior. To determine whether penguins are size selective feeders, and if selectivity has changed over time (or is associated with environmental controls), we will compare our full time-series data set of krill size-frequency structure from penguin diet samples for the north (Palmer Station region) and south (e.g., Avian I., Charcot I.) with net tow data collected from our ship and small boat surveys in the same region. To determine the effect of selective feeding on trophic transfer we will also assess the caloric content, lipids, and carbohydrates of the different size/stages of krill, to determine if the timing of peak penguin foraging and peak krill fat content impact chick fledging weight (complementary to Subtheme A2). We will incorporate the new findings on energy storage and flow and ecosystem structure from the Palmer Station field and lab studies into expanded versions of the regional food-web (Sailley et al. 2013) and 1-D PZND-biogeochemical (Kim et al. 2021, 2022) models. The ecosystem models will be extended to incorporate lipids and energy flow, with constraints on lipid and carbohydrate production, utilization, and requirements of different trophic compartments based on data from PAL 6B. This will be used to test predicted changes in carbon cycling in our conceptual model.

### **BROADER IMPACTS**

*Motivation.* The overall objective of the PAL education/outreach program is to promote the global significance of Antarctic science and research to educators, students, and broader public. Engaging with communities, sharing the knowledge and current findings of PAL is integral to promoting understanding of the tangible impacts of climate change on polar ecosystem. Even though polar regions are far from most of the world's population, they have a profound impact on lower-latitude weather patterns, raise sea level, and figure prominently in the world's economy and security (NSF 2020). National surveys and studies show that while people may be aware of local impacts of a changing climate, their understanding of the climate system and how it is connected to polar regions is limited (Ballew et al 2019; Leiserowitz et al 2010). The lack of polar literacy combined with the scientific importance of the WAP highlights the urgency of broadening the reach of polar science using effective educational materials and experiences that bring research and findings to learners in the lower latitudes.

How do we engage and excite broad audiences, while building a lasting knowledge of the issues facing our polar regions, without physically transporting individuals to the poles? What alternative virtual and cost-effective interventions can we construct that will help the public connect to these fragile habitats?



What are the key concepts and fundamental principles that we want the public to know and understand about the polar regions? What audience is best suited to investigate these ideas? To explore these questions, our efforts focus on bringing the poles to people by leveraging the availability of data and the stories of those collecting it. The Polar Literacy Principles (McDonnell et al. 2017, 2020) serve as the framework for our efforts to positively impact the education enterprise through development/dissemination of polar instructional materials and learning opportunities for K-12 educators facilitating their professional development/curricula. We will engage a range of learning communities through the development and implementation of: a) Out of School Time (OST) learning opportunities such as family science events, and afterschool and summer camp programs with a special focus on underserved and diverse audiences; b) art and science exhibitions with programming designed for use in higher education focused on engaging lifelong learners; and c) high quality science communication resources to build awareness of PAL research aimed directly for audiences in the cruise ship industry and indirectly through social media.

Our education and outreach work will have three key intended impacts: 1) *Reduce barriers to using PAL scientific data in teaching.* We will continue to focus on strategies to engage educators and students in understanding the value and wisdom of long-term data collection. 2) *Use art based pedagogical strategies to deepen appreciation and engagement of science-interested communities.* Our work will deepen appreciation and engagement of learners by promoting reflection, critical thinking, and creativity among collaborating scientists, artists, and educators. 3) *Improve STEM education and educator development and the full participation of women, persons with disabilities and underrepresented minorities in STEM (PAPGG 2020).* This is a cross cut intended impact that transcends all dimensions of our work.

### **Objectives:**

1. *Maintain and expand our virtual field trip schoolyard program: We will continue to offer 4-6 Video Teleconferences (VTCs) annually during each field season at Palmer Station, connecting with schools nationally (grades 5-12) (McDonnell, RU).* This program, which reaches ~200 youth/VTC, has been successful in engaging youth with PAL science (McDonnell et al 2020). We propose to update our virtual field trip activity package (maps, photos, and data visualizations) to schools. We will create and contribute a virtual field trip video to the Virtual Field project to expand the reach of our materials to undergraduates.

