PROJECT SUMMARY

Overview:

Seasonal sea ice-influenced marine ecosystems at both poles are regions of 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, decadal, and higher-frequency "pulse" changes driven by a range of processes, including natural climate variability, long-term climate warming, resiliency/recovery in the face of press versus pulse forcing, transformed spatial landscapes, and food-web alterations. We will contribute to fundamental understanding of population and biogeochemical responses for a marine ecosystem experiencing profound change.

Intellectual Merit:

Four multidisciplinary, but interrelated research themes guide our proposed work:

A. Ecological responses to long-term "press-pulse" and a recent decadal reversal. How do long-term "press" (climate warming) and shorter "pulse"(large storms, extreme seasonal anomaly in sea ice cover) pressures interact to drive changes across the WAP food web? What is the resilience of the ecosystem in the face of rapid change followed by a recent reversal in sea-ice loss?

B. Vertical & alongshore connectivity processes for physics and biology. How do both alongshore and vertical mixing dynamics along the WAP interact to modulate the distribution and variability of physical properties and marine organisms? What patterns in organism abundance and distribution result from physical transport vs. local transformation?

C. Food webs and carbon cycling. How will changes in the structure of the WAP pelagic food web affect cycling and export of carbon? How do changes in energy storage in primary producers affect higher trophic levels?

D. Disturbance from storms as a control on ecosystem structure. How do storms drive the productivity, behavior, and recruitment across all trophic levels in the WAP? Will increasing storminess be a tipping point for seabirds and land-based seals?

We will continue to address the influence of major natural climate modes (e.g., El Niño Southern Oscillation, Southern Annular Mode) that modulate variations in sea ice, weather, and oceanographic conditions to drive changes in ecosystem structure and function. Our sampling and analyses cover multiple time scales–from diel, seasonal, interannual, to decadal intervals, and space scales–from hemispheric to global scale investigated by remote sensing, the regional scale covered by an annual summer oceanographic cruise along the WAP, and the local scale accessed by daily to biweekly small boat sampling at Palmer Station. Autonomous vehicles, floats, moorings, and modeling enable us to expand and bridge time and space scales not covered by vessel-based sampling providing a seasonal to annual context. These observations are complemented with process studies that include manipulative experiments conducted on our annual research cruise and at Palmer Station.

Broader Impacts:

We will continue to build on our 30-year database of observations of climate change and ecological transformation, widely recognized as an exemplar of these trends. PAL research is harnessed through an education and outreach program promoting the global significance of Antarctic science and research. Using the newly-developed Polar Literacy Principles as a foundation, we will maintain and expand our virtual schoolyard program via dissemination of new polar instructional materials and learning opportunities for K-12 educators to facilitate their professional development and curricula. We will leverage the development of Out of School Time materials for afterschool and summer camp programs, sharing Palmer LTER-specific teaching materials with University, Museum, and 4-H Special Interest Club partners.

TABLE OF CONTENTS

For font size and page formatting specifications, see PAPPG section II.B.2.

	Total No. of Pages	**Page No.* (Optional)***
Cover Sheet for Proposal to the National Science Foundation		
Project Summary (not to exceed 1 page)	1	
Table of Contents	1	
Project Description (Including Results from Prior NSF Support) (not to exceed 15 pages) **(Exceed only if allowed by a specific program announcement/solicitation or if approved in advance by the appropriate NSF Assistant Director or designee)**	32	
References Cited	14	
Biographical Sketches (Not to exceed 2 pages each)	10	
Budget (Plus up to 3 pages of budget justification)	74	
Current and Pending Support	17	
Facilities, Equipment and Other Resources	2	
Special Information/Supplementary Documents (Data Management Plan, Mentoring Plan and Other Supplementary Documents)	32	
Appendix (List below.) **(Include only if allowed by a specific program announcement/ solicitation or if approved in advance by the appropriate NSF Assistant Director or designee)**		

Appendix Items:

*Proposers may select any numbering mechanism for the proposal. The entire proposal however, must be paginated. Complete both columns only if the proposal is numbered consecutively.

PROJECT DESCRIPTION

Results From Prior NSF Support

Hugh Ducklow, Douglas Martinson, **Oscar Schofield**, **Deborah Steinberg**, **Scott Doney**, **Ari Friedlaender**, Mark Ohman, William Fraser, **Janice McDonnell**, **Sharon Stammerjohn** "LTER Palmer, Antarctica (PAL): Land-Shelf-Ocean Connectivity, Ecosystem Resilience and Transformation in a Sea-Ice Influenced Pelagic Ecosystem" (ANT0823101, PLR-1344502, 01 Sep. 2014 – 31 Aug. 2020. $6,761,997) *[Bold indicates PAL LTER scientists in the LTER PAL-6 submission]*

Overview. The Palmer Long Term Ecological Research (PAL) program is focused on developing a comprehensive understanding of the seasonal sea ice-influenced ecosystem along the West Antarctic Peninsula (WAP) – the climate, plants, microbes, animals, biogeochemical processes, ocean, and sea ice south of the Antarctic Polar Front (northernmost extent of ice-influenced water). Since its inception in 1990, the central hypothesis of PAL has been that the seasonal and interannual variability of sea ice affects all levels of the Antarctic marine ecosystem, from the timing and magnitude of primary production to the breeding success and survival of top predators. At rates similar to the rapidly changing Arctic, the WAP ecosystem has rapidly changed due to significant declines in sea ice since at least the 1970s and rapid warming since at least the 1950s (Schofield et al. 2012, Stammerjohn et al. 2012, Ducklow et al. 2013). Over the last six years, the team made significant progress addressing major research themes proposed for PAL-5 with 123 publications since 2014 (PAL references denoted by italics in the Bibliography), many published in high profile journals (Nature, Proceedings of the National Academy, Geophysical Research Letters, Philosophical Transactions of the Royal Society, Ecology & Evolution). Data availability-access is provided as a supplementary document. Our Results from Prior Support highlights progress made by PAL-5 on research focus areas, highlighting our ten most significant (2014-19) publications (in bold, with full citations in the Reference section) and the results of prior support from our three new PIs.

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 continued change projected into the future (Boyd et al. 2016). The most rapid sea ice decreases in Antarctica have occurred along the WAP and the Bellingshausen Sea (Stammerjohn et al. 2012, Stammerjohn & Maksym 2017). Seasonal sea ice changes in the WAP region 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. 2008, Hobbs et al. 2016). There are latitudinal differences as the PAL sampling grid spans a climate gradient between the warmer northern and colder southern regions (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 1970's, in 2010 a reversal started (Schofield et al. 2018) (**Fig. 1a**). With this recent increase in sea ice days, there has been a weakening of longer-term warming trends, emphasizing the high natural variability of Antarctic climate (Hobbs et al. 2016). Nonetheless, documented long-term environmental warming and sea ice losses remain statistically significant (Henley et al. 2019). In the southern region of the PAL sampling grid, 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 satellite/ship observations showing concomitant increases in phytoplankton abundance (Montes Hugo et al. 2009, **Brown et al. 2019**) **(Fig. 1b)**. The increased biomass is consistent with observations/experiments that inner shelf primary productivity is light-limited, which is alleviated by a shallower MLD (Schofield et al. 2017, Carvalho et al. 2019). However, the recent sea ice reversal resulted in increased annual phytoplankton biomass in northern coastal waters (**Kim et al. 2018**), which reversed long-term phytoplankton declines previously observed there (Montes Hugo et al. 2009). While the base of the WAP food web has changed significantly, long-term trends in zooplankton communities are mixed. The keystone species *Euphausia superba* (Antarctic krill) exhibits no significant long-term directional change in the LTER study region (**Steinberg et al. 2015) (Fig. 1a)**, although their populations further north have significantly decreased (Atkinson et al. 2019). Other key macrozooplankton taxa show both increasing and decreasing trends in abundance, and some–such as salps and pteropods–are significantly correlated with ENSO or SAM climate cycles (**Steinberg et al. 2015**, Thibodeau et al. 2019). Higher trophic levels also show mixed responses. Antarctic baleen whales, specifically humpbacks (*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*) near Palmer Station (**Fig. 1a**). The Adélie penguin population has decreased by ~90% near Palmer, with no declines seen at colder southern colonies (Cimino et al. 2016a). While Adélie breeding phenology at Palmer tracks regional trends in sea ice over the last three decades (Cimino et al. 2019), the population decline from 1974 to 2010 leveled-off during the recent decade of sea ice trend reversal, despite the expectation that increased sea ice would lead to increased chick survival and recruitment. However, penguin populations are not only affected by shifts in sea ice in the ocean, but also shifts on land (Cimino et al. 2016a). For example, precipitation impacts breeding habitat quality on land that then influences breeding success and phenology, and wet and windy weather has been linked to Adélie penguin chick fledging mass (Fraser et al. 2013, **Cimino et al. 2014**, 2019). Going forward, we will focus on defining the relative effects on ecosystem response of extreme or episodic "pulse" disturbances (e.g., record low sea ice in 1989 and 2008, storm events) within the context of both short-term variability (e.g., the recent reversal) and long-term "press" of climate change (long-term warming and decreased sea ice).

Lateral connectivity and vertical stratification: Along the WAP lateral 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. 2019) that are structured by a combination of WAP geography, climate forcing (**Fig. 1a**), and ocean-atmosphere-ice connections. The warm (>1.5℃), 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 and above cross-shelf canyons (Klinck 1998, Dinniman & Klinck 2004, Couto et al. 2017b). UCDW enters the canyons as intrusions (Moffat et al. 2009) forming eddies that dissipate as they move inshore, mixing with colder, fresher shelf water (**Couto et al. 2017a**), and forming modified UCDW (mUCDW). As the eddies are transported shoreward they predominately lose heat laterally and downward, thus preserving subsurface heat, which is then available to melt marine-terminating glaciers (Cook 2016, **McKee et al. 2019**). The mUCDW transport terminates in coastal canyons that are biological hotspots associated with major Adélie penguin colonies (Schofield et al. 2013, Cimino et al. 2016a). These coastal canyons have significant and recurrent 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 using mUCDW from canyons show nutrients did not promote growth, indicating light is the more important factor (Carvalho et al. 2019). This is consistent with observations that macro- and micronutrient concentrations do not appear to be limiting even during peak bloom periods within these canyon systems (Carvalho et al. 2016). Additionally, the upwelling of mUCDW does not appear to control Fe flux to the surface; instead, shallow sediment-sourced Fe inputs are transported horizontally from surrounding coastlines, creating strong vertical gradients of dissolved Fe 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 surface waters of the mid-continental shelf and slope appear to be limited by micronutrients (especially Fe) (Annett et al. 2017, Sherman et al. submitted). PAL-6 will build on this current understanding to identify the drivers of ocean productivity as related to vertical and alongshore connectivity and circulation patterns.

Top-down controls and shifting baselines: During PAL-5, a cetacean component was added to address if the reemergence of whales following their near-extirpation by humans could regulate the demography of other krill-dependent predators such as penguins and seals through competitive exclusion (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 involving sea ice regulates predator populations based on evolved life histories (Fraser et al. 1992). PAL-5 focused on determining the status of WAP whale populations and how their sympatric penguin competitors utilized the available prey-scape. Humpback whales are expanding rapidly along the WAP (Bejder et al. 2016), consistent with observed high pregnancy rates. Humpback whales using the waters encompassing the PAL sampling grid are almost exclusively from a single population that breeds off the west coast of Central and South America (**Alberston et al. 2018**). These whales had an average annual pregnancy rate of 64%, with some individuals breeding every year (**Pallin et al. 2018**a,**b**). Given the energetic demands of such high fecundity (and release of competition with other krill-consuming blue and fin whales which have not recovered from whaling) it is unlikely that krill are a limiting resource for whales. Satellite telemetry demonstrated that whales utilize the entire PAL study area across the continental shelf in summer while moving to nearshore bays in fall (Curtice et al. 2015, Weinstein and Friedlaender 2017, Weinstein et al. 2017) where they encounter dense krill patches (Nowacek et al. 2011; Friedlaender et al. 2013, 2016; Tyson et al. 2016). This occurrence pattern is consistent with observed krill distributions (Lascara et al. 1999). Along the WAP, Adélie and gentoo penguin breeding colonies are often sympatric and possibly compete for prey. In the Palmer region, while their diets and foraging areas can overlap horizontally, each have separate core foraging regions and Adélies tend to feed at shallower depths than gentoos (Cimino et al. 2016b, Kohut et al. 2018, Pickett et al. 2018, Oliver et al. 2019). While penguin and whale foraging regions overlap vertically and horizontally, temporal partitioning occurs where penguins forage mainly during the day and whales at night (Cimino et al. in prep, Nichols et al. in prep). Furthermore, the presence of whales in the PAL region during these periods is episodic and largely driven by the presence of dense krill patches (Nichols et al. in prep). There is again no evidence that krill are a limiting resource during the penguin breeding season (Sailley et al. 2013, Pickett et al. 2018). Interestingly, variability in Adélie breeding phenology on two islands near Palmer was driven primarily by large-scale spring sea ice concentrations and secondarily by the influence of island-specific landscape aspect and wind scour on snow accumulation patterns (Cimino et al. 2019). Chick fledging mass was negatively affected by cold, wet, and windy weather, which could have increased thermoregulatory costs at the nest or altered the prey-scape (**Cimino et al. 2014**). Therefore, landscape may affect demography independent of, or in addition to, competition for krill resources (Fraser et al. 2013, **Cimino et al. 2019**). These findings suggest that if storms increase in intensity, duration and/or frequency, then they could lead to both negative landscape and seascape effects, which is a new research theme for PAL-6.

Foodweb structure and biogeochemical processes: The seasonally sea ice-influenced marine ecosystem of the WAP is characterized by high productivity concentrated in space and 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) as well as pCO_2 and dissolved inorganic carbon, with the carbon signal modulated by sea ice, glacial freshwater input, and air-sea exchange (Hauri et al. 2015, Eveleth et al. 2017). PAL hydrographic and biogeochemical data have been used to characterize time-evolving, spatial patterns of distinct ecological seascapes (Bowman et al. 2018). Waters south of Anvers Island are exhibiting changes in physical forcing with a decadal shallowing of the summer MLD that is correlated with increasing chlorophyll a and decreasing pCO_2 (**Brown et al. 2019**). On decadal time-scales, rising atmospheric CO_2 is projected to drive increasing pCO_2 and acidification of Southern Ocean surface waters (Boyd et al., 2016), but the acidification signal is yet difficult to detect in the PAL dataset because of substantial regionally-varying biological and physical factors and interannual climate variability (Hauri et al. 2015). Consequently, carbonate chemistry parameters, such as aragonite saturation, are not strong indicators of shelled pteropod abundance in the WAP (Thibodeau et al. 2019), likely because the WAP is not yet significantly undersaturated with respect to aragonite (Hauri et al. 2015). The high and seasonal net community production exceeds the export of carbon to depth via particle sinking suggesting losses from the surface ocean due to diapycnal mixing or other physical and biological mechanisms that 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, Sailley et al. 2013, Ducklow et al. 2015), results that are supported by observations of significant viral activity (Brum et al. 2016). Growth seasons following lower concentrations of winter sea ice are associated with declining phytoplankton biomass (**Saba et al. 2014**) and shifts in phytoplankton community composition and size structure (Moline et al. 2004, Montes Hugo et al. 2009, Schofield et al. 2017). The declines and shifts in phytoplankton affect pCO_2 as different phytoplankton taxa have differential drawdown rates (**Brown et al. 2019**). At the bottom of the food web there is tight coupling between phytoplankton and zooplankton, and years of large summer phytoplankton blooms are associated with positive recruitment of *E. superba* krill (**Saba et al. 2014**). Strong *E. superba* recruitment since 2011 is coincident with enhanced phytoplankton productivity and the recent sea ice reversal (Conroy et al. submitted-a). 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, originating mainly from krill, dominate sinking material captured by the sediment traps (Gleiber et al. 2012), and shifts in zooplankton community composition between "krill years" and "salp years" lead to considerable interannual variability in particulate organic carbon (POC) export (Steinberg in prep.). Furthermore, many taxa undergo diel vertical migration even in the austral summer (Conroy et al. submitted-b), indicating active carbon transport must be considered in models of biogeochemical cycling in the PAL region. Building on these findings, PAL-6 will examine how climate-driven changes in the planktonic food web can force changes in WAP productivity, export, carbon exchange, and energy storage.

Broader Impacts. During PAL-5, 19 PhD (10 graduated thus far) and 6 Masters (4 graduated) students, as well as 7 post docs, were all or partially supported by PAL. The education and outreach team designed education programs focused on communicating PAL research to predominantly K-12 educator and student audiences. We matched these efforts with a companion NSF award from the Polar Science Division (grant#1525635) called Polar Interdisciplinary Coordinated Education or Polar ICE. PAL offered a range of professional development programs for K-12 educators, Video Teleconferences (VTCs) for K-12 students, and science communication media projects. *VTCs:* To fulfill our Schoolyard LTER requirements, we offered 24 VTCs to virtually connect students and their 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 explain why they chose this rating for the effect of the VTC on 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 and analyze data?; 2) *Increase understanding and awareness of Polar Regions*– students were interested to learn especially 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. *Professional Training:* Since 2015, we engaged 75 K-12 educators in four, week-long professional development programs, reaching ~6,975 students. Our intended impact was to: 1) contribute to the engagement of youth in science, especially grades 6-9, and 2) 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. In addition to our formal education work, PAL collaborated with Public Radio (You're the Expert) where Dr. Schofield participated in a broadcast with three comedians and host Chris Duffy, with ~300 Rutgers students attending the show taping and ~250,000 downloads of the show's podcast to date. Dr. Friedlaender's whale research was featured by international news agencies including BBC and National Geographic reaching a viewing audience of > 70 million. Dr. Fraser's seabird research will be featured in the BBC's Frozen Planet II series, likely reaching millions of viewers.

Results From Prior NSF Support-New PIs.

Megan Cimino (UCSC): OPP-1744859, "Collaborative Research: Linking predator behavior and resource distributions: penguin-directed exploration of an ecological hotspot" (9/01/2019 – 08/31/2023; $234,938). Using propelled autonomous underwater vehicles with an integrated echosounder, the goal of this project is to assess the subsurface behavior of penguins, the distribution and characteristics of their prey, and the bio-physical properties of their environment. The field effort is slated for 2021 and 2023 at Palmer Station. By addressing the dynamic relationship between individual penguins, their prey, and habitat at the scale of individual foraging events, we can understand which processes play a role in regulating resource availability and what makes for profitable foraging habitat. ***Intellectual Merit:*** We will assess prey selection and penguin foraging behavior based on prey distribution (patch size, density, distribution, habitat associations) along with the traditional approach of prey abundance while also furthering development of robotic systems. We are in the fabrication phase for integrating the echosounder into the vehicle. Using 10 seasons (2009-2019) of penguin foraging location and dive data, we are analyzing penguin foraging behavior as a function of diel cycle and day of year to help design vehicle surveys for the coming year. ***Broader Impacts:*** Through integration, testing, and deployment of the underwater vehicles, we will ensure training takes place at the undergraduate, graduate and postdoctoral levels. We will engage schools and public through live interactions while in the field, and display the robotic vehicles. We are hiring a graduate student, and technicians/engineers are being trained as the vehicles are tested. No publications yet for this grant.

Carlos Moffat (UD): OPP-1703310, "The impact of oceanic forcing on the melting of west Antarctic Peninsula glaciers" (9/1/2016 – 5/31/2020; $211,861). Using existing observations and a state-of-the-art regional ocean model, the project aims to understand how glacier retreat is impacted by the structure and variability of along-shore and vertical ocean thermal gradients along the WAP. ***Intellectual Merit***: Results show supply of cold water from the Weddell Sea to Bransfield Strait results in stronger near-shore thermal gradients during winter/spring, suggesting larger along-shore glacier melt gradients during those seasons. Inflow from the Weddell is strongly modulated by wind forcing on both sides of the Peninsula and, on interannual time-scales, by SAM variability. Critically, these cold waters reach the southern PAL region, suggesting existing conceptual models of the heat and salt budgets of this region (Moffat and Meredith, 2018) lack a key component of along-shore exchange. Also, analysis of glider surveys and numerical models show that eddy dynamics are not only critical for the inflow of CDW to the shelf (Couto et al. 2017a) but also for the export of mUCDW to the open ocean (Brearley et al., 2019). ***Broader Impacts***: The project trained two post-docs, two graduate students, and two undergraduates. A website for dissemination of results and a database of historical hydrographic data from the region is in development. A manuscript, "Impacts of the Changing Cryosphere on Human Interactions with the Antarctic Peninsula," is in preparation.

Benjamin Van Mooy (WHOI): PLR-1543328, "Production and Fate of Oxylipins in Waters of the Western Antarctic Peninsula: Linkages Between UV Radiation, Lipid Peroxidation, and Carbon Cycling" (01/01/2017–12/31/2019; $582,484). The peroxidation of lipids is a physiological response to UV exposure that is often invoked in Antarctic plankton. However, this process had never been systematically studied under *in situ* conditions in Antarctica. The goal of this project, performed in close collaboration with PAL, was to use experiments and field sampling to examine the occurrence of lipid peroxidation, including production of oxylipins, in WAP plankton, and to assess whether production of bioactive oxylipins impacts food web dynamics and carbon export. ***Intellectual Merit***. We discovered the potential for massive rates of lipid peroxidation and oxylipin production in liposomes containing polyunsaturated phospholipids, which are abiotic surrogates for cell membranes (Collins et al., 2018). During a second set of experiments with natural communities during subsequent field seasons, we found slower rates of lipid peroxidation. Our hypothesis is that certain components of the WAP plankton community are adapted to oxidative stress from UV radiation, employing biochemical strategies to quench lipid oxidation. We saw substantial changes in other classes of lipids in response to light and UV radiation exposure, particularly in the pool of triacylglycerols (fats) which are used to store energy (Holm et al., in prep. *a*). In our final field season (2018-2019), we focused on the hypothesis that lipidomic changes catalyzed by light and UV radiation affect feeding behavior in krill (Holm et al., in prep. *b*). ***Broader Impacts***. This project supported all or a significant part of 3 Ph.D. dissertations. The project supports development of a lipidomic data analysis workflow, a publicly-available tool used by the oceanographic community. Lipidomic data are available as peer-reviewed articles, and we are archiving lipidomics datasets in online repositories.

Response to Mid-term Review

The mid-term review in 2017 offered a range of recommendations and suggestions which PAL-6 has responded to in this proposal. Specific actions include: ***Recommendation**: Explicitly identify the major ecological disturbances at the site and address phenological changes*. A central focus of PAL-6 is on disturbance in the WAP ecosystem (see themes A and D) to reconcile the role of long-term press (climate change), pulse (storm), and decadal (climate teleconnections) disturbances in structuring food web dynamics. We have and will continue to study shifting phenologies from the physical environmental to animal life cycles (see theme A). ***Recommendation**: Better estimates of krill biomass*. During PAL-5, we incorporated high resolution bio-acoustic sampling of krill by taking advantage of new Rigid Hull Inflatable Boat capabilities at Palmer Station. This is complemented with newly incorporated three-frequency bio-acoustic autonomous glider sampling, and increased tag deployments on penguins and whales, all which will be continued in PAL-6. For the WAP as a whole, we initiated a data recovery effort for all Acoustic Doppler Current Profiler (ADCP) data from US polar vessels to provide proxies for krill distribution and relative abundance over decadal and regional scales (Zhou et al. 1994, 2004). ***Recommendation***: *Use PI turnover from PAL-5 to PAL-6 as an opportunity to increase diversity amongs PIs*. We added 3 new PIs based on their scientific capabilities which has increased PI diversity. The new team includes an early career female PI and a Chilean PI, and now has a wider age distribution. ***Recommendation***: *Increase IM community investment, leverage national and international networks, and wider community resources*. We are increasing the links with international and national IM systems. PAL is unifying data standardization and availability through the Southern Ocean Observing System (see letter of support). PAL-6 is leveraging open access community data systems for new data streams. For example, glider data is being served via the NOAA glider Data Assembly Center (DAC) and dedicated NOAA ERDAP servers, image processing through the community ECOSCAPE, and whale data are used in the International Whaling Commission's Southern Ocean Research Partnership. Additional resources will be pursued to increase functionality of the system, which we note received high marks in a CCE-LTER midterm review in fall 2019 (PAL currently shares IM with CCE). ***Recommendation***: *Ensure budget flexibility for next PAL proposal*. We reorganized the budget, providing equal base increments with augmentations for field efforts. Management now retains an increment each year for equipment and a modicum of funding to entrain external partners (see letters of support). ***Suggestion***: *If resources are permitting then consider adding a second sediment trap*. The basis of this suggestion was to allow a north-south comparison of export. We will accomplish this instead with net and drifting sediment traps deployed along the latitudinal gradient during process studies, and with high resolution Thorium-234 measurements. ***Suggestion**: Project Management is to regularly reflect on when to sunset data streams or research themes*. Because moving forward we wish to focus our efforts on latitudinal and cross-shelf patterns in carbon export, we plan to phase out the moored sediment trap in PAL-6. We are also sunsetting a measurement (leucine uptake by bacteria) in order to pursue an energetic perspective of the food web (ecosystem lipodomics), and the high correlation in physical and biological parameters between Stations B and E near Palmer Station (Schofield et al. 2017) is allowing us to sunset Station B. ***Suggestion:** Organize around more integrative topics*. Our new themes are highly multi-disciplinary and cross-cutting, and not grouped by individual disciplinary components. ***Suggestion:** Determine measures of model uncertainties*. Uncertainties in stocks and flows from the inverse food web and data assimilation plankton ecosystem models are now being quantified using Monte Carlo approaches.

Scientific Background and Proposed Research

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 (e.g., Hauck et al. 2015, Moore et al. 2018, Gruber et al. 2019). Polar systems are among the most rapidly changing on Earth (Montes Hugo et al. 2009, Schofield et al. 2010, Brown & Arrigo 2012) and are sentinels of climate and ecosystem change, with iconic species serving as symbols of change. PAL-6 will build on three decades of research along the WAP to gain mechanistic and predictive understanding of ecosystem and biogeochemical responses to disturbances spanning long-term "presses" and higher frequency "pulses" driven by myriad of processes including natural climate variability, long-term climate change, resiliency/recovery in the face of press versus pulse forcing, altered species spatial landscapes, food-web alterations, and the impact of harvesting marine living resources.

Previous proposals: The major focus of all five previous PAL proposals was to explore 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 (i.e., diatoms, krill, penguins) in the context of high and low ice years. By PAL-3 (2002-08), we recognized that our study area was located in one of the most rapidly warming regions on Earth and focused on documenting ecological responses to long-term directional climate change. For PAL-4 (2008-14), our research group was reconstituted to provide a more comprehensive and process-oriented approach, involving a re-designed PAL sampling grid spanning the full WAP climate gradient with the aid of glider technology (**Fig. 1c**) and incorporating process-oriented experiments coupled to a range of system models. In PAL-5 (2014-20), we emphasized adaptive sampling, process studies, and modeling embedded in our local and regional-scale long-term observational program. During PAL-5 there was a significant recovery in sea ice (**Fig. 1a)** for which we expect the ecosystem response to be fully realized during this PAL-6 renewal. In PAL-6 we once again reconstitute the research team expand of our understanding of species-ecosystem resiliency in the face of multi-scaled disturbance and fundamental alteration of this polar ecosystem.