2. *Distribute Data to the Rescue: Penguins Need Our Help! program to Out of School Time (OST) afterschool and summer camp programs nationwide (McDonnell, leveraging our Polar Literacy NSF grant #1906897).* This program focuses on middle school age youth using art and creative expression to build data literacy skills. Efforts to date have focused on diverse audiences including OST youth ages 9-13 and their families from underserved and underrepresented communities; and informal educators at museums, science centers, zoos, and aquariums as well as YMCA, Boys & Girl Club, and 4-H Youth Development professionals. *Data to the Rescue* has been pilot tested with approximately 800 youth in NJ and PA. We will offer a professional development workshop with education professionals in the PI partner institutions in year 1. In addition, we will commercialize materials for distribution through the national 4-H network, reaching more than 20,000 youth through the 4-H STEM Challenge 2022. In addition, working with the National Association of Extension 4-H Youth Development Professionals, we will conduct a training for volunteers and 4-H professionals at their national conference.

3. *Expand education outreach through art and science exhibitions and programming beyond K-12 to engage college and university students and lifelong learners (Nelson, UCSC).* Dr. Rachel Nelson, Director of The Institute of the Arts and Sciences at UC Santa Cruz will help develop a traveling art and science exhibition to creatively engage audiences in issues impacting the polar regions (see letter of collaboration). Combining contemporary artworks by nationally and internationally acclaimed artists with analytics and data visualizations produced by associates of PAL, the exhibition and related programming will allow non-expert audiences to engage with and better understand issues of the changing climate in the Polar Regions. The exhibition will open in year 3 and travel with sustained programming in year 4.

4. *Connect science-interested audiences through collaborations with the cruise ship industry (Nelson and McDonnell).* Translating PAL research results into outreach products for audiences and measuring these audiences' understanding of and appreciation for Antarctica. We will focus on applying Visual



Thinking Strategies (VTS) to share images, art, and data visualizations with tourists to connect them to the environment and the changing climate in the WAP. The VTS technique connects the learner's aesthetic response to imagery with their understanding and connection to the conclusions they draw about climate change. We propose to train in the technique in year 2, with pilot programs in year 4.

**Evaluation.** For youth we will: 1) *Develop collaborative learning experiences, which allow learners to assume agency in their learning.* Collaborative learning strategies allow young people to leverage their own strengths, interests, and skills, while working with peers and adults. 2) *Meet the learners' need for programs that connect learning across settings.* We will collaboratively develop programming that creates productive learning partnerships. 3) *Provide youth access to LTER researchers sharing their connection, knowledge, and enthusiasm for polar science.* 4) *Develop a program that is culturally responsive by connecting to problems that are central to the learner's community (climate change, local natural settings) by leveraging the cultural orientation, resources, and practices of the project participants.* Research suggests that this can lead young people to see STEM as relevant to their lives, their family, and their culture.

LTER E&O budget is predetermined and modest, but we will strive to conduct a developmental evaluation program that provides a stream of just-in-time data to inform ongoing decision-making throughout program development (Patton 2011). We will deploy existing pre- and post-survey techniques to formatively evaluate our products and programs. Examples of dimensions and metrics include: 1) Personal Learning Plan (PLP) Knowledge Assessment: This assessment was developed to align with the PLP and will include items to measure knowledge. The assessment can be adapted to be administered to adult and youth learners, 2) Informal Educator Self-Efficacy Scale (Data Skills): Measures learners' self-reported attitudes towards data usage, 3) Science Process Skills Inventory (Knowledge): Identified through CAISE, this inventory was established by Oregon State University and the 4-H Youth Development program and measures the scientific inquiry skills among youth using an 11 item Likert scale. Reliability is 0.84-0.94 (Chronbach's Alpha) and a split-half reliability of 0.93. 4) Science Opinion Survey (Science Interest and Attitudes): Identified through CAISE, the Science Opinion Survey is a 30 item Likert scale assessment for measuring youth interest/attitudes towards science.