Conceptual framework. Our conceptual framework is based on a suite of biological processes, spanning a range of space/time scales that underlie ecosystem dynamics (Levin 1992). Environmental change also reflects physical/chemical forcing across a wide range of spatio-temporal scales with intra-seasonal "pulse" disturbances superimposed on long term "press" disturbances (Gaiser et al. 2020). The corresponding response of the ecosystem to change reflects how species evolved life histories are suited, or not, for the "new" dynamics of the altered system. The PAL LTER conceptual model (**Fig. 2**) is based on sea ice playing a critical role, directly or indirectly, in the population dynamics and life history strategies of organisms across all trophic levels of the food-web, spanning from the bacteria, to phytoplankton, to krill and other macrozooplankton, to penguins and other seabirds, and to marine mammals. The dynamics of the liquid-ice system underlies much of the biodiversity and productivity observed along the WAP, much like other polar ecosystems (Convey et al. 2014). Interannual variations in sea ice duration and extent along the WAP are driven by global-scale climate forcing through changes in regional winds, associated with the decadal variability and phasing of the SAM and ENSO that result in either high or low ice years (Stammerjohn et al. 2008a,b). High primary productivity, krill recruitment, and penguin breeding success follow high ice years (Ducklow et al. 2006, Saba et al. 2014, Steinberg et al. 2015, Schofield et al. 2017, Cimino et al. 2019), and conversely recruitment is poor during low ice years (Fountain et al. 2016).

During the first two decades of PAL, the WAP exhibited a trend toward a more positive phase of the SAM that drove changes in prevailing winds, heat input from the deep ocean, and warming air and ocean temperatures (Martinson et al. 2008, Couto et al. 2017a). Associated with this was a large decline in the annual sea ice season (**Fig. 1a**), which reflected and amplified a persistent ("press") disturbance from altered wind forcing and ocean and atmospheric warming. The cumulative impacts of sea-ice decline were shifts in species composition, changes in species' distributions, phenological adjustments, and mis-matches in trophic coupling (Smith et al. 1998, 2003; Ducklow et al. 2007, 2012, 2013). 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 could be approaching a tipping point (Bestelmeyer et al. 2011), and we were potentially witnessing a transition towards a new, ice-intolerant or ice-independent ecosystem (Sailley et al. 2013). However, there has been a recent cooling period associated with a phase shift in the Interdecadal Pacific Oscillation (IPO, Meehl et al. 2019), together with shifts in ENSO and SAM (Scambos & Stammerjohn 2019), resulting in a significant rebound in sea ice since 2010 (~30%, Schofield et al. 2018), providing an exceptional opportunity to assess the potential of the system to recover. The ecosystem responded with increased phytoplankton productivity (Kim et al. 2018, Schofield et al. 2018) and krill recruitment (Conroy et al. submitted-a); however, increases in other trophic levels have not yet occurred. This could reflect time lags associated with life history strategies. For example, Adélie penguin chicks leave their colonies for 3-6 years before returning to natal breeding areas (LeResche & Sladen 1970), so we require several more years to assess if there was a 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. Conversely, we can determine how ice-affiliated minke whale occurrence is affected by interannual and long-term changes in sea ice. Other drivers may be more important than previously appreciated in structuring WAP ecosystem dynamics, reflecting processes spanning from short-term local disturbances (an increase in storms, alterations to the landscape and seascape) to shifts in regional wind patterns and sea ice transport. Data from the last three years suggest that the cooling period has ended, which might ultimately explain the record high air temperatures recorded this past summer for the northern Antarctic Peninsula (65°F at -63°S and 51°F at -64°S, Washington Post). The ecosystem response to renewed warming after 6-years of cooling provides a unique opportunity to assess the resiliency of the system, noting that we may still see a lagged response to this regional-scale disturbance in some species with longer life spans (seabirds, whales, seals). Despite the recent cooling period during the last decade, there is a significant long-term warming trend (Henley et al. 2019) that is differentially expressed across the WAP. While 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, a process we term *climate migration*. PAL-6 will focus on better understanding the relative importance of short-term processes and feedbacks between local (snow cover, landscape geomorphology, storms), regional (wind, sea ice), and basin scale processes (climate change, climate teleconnections) that interactively underlie the food web dynamics and biogeochemistry.

In addition to sea-ice, regional ocean/atmosphere circulation and bathymetry play a major role in spatially structuring WAP ecosystem dynamics and species connectivity. The WAP is an open system, bordered by the ACC (Earth's largest ocean current) flowing along the continental slope (Martinson & McKee 2012). Interaction between the ACC and continental shelf-slope break initiates the transport of warm, nutrient-rich offshore oceanic waters across the continental shelf toward the coast, preferentially through submarine canyons (Couto et al. 2017a, McKee et al. 2019) (**Fig. 2**). As a result of region-specific transport and upwelling processes, cross-shelf canyons appear to be biological hotspots in the WAP (Kavanaugh et al. 2015). The major Adélie penguin colonies along the WAP are located near the coastal termini of these glacially carved cross-shelf seafloor canyons. We showed that canyon-heads are regions of predictable prey availability for foraging penguins, driven by shoaling of the upper mixed layer (Schofield et al. 2013, Carvalho et al. 2019). We now understand that specific interactions between the hemispheric to global climate modes, regional circulation, and local bathymetric features are major instruments of ecosystem and population connectivity in our region. Broadly, our conceptual framework recognizes the potential for well-established patterns of temporal (press, pulse, decadal) and spatial (regional-scale along-shore gradients, canyon-scale cross-shore circulation, vertical connectivity and mixing) variability (**Fig. 2**) to generate different ecosystem states (high and low primary productivity/krill recruitment years, within- and between canyon patchiness). Through comparative studies, we will continue to use these contrasting states to learn about the dynamics of ecosystem structure and function, and the resulting effects on regional carbon cycling. We will exploit the strong climate gradient along the WAP to frame questions about how ecosystem *responses* to climate and circulation might be changing as a function of ecosystem state. Consideration of these patterns through analysis and modeling of long-term data sets leads us to pose the following interrelated themes and questions that will guide our research over the next six years.

Major Research themes and Questions:

A. Ecological responses to long-term "press-pulse" and a recent decadal reversal. Changes in the WAP ecosystem reflect both long-term "press" pressures associated with a warming climate, and shorter-term extreme "pulse" events (e.g., a large storm, an extreme seasonal anomaly in sea ice cover). Additionally, the recent decade of cooling briefly reversed the long-term decreasing trend in sea ice. *How do long term "press" and shorter "pulse" pressures interact to drive changes across the food web? What is the resilience of the ecosystem in the face of rapid change followed by a recent sea ice reversal?*

B. Vertical & alongshore connectivity processes for physics and biology. Advection and mixing of waters on the WAP regulate the supply of heat, nutrients, and vertical stratification, which in turn affects sea ice growth/melt processes, modulates light availability for surface productivity, and affects transport of marine organisms on/off the shelf. *How do both alongshore and vertical mixing dynamics along the WAP interact to modulate the distribution and variability of physical properties and marine organisms? What patterns in organism abundance and distribution result from physical transport vs. local transformation?*

C. Food webs and carbon cycling. Polar ecosystems play a disproportionately large role in the global cycling of carbon, and climate-driven changes in the planktonic food webs may alter WAP productivity, carbon exchange, and energy storage. *How will these changes in the structure of the WAP pelagic food web affect cycling and export of carbon? How do changes in energy storage in primary producers affect higher trophic levels?*

D. Disturbance from storms as a control on ecosystem structure. Coastal Antarctica is one of the stormiest locations on Earth, and storm effects (strong winds and heavy precipitation) are known to have dramatic impacts on many coastal ecosystems, potentially affecting hydrodynamics, biotic community structure, and landscape conditions. Furthermore, the number and frequency of extreme weather events is predicted to increase. *How do storms drive the productivity, behavior, and recruitment across all trophic levels along the WAP? Will increasing storminess be a tipping point for seabirds and land-based seals?*

E. Education and Outreach. Never has it been more important to convey the importance of the Polar Regions on the planet, and address the critical public messages identified in the Polar Literacy Principles. *How does engagement with polar scientists, polar data, and local natural systems influence an informal science learner's understanding of and appreciation for PAL research? How best can PAL data be incorporated into informal learning environments? What role do PAL scientists play in enhancing learners understanding of the Antarctic ecosystem?* PAL will leverage the successful PAL-developed Data Jam model (Forster et al. 2018) to bring STEAM creativity to informal science learning programs.

Five core themes of the LTER Network. The above themes A-D incorporate the core LTER themes: primary production (see long-term trends, drivers, and disturbances in A-D), population studies (see long-term change and drivers of demographics from plankton to predators in A, D), movement of organic and inorganic matter (see alongshore and vertical connectivity in B and all C) and disturbance patterns (see press-pulse-decadal disturbances in A, and all D). We foresee our new disturbance theme, for example, could lead to a cross site LTER synthesis effort.

Overview of Sampling Strategy. An overview of our sampling/modeling strategy is provided below and is based on the logistical realities of working in an extreme environment (see Program Management section, appended). Details relevant to each research theme are provided below in sections A-E. Information Management, Project Management and Logistics are provided in the supplementary sections.

As ecological processes and press-pulse disturbances are expressed over a range of space/time scales, we developed a sampling plan to match our observations as best as possible to allow study of their interplay (Stommel 1963). This is accomplished through a combination of a multi-tiered and multi-platform sampling approach, process-based high-resolution sampling, and field experimental manipulative experiments. Whenever possible, new technologies are being added to increase sampling resolution in time, space, and biological diversity. The results of the sampling activities inform model efforts by filling gaps though improved parameterization of key processes and in turn models guide the development of future process studies in the field. The results are tightly coupled to development of Education/Outreach modules.

Long term observations. The PAL LTER program along the WAP (**Fig. 3**) has three complementary facets: a regional-scale oceanographic cruise, conducted every Austral summer (January) since 1993

(Waters & Smith 1992, Ducklow et al. 2008); continuous process-oriented regional scale instrumentation (moorings, gliders, and airborne drones); and local-scale, daily to weekly sampling in October-March at Palmer Station, including observations and measurements on breeding Adélie penguins, other seabirds, whales, and seals. Annual penguin observations were initiated in 1975 (Fraser et al. 1992, Fraser & Trivelpiece 1996) and hydrographic sampling began in 1991 (Moline & Prézelin 1996, 1997).

Annual research cruise in summer. The PAL regional sampling grid is occupied during a 28-science day cruise (see Project Management). The sampling grid has always included at least three stations per cross shore 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 in order to sample ice processes that were no longer prevalent in the northern grid (**Fig. 3a**). For PAL-6, we propose to expand once again to bridge the full north-south climate gradient by four sampling stations to the north of Palmer Station (the latter now residing in a transition zone) (**Fig. 3a**). Two stations would be added north of Low Island and two more between Low Island and Palmer Station. This will provide a Bransfield 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, and South Korea (see letters of support). This 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. 3a**, Clarke et al. 2007, 2008). Standardization of data between sites is the focus of the Southern Ocean Observation System (see letter of support; Schofield is co-Chair of the West Antarctic Peninsula and Scotia Arc Working Group).

During the January research cruise, along-track measurements yield continuous surface maps for a wide range of physical (temperature, salinity, currents), chemical (pCO_2, oxygen, argon) and biological (fluorescence, fast repetition rate fluorescence, phytoplankton species through automated imaging flow cytometry) properties. 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, dissolved oxygen, chlorophyll fluorescence, photosynthetically available radiation (PAR), and suspended particle abundance. Water is collected at twelve depths for discrete measurements (14C-uptake, chlorophyll, HPLC-pigments, dissolved oxygen, particulate inorganic carbon, particulate organic carbon, fast repetition rate fluorometry, eDNA, phytoplankton species identification, macronutrients, thorium deficits, lipidomics). CTD casts are complemented with net tows for macrozooplankton (e.g., krill, salps, pteropods) and mesozooplankton (e.g., copepods). Seabirds, whales, and seals are surveyed throughout the entire cruise to identify where high densities occur coincident to oceanographic features and enhanced biological activity. Skin and blubber biopsy samples are collected to examine whale population structure and demography (Albertson et al. 2017, Pallin et al. 2018b), while satellite tags are deployed to determine broad scale whale habitat use (Curtice et al. 2015). Finally, the seabird team conducts opportunistic censuses and diet sampling at islands of interest, which includes two decades of data collected at Avian Island during a 5-day field camp which will continue during PAL-6.

Palmer Station nearshore time series. PAL scientists have conducted seasonal sampling at Palmer Station during the October to March penguin breeding period each year since 1991-92 (Ducklow et al. 2013). The Palmer Station time series and partner time series to the north (AMLR, Carlini) and south (RaTS) capture seasonal dynamics in a local setting that complements the peninsula-wide annual sampling. The main objective of the Palmer Station sampling effort is to document and explain interannual variations in penguin demography in the context of responses of the plankton production system to physical forcing, krill recruitment (Saba et al. 2014), changes in prey distribution (Oliver et al. 2012, Bernard & Steinberg 2013), and landscape-related processes (Fraser et al. 2013, Cimino et al. 2019). Core measurements of penguin foraging ecology, breeding success, and population status along with water column studies are conducted daily to weekly via small boats at islands and hydrographic stations in the vicinity of Palmer Station (**Fig.**

3b,c). 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), which are all sensitive to ecosystem variability and/or penguin demographics and provide a holistic view of the ecosystem pressures seabirds must overcome to survive.

The cetacean component utilizes tagging biotelemetry methods, similar to the penguin component, to evaluate foraging behavior at fine scales (Friedlaender et al. 2016) around Palmer Station (Nichols et al. in prep.) (and throughout the entire PAL study area; Curtice et al. 2015, Weinstein & Friedlaender 2017). Skin and blubber biopsy sampling and photo-ID are also conducted to determine inter-annual changes in population structure and demography (e.g., pregnancy rates, Pallin et al. 2018b) as related to physical and biological ecosystem components. Unoccupied aerial systems (UAS; drones) have also been incorporated to evaluate changes in body condition throughout the foraging season (Beirlich et al. in prep) and link these to foraging behavior (Friedlaender et al. in prep) and inter-annual variability in pregnancy rates. UAS have also been used to conduct aerial surveys of islands surrounding Palmer Station throughout the summer to compliment ground surveys of penguins and seals and better understand the terrestrial habitat features that different species of seals utilize.

A seasonal data set of primary production, plankton community structure, and biogeochemistry, which also provides the environmental context for top predator demographics, is obtained by weekly sampling of a full suite of physical, chemical, optical, and biological measurements obtained from water samples collected in the upper 50-75 meters at Station E (**Fig. 3c**). The historical sampling at Station B (**Fig. 3c**) will be phased out in PAL-6 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 more capable boats (Rigid Hull Inflatable Boats), which now allows for bi-weekly high-resolution acoustic surveys and zooplankton net tows in penguin/predator foraging hotspots to provide proxy maps for krill resources. We will include nighttime zooplankton net tows to quantify diel vertical changes in zooplankton distribution, and to relate with diurnal patterns in krill predator foraging behavior. The facilities at Palmer also support a wide range of experimental incubation and manipulation studies which will continue in PAL-6. Our partnerships with 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, RaTS is located 400 km south of Palmer Station (**Fig. 3a**), where sea ice extent and duration today are about the level they were at Palmer 20 years ago (**Fig. 1a**). The RaTS ecosystem is thus at an earlier stage of response to climate migration. Thus, a British Antarctic Survey scientist (currently Mike Meredith, the RaTS Leader), has had full co-PI status in PAL since 2002 and also provides an annual cross calibration of hydrographic sensors at Rothera that will continue in PAL-6. This will now be complemented with the budding partnerships with Carlini and AMLR (the latter including Cape Shirreff) programs to the north (**Fig. 3a**) which will be developed during PAL-6 (as described above).

Experimental and Process Studies. Observational sampling is complemented with manipulative experiments conducted both on cruises and at Palmer Station. The manipulations often involve incubations that help define underlying physiological and growth responses for key species to changing environmental conditions (light, nutrients, temperature, pH, salinity anomalies, or combinations of predicted 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 remineralization, turbulence and particle aggregation rates). These experiments are generally conducted in bottles or tanks, which in part reflects 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_2 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. in prep) model approaches to build system-level descriptions of ecosystem processes. At Palmer Station these manipulations often focus on the seasonal variability in these processes (Luria et al. 2017), while onboard the RV *Gould* they capture the spatial variability across the latitudinal climate gradient along the WAP. Details on future process experiments are described in the thematic sections below; however many of these incubation experiments are conducted as part of our 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. We have been, and will continue, sampling over the Palmer Deep (Anvers Island), Marguerite Trough (Adelaide Island, Rothera Base) and Charcot Canyon, all associated with major penguin colonies.

Model simulations. The PAL field observations will be interpreted with a set of statistical, diagnostic, and prognostic models. Since no single model can capture the wide range of dynamics, time/space scales, and complexity inherent in the PAL dataset, models are chosen tailored to the specific research theme questions (see below). We will leverage a set of models, developed previously by PAL and collaborators, spanning from idealized process models to more realistic 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. A 1-D vertical physical model (Saenz et al. in prep.) 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). Sufficient observation-based information on mixed layer and seasonal thermocline physics are available for only a few situations: the Palmer Station near-shore time series; limited glider deployments at fixed locations (e.g., canyon head of Palmer Deep); and the mid-shelf bottom-moored temperature array (though this extends 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). In PAL-6, we propose to fill some of these observational gaps by conducting detailed sampling of surface properties and circulation using gliders and autonomous floats (see 'Theme B' below). Forced with atmosphere reanalysis and satellite data products, 1-D simulations over seasonal time-scales can be integrated either in full prognostic (predictive) mode or using data-based diagnostic constraints (e.g., assimilating sea-ice extent from satellite data or subsurface heating from lateral eddy injection from moorings or gliders). Pilot biological-physical experiments have been conducted by coupling to the 1-D physics model a phytoplankton-zooplankton-nutrient-detritus (PZND) module with bulk compartments tracking biological tracers (e.g., diatoms, iron).

Two 3-D ocean-sea ice circulation models are available 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. The model has been refined recently 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., submitted). Schultz (2019) reports preliminary results from a coupled PZND-biogeochemical module. The eddy-permitting resolution of MITgcm model allows for multi-decade experiments. Higher-resolution (approximately eddy resolving) simulations of the WAP shelf-slope come from a version of the Regional Ocean Modeling System (ROMS) (Dinniman et al. 2012, Graham et al. 2016). Again, the capability exists to add biological tracers and particle tracking to ROMS simulations to address targeted PAL science questions. For larger-scales, we will leverage Southern Ocean simulations of plankton biophysical dynamics (e.g., Rohr et al. 2017, Rohr et al. submitted A & B) using low-resolution and high resolution versions of the Community Earth System Model (Moore et al. 2018).

A similar span of complexity and scale exists for WAP biological models. Sailley et al. (2013) advanced an end-to-end food web model for the WAP (phytoplankton to seabirds and marine mammals). The inverse 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. Time-evolving, seasonal plankton dynamics are accessible through a new 1-D model for the WAP (Kim et al. in prep.). The PZND module, updated for the WAP 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, forms also a basis for the 1-D and 3-D coupled biophysical models above. 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).

Expanding sampling capabilities for time series. The WAP is a remote and harsh environment (high winds, high seas, sea-ice and icebergs, persistent cloud cover) hindering what can be sampled and when. Accordingly, PAL will continue to automate as much of our sampling as possible. Technical advances over the last decade also offer new proven approaches that will be continually integrated into the program. For field sampling, PAL will continue to expand our use of autonomous underwater gliders (to date 72 deployments, 908 days at sea–more than ships days sailed over the lifetime of PAL–spanning 19,941 horizontal kilometers), to provide high resolution data across and along the WAP continental shelf, and fill observational gaps between Rothera and King George Island (**Fig. 1c**). These surveys provide measurements of temperature, salinity, oxygen, phytoplankton fluorescence, and particle backscatter, to which we will add ocean currents (ADCP) to better resolve transport processes. Integrating sensors (e.g., LISST transmissometers to measure particles, multi-frequency bioacoustics) on gliders into standard sampling. Mooring operations will be extended to monitor along-shore exchange, with emphasis on the input of cold Weddell-origin water into the PAL study region, which is expected in Fall and Winter, while continuing to monitor influx of warm CDW along the shelf break and large submarine canyons. We will continue our collaboration with Elizabeth Shadwick (CSIRO) to measure carbon system parameters on our long-term mooring (see letter of support). The mooring measurements which complement glider surveys provide extended spatial coverage of the targeted exchange processes. Additionally, UAS (fixed wing and quadcopter) technology is maturing quickly and will be used during PAL-6 for census and phenological studies of land-based predators (e.g., seals and penguins) and mapping the dynamics of landscape processes (e.g., snow melt, topography, ice) and their ecological consequences.

RESEARCH THEMES

A. ECOLOGICAL RESPONSE TO LONG-TERM "PRESS-PULSE" AND A RECENT DECADAL REVERSAL

Motivation. The "press" of climate change is expected to accelerate, particularly in polar regions, while the magnitude and frequency of intra- to inter-seasonal extreme (or "pulse") events (e.g., a large storm event, an extreme seasonal anomaly in sea ice cover, snowfall, temperature) are also expected to increase (Smith 2011, Poloczanska et al. 2013, Harris et al. 2018). The PAL study area, which has been rapidly warming over the last 70 years (Vaughan et al. 2001, Schneider et al. 2012), with a history of pulse events (e.g., Fountain et al. 2016, see also Theme D), and now more recently, a trend reversal (Schofield et al. 2018, Henley et al. 2019) (**Fig. 1a**), is ideal for studying ecosystem response to 'press-pulse-decadal' forcing. Although PAL has documented changes in ecosystem structure and trophic linkages along this climate gradient over the long-term, impacts from this recent reversal as well as from expected increases in pulse events motivates a strong focus on ecological responses to press-pulse-decadal forcing, especially as such forcing may lead to major biodiversity impacts (e.g., Nielsen et al. 2012, Sanz-Lazaro 2016) and changes in the timing of occurrence of key life history events (phenological changes) (Lyon et al. 2008). Ecosystem responses can be characterized in terms of the system's resilience to disturbances of different type, magnitude, and time/space scale via metrics such as the extent to which the system deviates from and returns to its original state, and recovery times following the end of the disturbance or switches to a new state (e.g., Gunderson 2000, Müller et al. 2016, Jentsch and White 2019).

Background. WAP long-term changes (sea and air warming, sea and land ice loss, increased glacial melting and freshwater input) represent "press" or persistent perturbations on the polar ecosystem (**Fig. 1a, 4a**), expressed as shifts in species composition, changes in species' distributions, phenological adjustments, and mis-matches in trophic coupling. Additionally, climate-related impacts have affected the northern PAL for a longer period of time compared to the southern PAL due to the WAP climate gradient (**Fig. 4 b**). Phenological changes are also pronounced and include earlier sea-ice retreat in spring, and a later sea-ice advance in autumn. This has increased the summer open water season in the northern WAP from 6 to 8 months, and from 2 to 4 months in the southern WAP (from the late 1970's to the late 2010's) (**Fig. 4b**).

Sea ice phenological changes in turn can lead to phenological changes in the food web. At Palmer Station, the timing of egg laying in ice-dependent Adelie penguins parallels sea ice trends, with progressively earlier egg laying as the annual ice season shortened during 1979-2009 and later egg laying as the ice season recently lengthened during 2010-2016 (Cimino et al. 2019).

The WAP is characterized by high natural variability ranging from intraseasonal (days to months) to seasonal (phenological changes) to interdecadal scales (**Fig. 4a**). Seasonally, variability is highest during spring and autumn transitions, the timing of which differs north to south but also has changed with time as the ice seasons have shortened (**Fig. 4b**). On longer timescales, WAP variability is influenced by large-scale climate modes, including SAM, ENSO and the Interdecadal Pacific Oscillation (IPO) (Stammerjohn et al. 2008, Saba et al. 2014, Li et al. 2014, Meehl et al. 2019). The phases of these climate modes interact and can either amplify or dampen the environmental conditions. This includes changes in cloud cover, air and 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 cooling phase reflects these climate cycle interactions (Meehl et al. 2019, Scambos & Stammerjohn 2019).

Superimposed on WAP climate-driven trends/variability are events or "pulses" (extreme outliers falling outside the 10th to 90th percentile of a probability density function), which can amplify (or dampen) the ongoing press of climate change as observed in other ecosystems (Boucek & Rehage 2014, Smale & Wernberg 2013). While the duration of a pulse event could range from a few days to a few successive seasons, the ecological response to the pulse can be short-lived (representing resiliency), long-lasting, or even irreversible (a legacy effect or a tipping point) (e.g., Thibault & Brown 2008, Wernberg et al. 2016, Hughes et al. 2017; **Fig. 4a**). Although WAP biota are adapted to high climate variability, the underlying press of climate change over several years to decades can lead to unexpected amplified pulses in forcing. The biological or ecosystem impact from such pulse events will depend on the spatial scale, frequency, magnitude, seasonal timing, and duration, as well as the underlying state of the ongoing press of climate change (Harris et al. 2018). Additionally, when presses and pulses are exerted simultaneously (**Fig. 4a**), the potential for effecting a species shift or reaching a tipping point is enhanced (Scheffer et al. 2001). This is particularly true in nutrient-constrained, energy-limited polar environments, where episodic pulses occurring near a physio-ecological threshold can have long legacy effects (Fountain et al. 2016). Thus, the interaction of a long-term climate warming trend, the recent decadal reversal, and extreme pulse events has the potential to trigger complex, even catastrophic ecological responses (Harris et al. 2018). Similarly, commercial whaling in the early to mid-20th century was a major press of ecological disturbance that continues to impact krill and krill predators (Laws & Fuchs 1977, Ballance et al. 2006); the ecological and biogeochemical effects of yet another press, the krill fishery–which has been focused around the Antarctic Peninsula, are unknown (Laws & Fuchs 1977, Ballance et al. 2006, Cavan et al. 2019).

Proposed Research. We will assess the ecological response to: (1) the ongoing press of climate change (warming and decreased sea ice), in particular how mean states and variability have changed over the last 30-36 years, and (2) the most recent sea-ice reversal within the legacy of long-term warming and sea-ice loss. We will then characterize (3) the phenological changes in predator-prey relationships, and (4) the ecosystem response to the combined effect from press-pulse-decadal forcing using data synthesis and modeling (and insights gained from the other themes). Our aim is to improve predictive capability, as the press of climate change and frequency and magnitude of pulse events is expected to increase. The WAP climate gradient is useful for testing and assessing such ecological effects from press-pulse-decadal forcing, with the north providing a climatically-shifted and more variable baseline on which pulses and decadal variability are acting, in contrast to the south, where the baseline has only recently shifted and is less variable. This strategy allows us to assess the degree of recovery (if any) of the physical, chemical, and biological components of WAP ecosystem during the recent sea ice reversal. Trajectories of biological components will be analyzed within the context of life history strategies and generational time scales of organisms, as described below.