**BROADENING PARTICIPATION THROUGH A COORDINATED DIVERSITY, EQUITY, AND INCLUSION PLAN.** There is an overarching need to improve diversity in STEM disciplines. The traditional "pipeline" model, where a student follows a fairly linear, predictable, and structured path through K-12, undergraduate, and graduate education into career-length government or academic positions no longer captures the reality of a modern STEM career (Cannady et al. 2014). Instead, we propose to support a new model of a "braided river" concept where we vary the pathways into and within PAL opportunities to better recognize unusual entry points, evolving occupational goals, and opportunities for lifelong continuing education (Batchelor et al. 2021). We strive to support the recruitment and retention of underrepresented and under-tapped students, who might otherwise perceive themselves as STEM outsiders (Rahm & Moore 2016). The PAL science team, together with the E&O team has developed a strategic approach to leverage university resources to amplify impacts and outcomes, using PAL as a research and education focus. We focus on inclusive teaching and learning to improve recruitment and cultivate inclusive learning environments. **Virtual REU:** During the pandemic, Rutgers supported a cohort of 10 undergraduate students in a very successful 2-week virtual REU program, focused on developing and applying data analysis skills using Python notebooks to analyze and present ocean data. The program focused on: a) learning about ocean data collection methodologies and datasets; b) participating in a variety of professional development sessions, including scientific question development, science communication, the graduate school process, and diversity, inclusion, and research ethics; c) participating in career panels (Barr et al 2020) and d) developing, implementing, and presenting their research experience using an online dataset, under the guidance of a faculty mentor. We propose to use this model to create a PAL focused virtual REU as a short /intersession course between the PAL institutions. **Traditional REU:** PAL will leverage our existing university level REU and DEI focused programs to encourage diverse participation in PAL. PAL PIs will mentor students through the ACCESS summer research initiative and STEM diversity research programs at UC Santa Cruz (Friedlaender, Cimino) with a focus on Hispanic students,

the Virginia-North Carolina Louis Stokes Alliance for Minority Participation program at UVA (Doney), and REU site programs at Rutgers (Schofield), VIMS (Steinberg), and U. Delaware (Moffatt) aimed at minority students.

**OVERVIEW OF PAL SAMPLING, MODELING, AND SYNTHESIS.** Our integrated sampling/modeling strategy is based on a multi-faceted program that incorporates the logistical realities of working in this remote environment (see ‘Program Management’ section). The sampling strategy is designed to resolve key ecological processes influenced by press-to-pulse disturbances that are expressed over a range of space/time scales (Levin 1992, Stommel 1963). This is accomplished through a combination of multi-tiered and multi-platform sampling approaches, annual process-based high-resolution seasonal sampling, and field manipulative experiments. The results of the sampling activities inform modeling efforts by filling gaps through improved parameterization of key processes and provides data for assimilation modeling synthesis efforts. In turn, models guide the development of field process studies.

**Long-term observations.** The PAL program (Fig. 2) has four complementary facets: a regional-scale oceanographic cruise, continuous regional-scale autonomous instrumentation (moorings, gliders, and airborne drones), manipulative experiments, and local-scale daily to weekly sampling in October-March from Palmer Station, including observations and measurements at Adélie, gentoo and chinstrap breeding colonies (PAL is unique in that all three *Pygoscelid* penguins breed here), and of other seabirds and whales. At Palmer Station, the annual penguin observations were initiated in 1975 (Fraser et al. 1992, Fraser & Trivelpiece 1996) and hydrographic sampling began in 1991 (Moline & Prezelin 1996, 1997). *In situ* measurements are complemented with an extensive satellite remote sensing program focused on larger-scale physical, chemical, and biological dynamics along the WAP and adjacent Bellingshausen Sea. The