Characterize how the dominant spatial and temporal modes of variability changed over the last 30-36 years. PAL-3, using the first 12 years of grid-wide data (1993-2004), determined the dominant modes of spatial and temporal variability of key environmental, biological and biogeochemical variables (Ducklow et al. 2008, Martinson et al. 2008, Ross et al. 2008, Smith et al. 2008, Stammerjohn et al. 2008, Vernet et al. 2008). Now, with 16 more years of grid data (2005-2020), PAL-6 will revisit how those dominant modes of spatial and temporal variability have changed, both latitudinally and on-to-offshore with the ongoing press of climate change. In addition to traditional techniques of empirical orthogonal functions and reduced-space optimal analysis (Martinson et al. 2008), we will leverage a recent PAL multi-variate statistical study using "self-organizing maps" to define and track over time unique bio-physical seascape or geographical units along the WAP (Bowman et al. 2018). The rate of change in physical and chemical components will be compared to the lifespans of major trophic levels of the WAP ecosystem.

Characterize how the system responds to several-year periods of warm/less ice conditions and cold/more ice conditions. Superimposed on the press of climate forcing is high variability, including consecutive years of warm (less ice) conditions and cold (more ice) conditions. We will compare these warm/cold periods across time [warm periods (1998-2001 versus 2007-2010) and cold periods (2002-2006 versus 2011-2016)] to determine if the ongoing climate press alters the ecosystem response over time, reflecting changes in resiliency or legacy effects with base state (e.g., qualitative differences in the sign or nature of biological responses in food web; quantitative changes in the recovery times or magnitudes of biological responses to scaled perturbations). For example, our recent analyses suggest the following changes occurred during the recent colder period (more ice): (1) enhanced phytoplankton productivity in the south (Schofield et al. 2018); and (2) increased frequency of krill (*E. superba*) recruitment events (Conroy et al. submitted-a). These warm versus cold periods will be compared to determine how shifted baselines may alter the ecosystem response, and which life history traits (life span, foraging behavior, reproductive frequency/flexibility/timing) are associated with resiliency.

Characterize phenological shifts in predator-prey relationships. Climate change and variability is known to shift the distribution and phenology of animal populations (Lyon et al. 2008), and within PAL-5, phenological shifts were described for animals ranging from invertebrate pteropods (Thibodeau et al. submitted-a) to Adelie penguins (Cimino et al. 2019). However, it remains unclear how other environmental drivers are changing, and if other animals (e.g., krill and marine mammals) are responding similarly by shifting their phenology. PAL-6 includes opportunities to characterize the spatio-temporal scales of environmental change and determine how these affect the timing/presence of influential features including sea ice, weather conditions, water column stability, breeding/haul-out substrate, primary production, and krill availability (see also Themes B-D). Through detailed observational studies of the timing, presence, abundance, and behavior of krill predators (focused on penguins and whales) around Palmer Station, we can link population trajectories and reproductive success of different animals to both physical and biological variability and identify trophic mismatches (**Fig. 4c**). This will be combined with a new bioacoustics component initiated during PAL-5 and will continue as part of the PAL-6 Palmer Station sampling program. Small boat and glider surveys will focus on mapping prey resources for penguins and whales in the Palmer Station region. For penguins, phenotypic plasticity in egg laying exists (Cimino et al. 2019) but it is unclear how this relates to the timing of local primary productivity and krill availability to sustain chick rearing. For whales, we will quantify the timing of arrival and departure from the waters surrounding Palmer Station and the relationship with environmental properties such as timing of sea ice retreat and the availability of krill in suitable densities. 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, effecting the accelerated reproductive rates we have recently observed (Pallin et al. 2018b). This may be accentuated by the earlier retreat of winter sea ice opening foraging areas earlier in the summer. We will take advantage of the sampling strategies in the themes described below to link observed changes in the phenology of krill predator presence and behavior to temporal shifts in ecosystem properties (ice, storms, etc.).

Improve predictive capability of the ecological response to future press-pulse-decadal variability using data synthesis and modeling. During PAL-4 and PAL-5, we created a suite of new marine ecosystem and biogeochemical models for the WAP region that will form the basis for evaluating and predicting ecological response to future press-pulse-decadal variability. Ducklow et al. (2015), for example, used results from the data-inverse food-web model to evaluate geographic and interannual differences in WAP ecosystem carbon flow. Our modeling strategy will involve a combination of hindcast simulations: characterize ecosystem response to historical press trends and interannual to decadal variability in the context of the PAL data synthesis described above; idealized simulations with specified changes in future climate and disturbance frequency and magnitude; and climate projections using realistic future forcing output from global Earth System Models. The hindcast simulations, in particular, 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 (e.g., 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).

Characterize the full climate gradient spanning the WAP. Core spatial sampling by the ship and underwater gliders (Schofield et al. 2013) now span 2 of 3 zones of the WAP climate gradient. Sampling currently begins mid-WAP (centered on Palmer Station), which represents the transition between a more maritime versus continental climate regime, the former characterized by highly variable sea ice, air moisture, and storms. From here, PAL sampling extends southward into a more continental climate, characterized by heavy sea ice and cold, dry atmospheric conditions. The PAL grid currently inadequately samples the far northern WAP region that appears to have already transitioned to a more subpolar climate characterized with minimal sea ice (Kim et al. 2018), and a long-term decrease in abundance of Antarctic krill, *E. superba* (Atkinson et al. 2019) that has yet to manifest to the south, i.e., in the PAL region (Steinberg et al. 2015). The sampling will be accomplished by adding process stations to the north to overlap with the newly deployed NOAA ocean observing array near Cape Shirreff in the Bransfield Strait (**Fig. 3a**). The PAL data will provide a useful spatial annual reference dataset for NOAA and the long-term sampling at Carlini Station (**Fig. 3a**). This partnership between PAL, NOAA, and Carlini has produced open access data and synthesis publications (Kim et al. 2018, Henley et al. 2019, see letters of support from Drs. Schloss, Watters, and Meredith). Combined, the WAP science community will have unique access to three decades-long time series, each located within one of the distinct sectors spanning the climate gradient of the WAP. PAL-6 will link these sites across the WAP by ship and glider deployments (**Figs. 1c, 3a**).

B. VERTICAL & ALONGSHORE CONNECTIVITY PROCESSES FOR PHYSICS AND BIOLOGY

Motivation. Physical processes controlling the advection and mixing of waters on the WAP are critical because they determine nutrient supply from the open ocean and land, affect sea ice growth/melt processes, modulate light availability for surface productivity, and generate transport pathways for plankton on the shelf. This theme is focused on understanding how both (1) along-shore property distribution and exchange processes, and (2) connectivity between surface and deep ocean layers modulate the distribution and variability of physical properties and marine organisms along the WAP. This will provide a key local context for interpreting "transport vs. transformation" processes on the scales of local plankton and predator populations. We build on a new understanding, developed during PAL-5, of how rapid environmental change, natural variability, and local conditions impact the WAP ecosystem.

Background. An important focus of PAL research has been understanding the role that cross-shelf lateral transport of heat, freshwater, and nutrients play in modulating the distribution of organisms and biological productivity across the WAP. This modulation results from a combination of local conditions such as benthic topography and strong large-scale forcing from the atmosphere, open ocean, and sea ice. A fundamental model for the modulation of shelf physical and biological properties is the transport of warm CDW, carried by the ACC, onto the shelf (**Fig. 5a**). This process occurs in the form of small ocean eddies entering the shelf through large submarine canyons (Moffat et al. 2009, Martinson & McKee 2012, Brearley et al. 2019). Glider datasets collected during PAL-5 provided the first shelf-wide surveys of subsurface eddies (**Fig 5b**, Couto et al. 2017a), and process studies combining moorings and hydrographic surveys revealed key aspects of the eddy dynamics, including the loss of heat laterally, not vertically, as eddies move onshore (McKee et al. 2019). These findings are important because they show that eddy-driven CDW intrusions are widespread across submarine canyons (**Fig 5b**), which are biological "hotspots" of elevated phytoplankton productivity and which are associated with major Adélie penguin breeding colonies and foraging areas near canyon heads (Schofield et al. 2013, Kavanaugh et al. 2015, Carvahlo et al. 2019). However, evidence thus far suggests that modulation of light availability best explains the enhanced phytoplankton productivity (Carvalho et al. 2016), a fact consistent with the lateral, rather than vertical, loss of heat from the eddies (McKee et al. 2019).

Building upon the above results, a goal of PAL-6 is to examine the processes that modulate the generation of biological hotspots in space and time. Vertical exchanges can be forced from above or below. For example, changes in storm activity are likely to enhance vertical mixing, a process that is heavily modulated by the presence of sea ice (Brearley et al. 2017). But storms also affect sea ice growth/melt, which in turn affects vertical stratification (thus vertical exchanges) and mixed layer depth. Sites of complex topography on the WAP shelf also appear to enhance vertical mixing of deep nutrient rich warm waters from below (**Fig 5a**, Venables et al. 2017). While canyons continue to be a focus for understanding biological hotspots in our study region, the broader question is how and when the nutrient rich warm CDW water entering the shelf is ventilated to the surface. Addressing this question will improve our understanding of how heat and nutrients are supplied to the surface layer, and how those processes affect the growth/melt of sea ice. These same dynamics (e.g., vertical advection, mixing, sea ice growth/melt) modulate the vertical structure of the water column (e.g., strength of stratification and MLD) that determines light availability near the surface. Understanding these processes has been hindered by the difficulty of generating continuous time series of the surface properties and ocean circulation, particularly in the more ice-laden coastal WAP. The surface circulation, in particular, is poorly known. The use of ocean gliders, proven successful in PAL-4&5, will be expanded, along with the use of autonomous floats, to address these observational gaps.

The PAL study region exhibits significant and persistent physical and biological variability along the coast (**Fig 5c**) and there is growing evidence that a significant amount of the variability reflects north and south connectivity of freshwater, sea-ice (**Fig 5d**), and organisms (Piñones et al. 2013). Thus, a focus of PAL-6 is to study how physical and biological characteristics of different coastal regions are propagated along the peninsula. This physical and biological variability is partly a result of the influence of the Weddell Sea, which acts a source of cold, fresh water to the northern WAP through the Bransfield Strait (**Fig 5c**). Along-shore WAP property gradients strongly modulate glacier retreat (**Fig 5e**, Cook et al. 2016) and primary productivity (**Fig 5f**, Montes-Hugo et al., 2009). While the physical processes modulating the variability of along-shore gradients are yet poorly resolved, recent research has also revealed significant along-shore variability that can affect key aspects of the ecosystem structure. Modeling (Wang et al. in prep.) and observational (Aguiar-Gonzalez et al. in prep.) studies of the WAP show that cold water in Bransfield Strait, of Weddell Sea origin, is a substantial source of cooling for the shelf to the south. This process is wind-forced and strongly seasonal, with influx in fall and winter, and with substantial interannual variability modulated by SAM. The ecological implications of this exchange have not yet been explored, but are a new and potentially significant driver of observed environmental variability in the PAL study region. These dynamics are closely connected to our goal of understanding vertical connectivity on the shelf, as this along-shore exchange modifies the water column properties and circulation, and thus vertical transport and mixing.

Proposed Research. We aim to understand processes modulating along-shore variability and vertical connectivity that play key roles in structuring the ecosystem. Focus areas are: (1) understanding the competition between warm CDW intrusions from the open ocean and along-shore cold water transport through the Bransfield Strait in shaping along-shelf gradients in temperature, salinity, and nutrients; (2) quantifying the mechanisms that supply cold water and sea ice to the PAL study region from Bransfield Strait; and (3) determining the seasonal-to-interannual variability of along-shore physical gradients in the WAP. To address vertical connectivity on the shelf, we will (4) characterize the dynamics that lead to canyons acting as biological hotspots by modulating the vertical structure of the surface layer, and (5) understand the spatial distribution, timing, and frequency of vertical exchange events on the shelf, and their impact on supply of nutrients, organisms, and productivity. All of these questions will be considered within the context of press-pulse-decadal forcing.

Alongshore variability and connectivity. This strategy uses a multiplatform observational approach with a substantial modeling effort. PAL currently maintains a long-term mooring, measuring temperature and currents that has proven critical for understanding the inflow of CDW water onto the shelf (**Fig. 3a**). We will expand this effort by installing additional moorings to study along-shore exchanges between the PAL study region and the colder Bransfield Strait to the north (**Fig. 3a**), which historical hydrographic observations and modeling studies show is substantial and varies strongly on seasonal to interannual time-scales. Ocean gliders, in turn, will be used to provide shelf-wide surveys of the vertical structure of water properties and ocean currents, with particular emphasis on the surface layer (**Fig. 3a**). Repeated and sustained sampling across key topographic features, some considered to be predictable predator foraging habitats, will elucidate processes that lead to canyon-generating biological hotspots. Focused, repeated glider sampling will consist of two modes: in stationary mode as a mooring (Clark et al. 2019), and in high density survey mode (e.g., of a topographic feature), extended over austral summer to capture the response of the surface layer to storm events and to monitor topographic mixing processes.