*Table 1. Core measurements of PAL LTER program. Ships provide bi-annual regional maps of variables, Palmer Station provides continuous weather data and daily to biweekly sampling, gliders provide several month long adaptive regional sampling, moorings provide continuous time series. Satellite coverage varies within the WAP region.*

LTER Research Theme	Sampling Platform	Observation Measurement (PI)
<b>Physical System Characteristics</b>	Ship, Glider, Moorings, Palmer Station Ship, Glider, Moorings, Palmer Station Ship, Glider, Moorings, Palmer Station Ship, Glider, Moorings, Palmer Station Ship, Glider, Palmer Station Ship, Glider, Palmer Station Ship Ship, Palmer Station Ship, Palmer Station Satellites	Temperature (Moffatt) Salinity (Moffatt) Ocean Circulation (Moffatt) Oxygen, Chlorophyll Fluorescence (Schofield) Light Intensity (Schofield) Light Scattering (Schofield) Water Clarity (Schofield) Weather (Light, Winds, Temperature, Snow) (NSF) Glacial and Sea Ice Meltwater Fraction (Meredith) Temperature, Sea Ice, Wind, Light Flux, Ocean Height, Ocean-Ice-Snow Color (Stammerjohn, Doney)
<b>Primary Production</b>	Ship, Palmer Station, Glider Ship, Palmer Station Ship, Palmer Station Ship, Palmer Station	Photosynthetic Electron Transport (Schofield) Primary Production (14C-uptake) (Schofield) Net Community Production (Oxygen/Argon) (Schofield) pCO <sub>2</sub> (NSF)
<b>Populations/Diversity</b>	Ship, Palmer Station Ship, Palmer Station, Glider Ship, Palmer Station Ship, Palmer Station Ship, Palmer Station Ship, Palmer Station Ship, Palmer Station	Phytoplankton Pigmentation (Schofield) Particle Size Distribution (Schofield) Algal-Bacterial Abundance/Diversity (Schofield, van Mooy) Zooplankton Abundance/Diversity (Steinberg) Sea Bird Abundance/Diversity (Cimino) Penguin Fecundity (Cimino) Marine Mammal Abundance/Diversity (Friedlaender)
<b>Organic Matter</b>	Ship, Palmer Station Ship Ship, Palmer Station Ship, Palmer Station Ship, Palmer Station Ship, Palmer Station	Particulate Organic Carbon (van Mooy) Lipidomics (multiple trophic levels – van Mooy) Carbohydrates (van Mooy) Thorium Deficits (van Mooy w/ Stukel) Drifting Sediment Traps (van Mooy) Calorimetry (van Mooy)
<b>Inorganic Matter</b>	Ship, Palmer Station Ship, Palmer Station Ship, Palmer Station Ship, Palmer Station Ship, Palmer Station	Particulate Inorganic Carbon (van Mooy) Nitrate-Nitrite-Ammonia (Schofield) Phosphate (Schofield) Silicate (Schofield) Drifting Sediment Traps (van Mooy)

PAL core measurements that address core research themes of the LTER network are provided in Table 1.

*Regional-scale oceanographic observations (research cruise, gliders, land-based sampling).* The research cruises are conducted in austral summer along the WAP (Waters & Smith 1992, Ducklow et al. 2008) and were performed annually. New to PAL-6B due to a reduction in NSF/OPP-supported ship availability, ship surveys will be conducted every other year. To fill the gap, autonomous sampling by underwater gliders (Fig. 2) will be expanded in non-cruise years to provide shelf wide measurements of temperature, salinity, oxygen, phytoplankton abundance, and particles throughout the PAL grid normally covered by the cruise. This expansion incorporates regional glider active acoustics measurements to provide proxies for zooplankton and fish biomass, as well as passive acoustics to determine the presence, relative abundance, and behavior of baleen whales. PAL has conducted 63 glider missions, representing 978 days at sea since 2007, demonstrating the ability to provide sustained measurements when ships are not available. Gliders cannot collect water samples but will provide much higher horizontal/vertical resolution (meters) than the cruise, a trade-off that augments our ability to resolve variability at smaller spatial scales. Additionally, NSF will support annual ship turn-arounds of year-long mooring deployments (Fig. 2) providing high resolution temporal annual *in situ* seasonal coverage. Finally, in every year we will also be able to sample the Palmer Deep station once per month from Oct-to-March (Grid Station 600.040) via available Rigid Hull Inflatable Boats (RHIBs) from Palmer Station. This station was historically sampled during the annual research cruise, but now we can provide in a key location seasonal sampling for nutrients, phytoplankton and zooplankton taxonomic composition (variables that cannot be sampled remotely).