Vertical exchange processes. During the ice-free season, we will rely on gliders in combination with subsurface moorings. As seasonal ice cover and presence of large icebergs pose a significant challenge to characterize surface properties, we also plan to use newly-developed coastal profiling floats equipped with temperature, salinity, oxygen, fluorescence and pressure sensors. These floats are designed to rest on the bottom between vertical profiles with set periodicity, and to transmit data when they can access the surface through openings in the ice cover. The instruments will be deployed at mid-shelf sites (e.g., Palmer Canyon, **Fig. 3a**) and will provide the first set of year-round, full-depth observations on the shelf away from the manned research stations, to complement mooring deployments limited to subsurface layers. Together, these new data will allow us to examine processes modulating MLD and vertical mixing, key processes affecting biological productivity (through light availability and nutrient supply), especially during critical periods of atmospheric forcing by storms, as well as during spring melt-back and autumn freeze-up.

Modeling synthesis of WAP across- and along-shore, and vertical circulation. A complementary modeling effort will be used investigate processes captured by the new observations described above, guide instrument deployment and surveys, and resolve key processes on seasonal to interannual time-scales. A regional version of ROMS has been developed at Old Dominion University (e.g., Graham et al. 2016; see ODU letter of support). The configuration includes a 1.5 km horizontal resolution, 24 vertical levels, a dynamic ice model, realistic topography and boundary conditions, and atmospheric forcing provided by the Antarctic Mesoscale Prediction System (Powers et al. 2012). Of particular interest is to better understand shelf-wide impacts of hotspot-generating mechanisms identified by our small-scale surveys, the role of sea ice growth/melt in modulating vertical exchanges, and the dynamics of along-shore exchanges. Impact of these physical dynamics on plankton distribution and temporal variability will be examined with particle tracking experiments coupled to the circulation model, with a focus on the generation of horizontal retention and enhanced hotspots of vertical exchange. These modeling efforts will also inform work described in other themes, such as impacts of vertical exchange of nutrients on the shelf for WAP biogeochemical cycling (Theme C), and of pulse events (e.g., storms) on ecosystem structure (Theme D).

C. FOOD WEBS AND CARBON CYCLING

Motivation. The structure of the pelagic food web plays a fundamental role in regulating net community production, air-sea exchange of carbon dioxide (CO_2), and the export of organic carbon to the deep ocean (the biological pump) (Ducklow et al. 2001, 2015; Sailley et al. 2013; Steinberg & Landry 2017). Furthermore, energy storage and food web interactions affect assimilation and trophic transfer efficiency of energy and carbon throughout the food web. Our previous observational and data 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 web can force changes in productivity, carbon exchange, and energy storage, but these changes are only discernable in the context of a long-term program. In PAL-6 we build upon two decades of plankton and biogeochemical measurements to quantify these changes.

Background. The structure of the pelagic food web varies across the WAP continental 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 characterized by low biomass and micronutrient limitation (Annett et al. 2017). Coastal waters characterized by >20 μm diatom phytoplankton (Hart 1942, Nelson & Smith 1991, Prézelin et al. 2000), are regulated by water column stratification and light limitation (Moline et al. 1998; Vernet et al. 2008; Carvalho et al. 2016, 2019; Schofield et al. 2017; Rozema et al. 2017). Offshore waters are characterized by seasonal spring blooms associated with the retreat of sea ice (Smith & Nelson 1985) that terminate as micronutrients become limiting (Sherman et al. submitted). Cryptophytes are an abundant WAP phytoplankton taxa associated with lower salinity coastal waters (Moline et al. 2004, Schofield et al. 2017, Rozema et al.2017), leading to the hypothesis that they will thrive under conditions of increased warming and sea-ice melting (Moline et al. 2004). Mixed flagellates, dominated by dinoflagellates are likely responsible for high rates of microzooplankton grazing (Garzio et al. 2013). The relative abundance of these respective phytoplankton taxa affects ocean CO_2 assimilation (Brown et al. 2019) (**Fig. 6a**), therefore PAL-6 will study the environmental drivers of not only phytoplankton biomass but also expand our focus on physiology and diversity.

Vertical export of POC is a key process in the WAP biological pump. POC export over the northern WAP shelf is dominated by krill fecal pellets (Gleiber et al. 2012), and a recent modeling effort shows that fecal pellet production in the marginal ice zone is equivalent to 13-18% of annual POC export in the Southern Ocean (Liszka 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 in prep.). 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 also 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). Analysis of WAP zooplankton diel vertical distribution patterns collected during PAL-5 indicates strong DVM by a number of key taxa (e.g., salps, ostracods, copepods, pteropods), controlled by photoperiod and MLD (Conroy et al. submitted-b; **Fig. 6b**). 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 the surprisingly low particle export to primary production ratios observed for the WAP (Stukel et al. 2015, Ducklow et al. 2018).

Given emerging observations that light availability is a fundamental feature structuring productive coastal systems and export of carbon, understanding energy flow through the ecosystem is critically important. 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 (Holm et al. in prep a.; **Fig. 6c**). 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 prep). 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, differences in prey quality (i.e., lipid and caloric content) affect the ability of predators to meet their energetic demands, and have implications for key life history stages, such as penguin chick fledging and recruitment 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). These observations suggest that prey quality may also be affected by climate migration, which we will examine in PAL-6 using new lipodomic approaches.

Proposed Research.

Phytoplankton primary productivity, diversity, and carbon dynamics. Phytoplankton community structure will be examined within the context of continued measurements of physical (e.g., mixed layer depth) and bulk biogeochemical properties including patterns of seasonal nutrient drawdown (Kim et al. 2016), oxygen, dissolved inorganic carbon and alkalinity (Hauri et al. 2015), surface pCO_2, POC, and total chlorophyll as well as biological rate measurements of 14C-incubation net primary production and net community production derived by underway O_2/Ar data (Eveleth et al. 2017, Ducklow et al. 2018). Measurements of the energy budget for photosynthesis will be as added as a new core measurement providing the fundamental estimate of the available biological energy for the ecosystem, with which we will combine profiles of the energy storage across the foodweb through advanced lipidomic analyses (see below). This energy budget is measured by combining data from a PicoLiF (Picosecond Lifetime Fluorescence), developed to measure fluorescence lifetimes in the picosecond time domain (Kuzminov & Gorbunov 2016, Lin et al. 2016) with fast repetition rate fluorometry (Lin et al. 2016, Park et al. 2017, Falkowski et al. 2017). Calorimetry will be used to affirm this approach. We will combine measurements with detailed time/space measurements of phytoplankton species diversity beyond the taxon-level chemotaxonomic phytoplankton accessory pigments. We will map communities at species level using automated microscopy (Sosik & Olson 2007), particle size distribution (Karp-Boss & Boss 2007), community eDNA/RNA profiling (Djurhuus et al. 2018), as well as traditional and SEM microscopic analyses for cells under 10 μm that are uncharacterized on the WAP. These morphology approaches will be complemented with community profiling using 16S/18S working in collaboration with Dr. Bowman (see letter of support). The spatial and temporal maps will be complemented with controlled manipulative incubations of natural communities (light, nutrients, dynamic light regimes) onboard the Gould and at Palmer Station. This will complement a range of similar efforts at other marine LTER sites (Northeast US Shelf, Northern Gulf of Alaska, California Current, Beaufort Lagoons).

Food webs, carbon cycling, and export processes. We will combine the above with ongoing measurements of zooplankton abundance and diversity across the PAL grid. 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 (e.g., Thibodeau et al. submitted-b). Preliminary estimates suggest active transport is a substantial, unaccounted for export term in the WAP C budget, with mean active C transport below 150m by summed DVM taxa equivalent to or exceeding passive POC export measured by sediment traps in summer. We will add active transport by seasonal vertical migrants such as hibernating copepods (e.g., *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. We will examine assimilation efficiencies of key lipids by krill and copepods (see below), in parallel with spatially resolved surveys of lipidomes in sinking particulate organic matter (POM), collected in drifting net traps (Collins et al. 2016, Fulton et al. 2017) deployed at Process Study stations representative of the WAP latitudinal and coastal-shelf-slope gradients. 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). We will further combine our ongoing experiments of zooplankton fecal pellet production with zooplankton abundance and size data to develop size-based algorithms of fecal pellet production and export. These will be tied to PAL data to make predictions of the changing role of zooplankton-mediated carbon export in the WAP that will be compared with geochemical estimates of net community production (from surface O_2/Ar and seasonal nutrient drawdown) and export via ^{234}Th deficit (Stukel et al. 2015, see letter from Stukel) and particle flux measured by drifting sediment traps.

Energy storage and food web interactions. Lipids have a long history as tools for understanding trophic interactions in Antarctic marine communities, (Bottino 1974, Hagen et al. 1996, Kattner et al. 2012, Nichols et al. 1989, Skerratt et al. 1995, Ruck et al. 2014), and our state-of-the-art lipidomics workflow will allow us to routinely obtain nearly complete lipidomes (1,000 + molecules) from the many hundreds of samples we expect to collect each season (Becker et al. 2018, Collins et al. 2016, 2018). We will examine how the molecular diversity and energy content of lipids vary between major taxa along the latitudinal and cross-shelf gradients of the WAP, and from time scales from 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), key phytoplankton taxa (flow sorting; Popendorf et al. 2011), and major zooplankton taxa (net tows). We will analyze sea-ice algal communities in ice cores. We will also estimate lipid digestion efficiency through comparative analysis of prey and fecal pellets in krill, as well as diet samples (via lavage) and excreta of penguins. Finally, we will assess the propagation of energy storage molecules into the energy reserves of humpback whales within and across seasons by conducting lipidomic analyses of blubber biopsy samples collected throughout the summer season. Bomb calorimetry on representative subsamples will estimate total energy content and the relative contribution of TAGs, wax esters, and other lipids. These lipidomic and caloric data will provide a framework for developing hypotheses connecting spatial and temporal distributions of chemical energy in phytoplankton, zooplankton, and representative predators (penguins and baleen whales).

Complementary lipid and energy contents data will provide novel insights on how 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 asses the energy densities and lipidomes 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.

Food-web and biogeochemical modeling. 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. in prep.) models. Both ecosystem models will be extended to incorporate lipids and energy flow, with constraints on lipid production, utilization, and requirements of different trophic compartments based on the new Palmer data and literature values. Active zooplankton carbon export will be included using a new zooplankton DVM parameterization (Archibald et al. 2019) adapted to polar summer conditions.

D. DISTURBANCE FROM STORMS AS A CONTROL ON ECOSYSTEM STRUCTURE

Motivation. Disturbance of the WAP ecosystem occurs across a range of temporal and spatial scales and from a number of phenomena, some of which have been the focus of prior PAL research (e.g., mesoscale ocean eddies; upwelling events; sub-annual to interannual climate modes). The purpose of this new focus is to understand a disturbance process that has received little systematic focus–the short and long-term impacts of pulsed storm events on the WAP ecosystem. Throughout the PAL time series, we have concrete but often anecdotal evidence of the effects of storms on the physical and biological environment. We now have the scientific capacity/instrumentation to study storm effects in this remote ecosystem, and propose to conduct targeted studies to understand storm properties, determine long-term changes in these properties, and identify storm effects on the food web and the demography/survival of krill predators.

Background. Storm effects, including strong winds and heavy precipitation, are known to have dramatic impacts on coastal ecosystems, ranging from hydrodynamics, biotic community structure, to landscape conditions (e.g., Valiela et al. 1998, Johnson et al. 2015, Kearney et al. 2019). Despite this knowledge and even acknowledgement in prior PAL research, previous proposals primarily focused on long-term warming and sea ice loss. However, recent PAL observations highlight significant ecological impacts from storm events (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). This has led to the development of a storm intensity hypothesis: that any increase in the frequency or duration of storms will impact both landscape and seascape environments, such that survivorship, recruitment success, and the health of animal populations will be critically impacted. As each trophic level is affected differently by the direct and indirect impacts of press-pulse disturbances (see Theme A), it is necessary to consider how both long-term sea ice trends and episodic atmospheric conditions simultaneously alter ecological processes. Already many other LTER sites report changes in storm frequency and magnitude as key factors structuring their ecosystems; thus, this topic offers a rich opportunity for cross-site synthesis. For PAL the significance of storm effects, whether storm characteristics are changing, and the consequences for the food-web, have not yet been a specific focus.

Antarctic wind patterns and storm intensity are linked to global and synoptic-scale climate change and variability through tropical teleconnections and other climate modes (e.g. ENSO, SAM) (Yuan et al. 2018, Holland et al. 2019). There is considerable inter- and intra-annual variability in storm characteristics in the Antarctic (Hoskins & Hodges 2005) including the WAP (**Fig. 7a,b**), with storm intensity (as measured by wind speed and snow accumulation) highest during austral winter. During summer, storm frequency varies quasi-weekly over local to regional spatial scales, and stormy conditions range from high winds with no precipitation, to calm winds with high rain or snow precipitation, to blizzard conditions. The physical effects of these episodic storms on biological processes are hypothesized to be related to wind-driven ocean mixing and transport, sea-ice break-up, and cloudiness, thus affecting light/nutrient availability in the seascape, as well as snow deposition/accumulation affecting the landscape.

Wind forcing drives sea-ice distributions, waves and surface currents (Kohut et al. 2018, Kohout et al. 2014), ocean mixing, MLD and stratification, and thus also the distribution/abundance of plankton. Vertical mixing dilutes phytoplankton concentrations (Moline and Prezelin 1996, Saba et al. 2014), while ocean currents can provide a flux of nutrients, causing secondary phytoplankton blooms after clouds disappear and the ocean restratifies (Moline & Prezelin 1998, Warren et al. 2009, Nardelli et al. in prep). Stormy cloud cover may impact the light energy available to fuel total production (see Theme C). High winds may affect krill, through passive advection or cue active vertical migrations to depths below the turbulent mixed layer (Croll et al. 2009, Warren et al. 2009), and the wind-related response of krill and other zooplankton will vary by swimming ability or size class.