The PAL regional cruise sampling grid is occupied during a 28-day science cruise (Fig. 2). The sampling grid has always included at least three stations per across-shelf sampling line (coastal, mid-shelf, and continental slope). Early on (1993-2008), the grid consisted of 55 stations within 5 sampling lines; however, as PAL began to appreciate the strong climate gradient along the WAP, the grid was expanded farther south by 6-9 stations (ice dependent) to sample processes that were no longer prevalent in the northern grid (Fig. 2). For PAL-6A, we expanded the grid to bridge the full north-south climate gradient by adding four sampling stations north of Palmer Station (the latter now residing in a transition zone) (Fig. 2). Two stations were added north of Low Island and two more between Low Island and Palmer Station. This provides a Bransfield Strait sub-polar “end member” and better links to ongoing sustained sampling by NOAA as part of the Antarctic Marine Living Resources (AMLR) program and to the nearshore time series at Carlini Station maintained by Argentina-Germany-South Korea (see letters of collaboration). This also complements our existing long-term partnership with the United Kingdom’s Rothera Oceanographic and Biological Time Series (RaTS) at Rothera Station located 400 kilometers to the south of Palmer Station (Fig. 2, Clarke et al. 2007, 2008). Standardization of data between these international time series sites is the focus of the Southern Ocean Observation System as part of a Regional Working Group chaired by Schofield (see letter of collaboration). Our partnerships with these other time series along the WAP climate gradient have become a valuable part of the program (Kim et al. 2018), especially as altered ecosystem properties are projected to propagate southward over time. For example, at RaTS, the sea ice extent and duration today are about the level they were at Palmer 20 years ago (Fig. 1B). The RaTS ecosystem is thus at an earlier stage of response to climate migration. A British Antarctic Survey scientist (currently Mike Meredith, the RaTS Leader) has had full co-PI status in PAL since 2002; cruise cross calibration of hydrographic sensors and oxygen-18 isotopic measurements at Rothera Base will also continue in PAL-6B. Satellites provide the seasonal regional context for the ocean physics and primary productivity (Kavanaugh et al. 2015, Li et al. 2016) and discolored landscapes indicative of seabird and seal colonies (Lynch et al. 2012, LaRue et al. 2014, Lynch and LaRue 2014).

During the January research cruise, along-track measurements yield continuous data for a range of physical, chemical and biological properties (Table 1). These surface maps are complemented with vertical water column sampling at historical locations occupied since 1993. At these stations, vertical casts are collected from the surface to bottom providing continuous profiles of temperature, salinity, oxygen, chlorophyll fluorescence, visible light, and water clarity. Water is collected at twelve depths for discrete measurements (Table 1). CTD casts are complemented with zooplankton net tows. Seabirds, whales, and seals are surveyed throughout the entire cruise to identify if coincident to oceanographic features. Skin and

blubber biopsy samples are collected to examine whale population structure and demography (Albertson et al. 2018, Pallin et al. 2018b), while satellite and motion-sensing tags are deployed to determine multi-scale habitat use (Friedlaender et al. 2016). Finally, the seabird team conducts censuses and diet sampling at islands of interest, which includes two decades of data collected at Avian Island (towards the southern end of our sampling grid, Fig. 2).

*Palmer Station nearshore time series.* PAL has conducted seasonal sampling at Palmer Station during the October to March penguin breeding period each year since 1991 (Ducklow et al. 2013). The Palmer Station time series and partner time series program to the north (NOAA-AMLR sampling initiated in 1986, Carlini-sampling initiated in 1994) and south (RaTS-sampling initiated in 1997) provide multiple coastal time series spanning the WAP climate gradient. Palmer Station sampling is documenting interannual variations in the ecosystem, including responses of plankton production to physical forcing, krill recruitment (Saba et al. 2014), changes in prey distribution (Oliver et al. 2012, Bernard & Steinberg 2013, Nardelli et al. 2021), and landscape-related processes (Fraser et al. 2013, Cimino et al. 2019). The marine sampling capabilities at Palmer Station have been expanded with the RHIBs which are outfitted with A-frames. Core measurements of penguin foraging ecology, breeding phenology, and population status along with water column studies are conducted daily to weekly via small boats at islands and hydrographic stations (Fig. 2). This includes monitoring of other seabirds that are penguin predators or potential competitors (including giant petrels, brown and south polar skuas, blue-eyed shags, and kelp gulls). In total this effort provides a holistic view of the ecosystem pressures seabirds must overcome to survive. The whale component utilizes tagging methods, similar to the penguin component, to evaluate foraging behavior at fine scales around Palmer Station and throughout the entire PAL study area (Friedlaender et al. 2016). Skin and blubber biopsy sampling and photo-IDs determine inter-annual changes in population structure and demography (pregnancy rates, Pallin et al. 2018b) as related to physical and ecosystem components. Personnel conduct daily surveys of the boating area around Palmer and sample all whales encountered (and whales encountered during the research cruise); biopsy sample sizes are 100-300 annually.

Unoccupied aerial systems (UAS; drones) have been incorporated to evaluate changes in body condition throughout the foraging season (Bierlich et al. 2021) and link these to foraging behavior and inter-annual variability in pregnancy rates. UAS's have also been used to conduct aerial surveys of islands surrounding Palmer Station throughout the summer to compliment ground surveys of penguins. A new component using continuous passive acoustic monitoring via moored hydrophones will allow for testing of hypotheses related to the phenology of whale presence annually as well as coincident with storms. Moorings are now near Palmer Station and offshore in the Palmer Canyon. During summer, these moorings will be augmented with physical (temperature, salinity) and biological (zooplankton acoustics, chlorophyll, oxygen) sensors throughout the upper water column (100-200 m) to understand how storms, meltwater discharge, and sea ice impact the evolution of the upper ocean in the vicinity of key penguin and whale foraging grounds.

A seasonal data set of primary production, plankton community structure, and biogeochemistry provides the environmental context for top predator demographics and is obtained with twice-weekly sampling of the same parameters as the regional oceanographic cruise, including discrete water samples collected in the upper 75 meters at Station E (Fig. 2, map inset). The historical sampling at Station B was phased out in PAL-6A as biological and chemical data at both stations are highly correlated, and Station E provides the clearest ocean signal. Over PAL-5, the sampling expanded with the addition of the RHIBs, which now allow for bi-weekly high-resolution acoustic surveys and zooplankton net tows in penguin/predator foraging hotspots to provide proxy maps for krill resources (Nardelli et al. 2021). We will include nighttime zooplankton net tows and CTD casts to quantify diel vertical changes in zooplankton distribution and phytoplankton physiology, and to relate those to diurnal patterns in krill predator foraging behavior. Palmer facilities also support experimental incubation and manipulation studies which will continue in PAL-6B.