Storms have apparent consequences for krill predators while breeding on land (seabirds) and when foraging at sea (seabirds and whales) (**Fig. 7c**). For seabirds nesting on land (e.g., penguins, skuas, giant petrels), island-specific landscape geomorphology influences snow deposition and accumulation patterns, which drives nest microclimate conditions, breeding phenology, and reproductive success (Patterson et al. 2003, Fraser et al. 2013, Cimino et al. 2019). Snow or meltwater can bury or flood nests (**Fig. 7d**), 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, Mcclintok et al. 2008, Boersma et al. 2014). Similarly, Adelie penguin chick fledging mass, a key indicator of chick survival, is negatively related to cold, wet, and windy weather (**Fig. 7e**), though it is unclear if the mechanism is through increased thermoregulatory costs or decreased chick feeding frequency related to wind-driven changes in the marine preyscape (Chappell et al. 1989, Chapman et al. 2011, Cimino et al. 2014). Even a single catastrophic summer storm is capable of causing massive breeding failures (Massom et al. 2008). At sea, predator foraging behavior is linked to wind forcing, presumably through alterations the seascape and prey characteristics. After strong wind events, penguins and whales dive deeper and shift foraging locations, which often for penguins results in longer foraging trips (Fraser & Hofmann 2003) (**Fig. 7f**). For larger krill predators (baleen whales) that require high density krill patches to meet their energetic demands, the effect of storms on the availability of profitable prey may be significant. Decreases in foraging efficiency and increases in effort ultimately affects adult fitness, body condition, and reproductive rates, as well as offspring survival.

Proposed Research. We will investigate storm disturbances on the physical and biological environment and if storm characteristics have changed over time to more strongly affect food web connectivity and population dynamics for key indicator species (**Fig. 7c**). Specifically, we will: (1) develop metrics for defining storm characteristics to test for long-term changes in storm forcing across the WAP; (2) quantify the relationship between regional-scale storms with local-scale weather at Palmer Station, (3) at Palmer Station, identify local effects of storms on water column structure, ocean currents, plankton dynamics and predator behavior; and (4) relate storm frequency/intensity to predator demographics, while also considering sea ice effects. While storms are short-term events (days to weeks), the integration of atmospheric, oceanographic, terrestrial, biological, and animal behavior data across multiple time-scales is needed to test for changes in storm properties and consequent cascading effects on the ecosystem (complementary to long-term changes in Theme A and shelf-scale dynamics in Theme B).

Defining metrics for biologically-relevant storm disturbances. To identify long-term changes in storms, we will develop metrics for storm characteristics at the local- (Palmer Station) and regional- (WAP) scale. These metrics may include precipitation (rate, frequency, and duration), wind speed and direction, cloud cover and storm intensity (magnitude of low-pressure center), and ocean physics (e.g., retrospective analysis of variation in mixed layer depth used to infer wind-driven mixing; Kim et al. 2018). We will use these metrics to calculate mean storm characteristics and test for decadal trends, where the interpretations of decadal trends will rely on understanding other long-term changes outlined in Theme A. We are particularly interested in how these storm metrics have changed with time, how they differ along the WAP climate gradient, and how they are linked to large-scale sea ice patterns and climate modes. Multidecadal reanalysis datasets for the Southern Hemisphere (ERA-Interim, Dee et al. 2011) will be used to calculate storm timing and location using relative vorticity data. Following Grise et al. (2013), algorithms can be used to identify storms based on changes in direction and speed using a threshold level for 'cyclone vorticity units'. These regional-scale storm metrics will be compared to Palmer Station meteorological data to understand how regional-scale processes influence local weather. For example, 2001-02 was an extreme weather year (Massom et al. 2008) and resulted in multiple storms crossing Palmer Station (**Fig. 7b**).

Storm impacts on the food web. Few studies have examined the effect of storm disturbances over small spatial (10s kms) and temporal (days) scales on Antarctic marine food webs. Using our storm metrics, we will focus on periods before, during, and after storms to identify effects on water column properties and biological community response, and how this varies between years. We are interested in determining how much wind energy is required to destratify the upper water column (e.g., Hauri et al. 2013) and how this destratification or increased turbulence affects food web connectivity. Quantifying these links involves multiplatform observational and modeling approaches (Theme B). Bi-weekly sampling at Palmer Station will continue to provide a time series of upper water column physical properties, chlorophyll concentration, and community structure from October-March, and bi-weekly acoustic surveys of krill aggregations within commonly used penguin and whale foraging areas from December-March (**Fig. 3b**). Similarly, shorter-term glider sampling in January-February provides high-resolution measures of optical properties, chlorophyll, and acoustic characterization of zooplankton. Satellite-tags paired with time-depth recorders on penguins and whales in January-February provides information on animal behavior including foraging locations, dive profiles, and foraging effort (i.e., foraging trip duration for penguins and foraging bout length for whales). Whale relative abundance will be determined daily to compare with local prey abundance. Merging these time series provides a seasonal view of the evolution of oceanographic conditions and biological response, with higher resolution observations in January and February occurring within the critical penguin chick-rearing period and the resumption of whale feeding after ~6 months of fasting during the breeding season.

Preliminary data collected during PAL-5 revealed an apparent relationship between increased wind speeds and deeper MLDs and predator dive depths (**Fig 7f**). However, it was unclear how krill responded to wind-driven effects. Do winds create increased turbulence that cause krill to actively migrate deeper, or are krill being advected out of the system causing predators to target deeper prey patches that are not subject to wind forcing? Or are krill aggregations being dispersed below a threshold level for successful foraging? Our acoustic surveys provide data on the local availability of krill that dictates foraging behavior. Penguins and whales have different energetic demands, abilities to detect and exploit prey, and capacities to extend foraging range. For example, whales require high-density prey patches to make feeding energetically viable while penguins may utilize smaller or lower-density patches as they consecutively target a single prey animal, suggesting there may be contrasting responses of predator species to storm-related alterations in prey aggregations. Parallel tagging of the two predator groups will allow statistical comparison of foraging behavioral responses. As whales are highly mobile and not tethered to a breeding colony, we expect whales may leave the Palmer region to seek out more profitable foraging habitat if storms affect local prey quality. To address this, we will deploy longer-lived tags during the summer (2-3 months). We will use the Population Consequences of Disturbance conceptual framework to better understand how storms affect the behavior and physiology of these two krill predators and if there are signals that can be detected from acute and chronic exposure to storms that manifest as changes in individual fitness that then lead to changes in population dynamics (outlined in Pirotta et al. 2018, New et al. 2015) (**Fig. 7c**). In this framework, we can determine differential effects of disturbance and resilience on krill predators with significantly different life histories, foraging behaviors, and demographic patterns.

Understanding predator demographic responses: storm effects relative to sea ice winter preconditioning. Long-term Adélie penguin population trends in the WAP reflect the interaction between two scales of forcing: regional decreases in winter sea ice and local-scale increases in spring snow accumulation. The recent cooling period, resulting in more sea ice and the near-immediate response of phytoplankton production and krill recruitment events, suggests that the ice-dependent Adélie penguin would respond positively via a population increase–but this has yet to be seen. Could negative storm effects dominate over positive sea ice effects, or did the short-term sea ice increase not surpass a threshold to initiate an Adélie population increase? Even with the recent increase, sea ice is still lower than in the 1990s when Adélies were already declining. Possibly more frequent and intense spring/summer storms counteract the positive influences of sea ice, posing a barrier to the recovery of Adélie penguins. Similarly, while whale populations are increasing, sea ice conditions and storm disturbances may affect female pregnancy rates at a one-year lag manifested in decreased foraging efficiency (measured from tags) and body condition (from UAS and blubber lipid concentrations). Results from PAL-5 indicate significant inter-annual variability in humpback whale pregnancy rates (~35-70%) (Pallin et al. 2018b) that cannot be correlated to our current environmental sampling strategy. Therefore, we will conduct statistical analyses (e.g., generalized linear or additive models) that include both sea ice conditions (informed by Theme A) and summer storm metrics to determine drivers of penguin demographics (e.g., breeding success, chick mass) and whale pregnancy rates. Using a combination of these metrics will aid in deciphering the relative magnitude of landscape versus seascape storm effects on penguin demography.

E. EDUCATION AND OUTREACH

Motivation. One of the main aims of PAL Outreach is promoting the global significance of Antarctic science and research. Bringing the knowledge and current findings of PAL to the public is integral to their understanding of our global systems. It is a critical time to broaden the reach of polar science to as many audiences outside of academia as possible to increase awareness of polar change and its consequences. 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 means can we construct that would 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 test these ideas? To investigate answers to these questions, our efforts have focused on bringing the poles to people by leveraging the availability of authentic scientific data and sensor networks deployed in the Polar Regions. The newly-developed Polar Literacy Principles (McDonnell et al. 2017, 2020) serve as the framework for our efforts to 1) ***positively impact the formal***

education enterprise through the development and dissemination of polar instructional materials and learning opportunities for K-12 educators to facilitate their professional development and curricula; 2) ***engage communities in polar science research*** through the development and implementation of Out of School Time (OST) learning opportunities such as Family Science events, afterschool short-term exploratory learning programs, and summer camp programs focused on underserved and diverse audiences; and 3) ***develop high quality science communication products*** to build awareness of PAL research directly to audiences in the cruise ship industry as well as indirectly through social media.

Proposed Research. Moving forward and using the Polar Learning Principles as a foundation, we propose to focus on two new key audiences: 1) OST youth ages 9-13 and their families from underserved and underrepresented communities; and 2) informal educators such as those that work in museums, science centers, zoos, and aquariums, as well as YMCA, Boys & Girls Clubs, and 4-H Youth Development professionals. We will develop programs grounded in real-world phenomena related to PAL, designed from a youth-centered view. By leveraging our NSF grant (#1906897) Polar Literacy: A Model for youth engagement in learning, we will focus on creating inclusive curriculum and program opportunities that focus on diverse and underserved audiences. We have two key objectives:

1. Maintain and expand our virtual schoolyard program. We propose to formalize our school materials by engaging a graphic designer to put together a professional and polished lesson package for schools complete with photographs, graphics (food web), and maps. We will continue to offer 5-6 VTCs annually during the field season, serving twenty 5-12th grade schools nationally. The PAL website will be overhauled and updated to add new virtual field experiences and scientist interviews to improve the user experience. We currently have several graduate students in the field collecting video appropriate for virtual reality experiences. We will work with the Bryd Polar Climate Research Center at The Ohio State University to develop engaging video products to enhance our web experience.

2. Leverage the development of Out of School Time (OST) materials for afterschool and summer camp programs. McDonnell and Schofield plan to leverage our efforts with the Byrd Center, The Franklin Institute (Philadelphia PA), and both the Jordana Basin and McMurdo Dry Valleys LTER programs to develop informal science learning programs, called short-term exploratory program (STEP) clubs. We will target youth from underrepresented groups (low income households; first-generation Americans; including first-generation college students from Appalachia). The participating club and camp audiences are in locations that support both rural and urban youth who are underserved and underrepresented. Youth will closely represent the demographics of NJ cities including Newark (51% African American, 41% Hispanic, 7% white and 19% other). Approximately 70% of Newark youth live below 200% of Federal Poverty Level, including Long Branch (14% African American, 28% Latino, 63% white) and Trenton (52% African American, and 28% Latino, 32% white). Our partner, The Franklin Institute, serves a majority-minority population in Philadelphia, PA and summer camp demographics are 95% African American, 3% Caucasian, and 2% Other. Finally, our partner, Rural Action works with high-needs schools in counties that have between 56% and 58% of youth qualifying for free and reduced lunches and less access to healthcare and preschool options than elsewhere in the state of Ohio. Polar CAP will facilitate innovations in STEM OST by focusing on: 1) leveraging data from NSF assets and research programs to connect non-expert audiences to the most remote and perhaps the most important regions for measuring/monitoring climate change; and 2) translating polar research results into outreach products for audiences and measuring these audiences' understanding of and appreciation for Polar Regions. We will develop PAL teaching materials that will be shared among grant partners, including nationally through the 4-H Youth Development network. This networking leverages existing programs to facilitate collaborative development of new programs and resources as well as valuable data on learning experiences in OST environments. We will create transferable informal educator professional development and educational networking opportunities for PAL.

Related Research Projects. PAL-6 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.