*Experimental and process studies.* Observational sampling is complemented with manipulative experiments conducted both on cruises and at Palmer Station. The manipulations involve incubations (1 to 100s of liters) to help define underlying physiological and growth responses for key species to changing

environmental conditions (light, nutrients, temperature, pH, salinity anomalies, or combinations of stressors, changes in landscape features), organismal interactions (macro- & microheterotroph grazing rates and efficiencies), and processes regulating biogeochemical fluxes (particle sinking and remineralization rates, fecal matter production and remineralization, turbulence and particle aggregation rates). These experiments are generally conducted in bottles or tanks, which in part reflect the Antarctic Treaty's tight regulation of natural manipulations. This precludes us from using *in situ* experimental strategies used by some coastal and terrestrial LTER sites (soil warming, enclosure/exclosure, whole community CO<sub>2</sub> enrichments). Our experiments are designed to support modeling efforts, and results are analyzed with inverse (Sailley et al. 2013) and data assimilation (Luo et al. 2010, Kim et al. 2021, 2022) model approaches to build system-level descriptions of ecosystem processes. At Palmer Station these manipulations often focus on the seasonal variability of these processes (Luria et al. 2017), while onboard the regional oceanographic cruise these experiments capture the spatial variability across the latitudinal climate gradient along the WAP (Carvalho et al. 2019), described in the thematic sections above. Many of these incubation experiments are also conducted as part of a larger comparison study we began in 2009, where we have used the climate gradient combined with interannual sea ice variability to assess the variability between three submarine canyons located along the WAP. In PAL-6B, we will add a new focus on how storminess and ocean mixing impact these processes. We have been, and will continue, sampling over the Palmer Deep (Anvers Island), Marguerite Trough (Avian Island, Rothera Base), and when accessible, Charcot Canyon in the southern WAP (heavy sea ice can make this location inaccessible some years); all of these canyons are associated with major penguin colonies.

**Model simulations.** PAL field observations will be interpreted with a suite of statistical, diagnostic, and prognostic models. No single model can capture the wide range of dynamics, time/space scales, and complexity inherent in the PAL system, therefore a suite of models are chosen and tailored for specific research questions (see below). We will leverage a set of models, developed by PAL and collaborators, spanning from idealized process models to realistic numerical simulations coupling physics and biology.

Variations in atmosphere-ocean-ice exchange, MLD, and vertical transport of heat, salt, nutrients and plankton are central to polar ecosystem dynamics and to all three Research Themes. Our 1-D vertical physical model (Saenz et al. submitted) is now available for the WAP system incorporating the K-Profile Parameterization (KPP) for the ocean planetary boundary layer (Large et al. 1994) and a sophisticated snow-sea ice model component (Saenz & Arrigo 2012). Forced with atmosphere reanalysis and satellite data products, 1-D simulations over seasonal time-scales are integrated either in full prognostic (predictive) mode or using data-based diagnostic constraints (e.g., assimilating sea-ice extent from satellite data or subsurface ocean observations from moorings and gliders capturing heating and nutrient injections from eddy activity). Pilot biological-physical experiments also have been conducted by coupling the 1-D physics model a phytoplankton-zooplankton-nutrient-detritus (PZND) module with bulk compartments tracking biological tracers (e.g., diatoms, iron). In PAL-6B, the 1-D modeling framework will be used to analyze physical and bio-physical responses and interpret field data across time scales from storm and mesoscale disturbance events to interannual, decadal, and climate scales. PAL field data provide key information on mixed layer and seasonal thermocline physics for model-data comparisons, with data on different scales, including: our Palmer Station near-shore time series, glider deployments at fixed locations (e.g., canyon head of Palmer Deep), and the mid-shelf bottom-moored temperature array (though only to a maximum of 50m below the surface so does not capture the surface mixed layer to avoid damage during winter from sea-ice and icebergs).

We will use our newly developed 3-D ocean-sea ice circulation model (Schultz et al., 2020) with a biophysics module (Schultz et al., 2021) to simulate lateral and vertical transport on the WAP shelf-slope domain. A regional version of the MIT Ocean General Circulation Model (GCM), originally designed by BAS collaborators to study regional freshwater dynamics (Regan et al. 2018), includes a fully active sea-ice component based on Hilbler-type ice thermodynamics, elastic-viscous-plastic (EVP) ice rheology, and an ice-shelf component to include the freshwater input from ice shelf melt. We refined the physical model to improve seasonal and interannual sea-ice dynamics and mixed layer dynamics using satellite data and

the PAL ship survey as the basis for model skill evaluation (Schultz et al., 2020). We also coupled into the physical simulation a PZND-biogeochemical module, and the resulting biophysical simulations exhibit considerable skill in capturing regional primary productivity and carbon cycling patterns observed in PAL ship survey data and satellite remote sensing (Schultz et al. 2021). Our eddy-permitting resolution of MITgcm model allows for multi-decade biophysical experiments for the PAL domain and adjacent Southern Ocean sector, and higher resolution (approximately eddy resolving) simulations of the WAP shelf-slope sub-region are feasible for shorter time-periods and targeted model process studies.

A similar span of complexity and scale exists for WAP biological models relevant to all three Research Themes. We developed an end-to-end food web model for the WAP (bacteria and phytoplankton to seabirds and marine mammals) in PAL-4 (Sailley et al. 2013, Ducklow et al. 2015). Using inverse techniques, the box model solves for steady-state carbon flows through the depth-integrated food web using observational constraints on biological stocks and rates and literature prescribed allometric relationships. A new 1-D time-evolving model for WAP seasonal plankton dynamics (Kim et al. 2021,2022) can be used with either diagnostic physics or in fully coupled 1-D biophysical simulations. The plankton module is updated based on recent PAL studies to include size structure in phytoplankton production, microzooplankton grazing, and a more sophisticated treatment of bacterial and dissolved organic matter interactions. The model has built-in capabilities for assimilating physical forcing data (e.g., time-series, glider, and mooring data) and optimizing biological model parameters using a variational adjoint method (Luo et al. 2010). Drs. Schultz and Kim are joining the PAL team as formal collaborators (see letters of collaboration).

### SYNTHESIS

In continuing our 31-year time series of daily observations at Palmer Station and annual oceanographic cruise in a climate change hotspot, we will utilize these historical and new observations to understand three interrelated ecological topics: drivers of disturbance across a range of spatiotemporal scales as they relate to ecological change along a latitudinal climate gradient (Theme A), vertical and alongshore connectivity in the ocean as a driver of ecological change/variability (Theme B), and food webs as drivers of changes in carbon export and trophic interactions (Theme C). Since PAL's inception, multidisciplinary ecological questions have been addressed by combining boat-based observations, satellite remote sensing, moorings, manipulative experiments, models now spanning idealized processes to numerical simulations, and recently, modern technologies (acoustics, biologging tags, gliders, drones). Now, we are poised to unravel complex drivers of ecological change to address theory related to ecosystem state change in response to press-to-pulse disturbances. Our data span a sea-ice rebuild period and subsequent return to sea-ice decline, providing an exemplary natural experiment to study ecosystem resiliency or legacy effects. Specifically, we propose to test if earlier sea-ice retreat shifts ecosystem phenology and results in decreased productivity and carbon export, causing mismatches for high trophic levels. Another major focus is on storm impacts, including how a southward shift in storm activity affects demographic rates of top predators by leading to more snow on land and altering upper ocean and prey dynamics. Further, storm-driven cloudiness may lead to reduced energy capture by phytoplankton, resulting in low-quality prey for predators. Interestingly, the intrusion of cold Weddell Sea water to our northern study region may support polar species, providing a resiliency to maintain polar community composition that we aim to understand. Our focus on disturbance will provide rich opportunity for cross-site comparison in the LTER network. Our integrated research program and synthetic approach will be critical for identifying dominant mechanisms responsible for long-term ecological changes, especially for our indicator species (Adélie penguin demise) that are responding to multiple stressors (land, sea, and prey effects). Using our infrastructure and data archive, we plan to facilitate new research through collaborations and build a multinational consortium of diverse partner programs focused on the WAP pelagic ecosystem.

**Related Research Projects.** PAL-6 B has multiple collaborations/partnerships (see letters of support), and PAL-6 members compete for independent grants building on the LTER. Given the nature of polar program funding, we are not specifically leveraging our own additional funds from other sources.

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