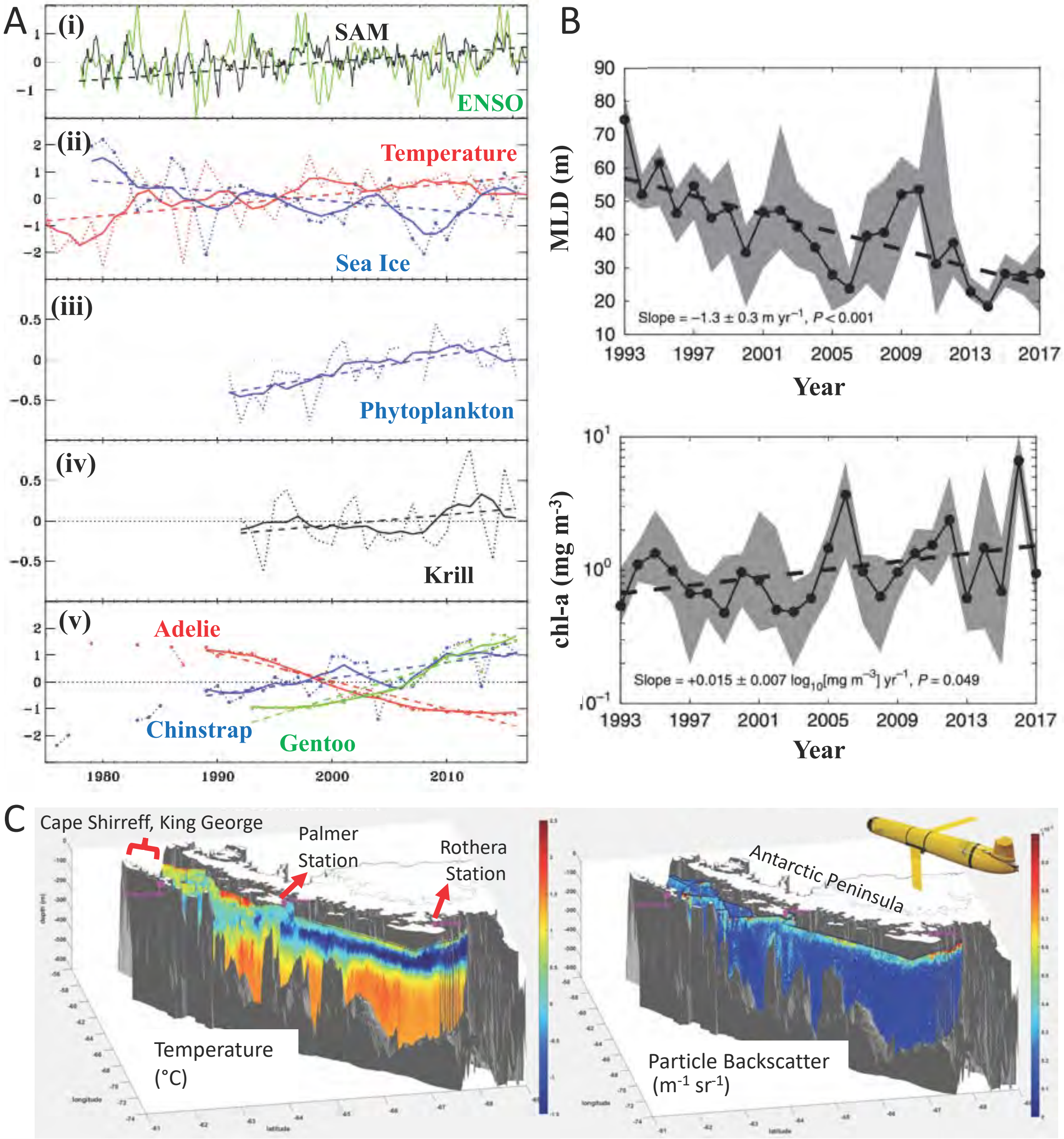

Figure 1. PAL signature long-term datasets and innovative approaches. (A) PAL signature datasets showing annual (dotted) standardized data anomalies, smoothed multi-yearly (solid) variability, and long-term trends (dashed): **(i)** monthly El Niño Southern Oscillation (ENSO) (green), Southern Annular Mode (SAM) (black); **(ii)** winter (Jun-Aug) air temperature (red), PAL annual sea ice season duration (blue); note the sea ice increase during the last decade- the ecosystem response to this reversal in the long-term trend is a focus of PAL-6; **(iii)** seasonally/depth integrated summer phytoplankton (chlorophyll) at Palmer Station; **(iv)** January Antarctic krill abundance in the northern WAP survey grid; **(v)** penguin breeding pairs at Palmer Station by species. **(B)** Time series showing decreasing trends in average mixed layer depth (MLD) and increasing phytoplankton standing stocks (chlorophyll *a*), which are driven in part by increasing sea ice melting, particularly in the southern end of the WAP grid (Brown et al. 2019). **(C)** A nearly 800-km continuous Slocum glider survey along the WAP mapping the water temperature (left) and optical backscatter (right; proportional to particle number and type) from the surface to 1000 m depth. The surveys spanned between the local time series collected by our international collaborators: NOAA and the Argentinians and Germans in the north (Cape Shirreff and King George), and the British in the south (Rothera Station).

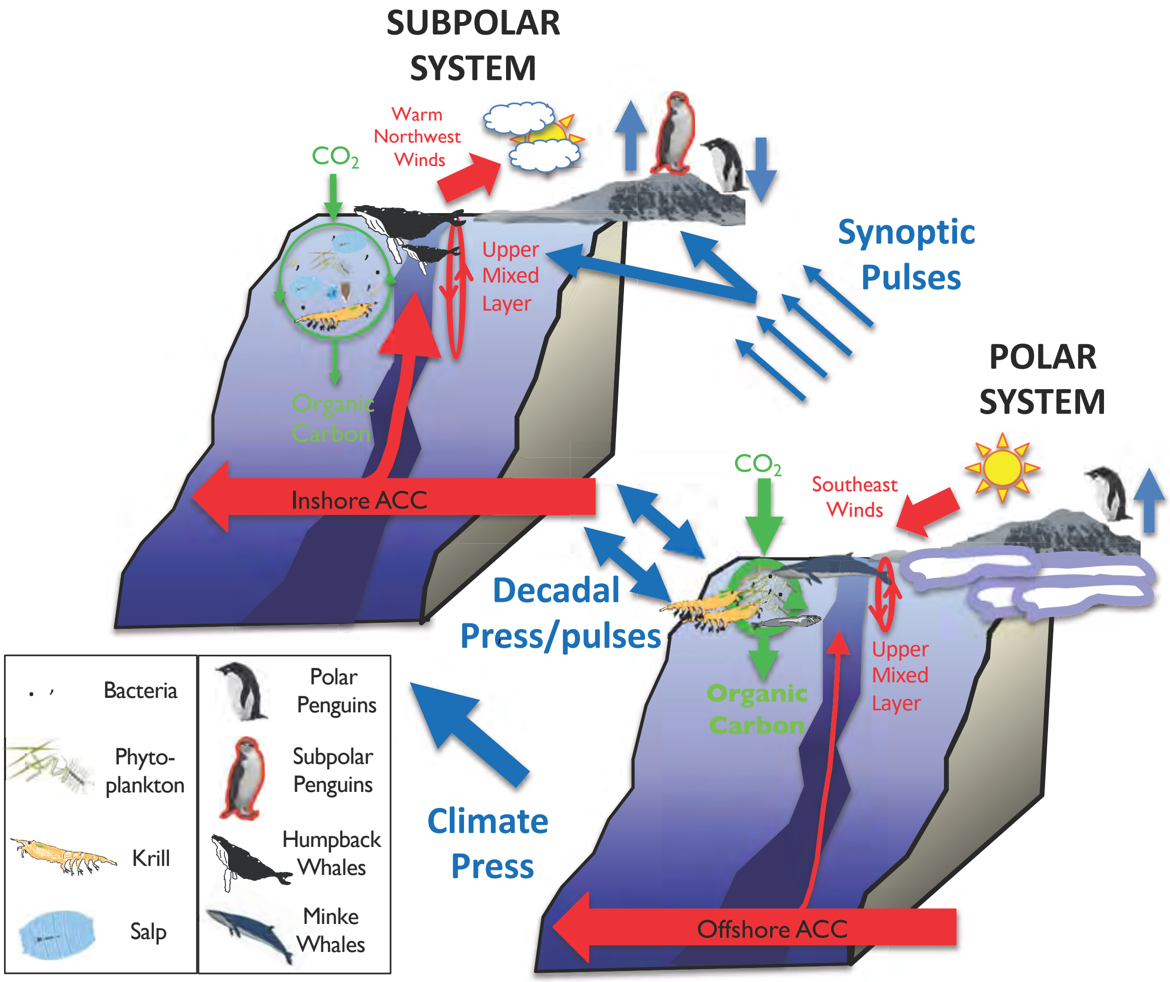

Figure 2. Conceptual Model. PAL spans a space and time climate-biogeographic gradient that has shifted during the program due to local and global atmospheric circulation changes affecting the ocean. The shifting sea-ice structured polar system is being affected by a range of disturbances spanning climate press (long-term warming), interannual to decadal variability (e.g., from ENSO, SAM) and synoptic weather pulses (storms) that affect land and seascapes. The rates/mechanisms of these induced shifts are the focus of PAL-6 research themes. Within the PAL study area, the northern region has/is shifted to a subpolar system whereas the southern region remains a polar system. Shifts from a polar to subpolar system include decreased sea ice, deeper mixed layers, and alterations in winds, cloudiness, snowfall, ocean currents, carbon cycling and predator populations. The polar food web is relatively linear (bacteria-diatoms-krill-fish-predators) and dominated by ice-obligate species including ice fish, Adélie penguins, and Minke whales. The higher primary production and shorter food webs in this system result in high carbon uptake, exchanges, and export. The subpolar system has a more diverse food web (bacteria-multiple phytoplankton-microzooplankton-krill/salps-predators) and includes ice-intolerant species, such as cryptophytes, salps, chinstrap and gentoo penguins, and humpback whales. Lower primary production and multiple trophic transfers makes this primarily a recycling system, leaving less organic carbon for export. How large-scale forcing is structuring local food-webs, oceanography, and biogeochemistry are the focus of Themes A and B. Theme C assesses how changes in the food-web alters biotic interactions from primary producers to predators, and regulates carbon cycling and export. The impact of weather pulses in driving land and seascape environments and food webs is addressed in Theme D.

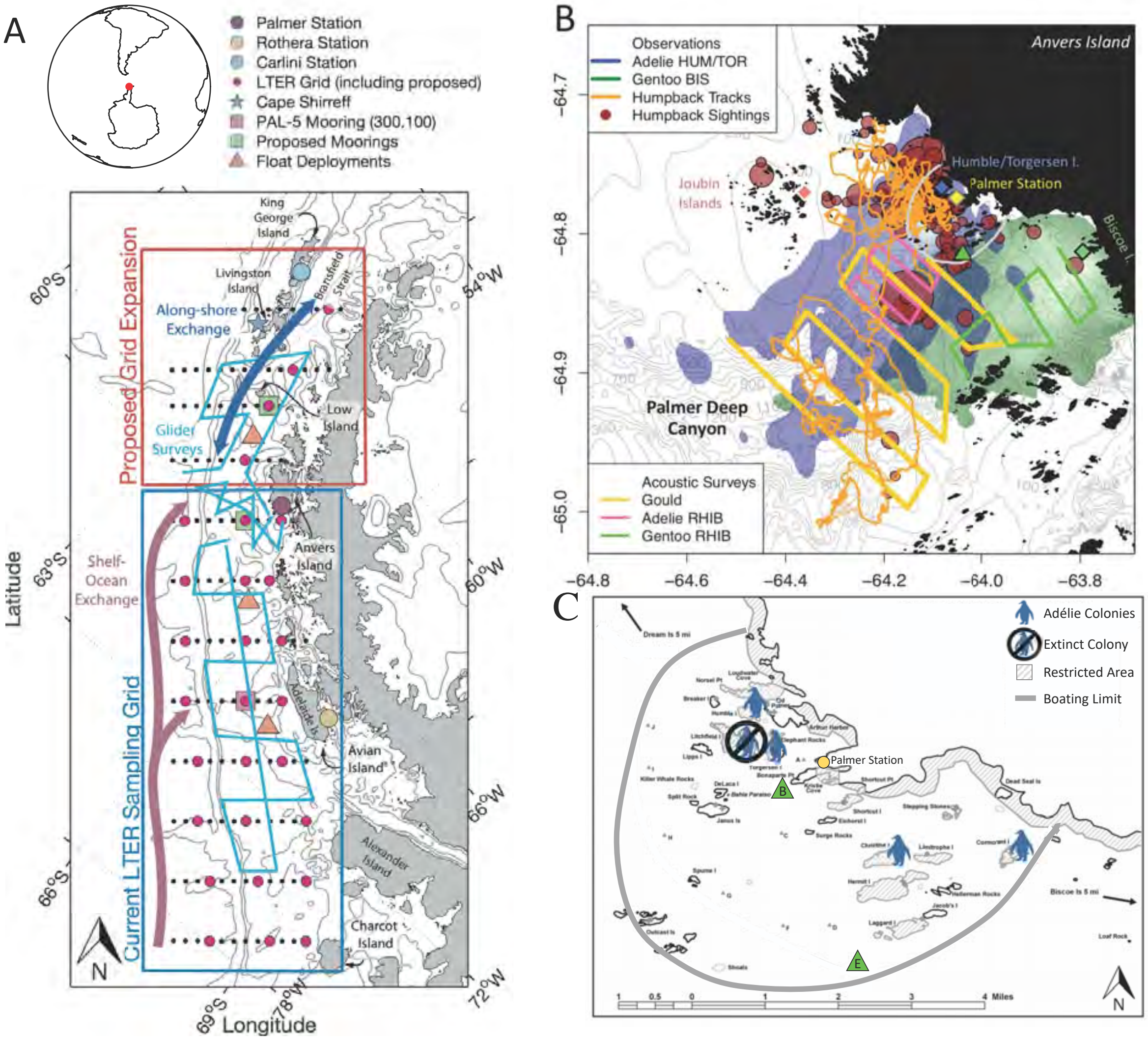

Figure 3. PAL study regions along the WAP, Southern Ocean. (A) Locations of shelf, slope and coastal hydrographic stations within our current sampling grid occupied during the annual summer cruise and proposed expansion, research stations, and proposed instrument deployment locations. Sampling grid lines are 100 km apart in alongshore direction and stations (black and pink dots) are 20 km apart in the onshore-offshore direction. Our main penguin study colonies are on/near Anvers, Avian and Charcot Islands. **(B)** Map of the Palmer Deep Canyon study region near Palmer Station, showing potential acoustic survey grids from the *RV Gould* and Rigid Hull Inflatable Boats (RHIBs), multi-year kernel density estimates of penguin foraging locations, and example humpback whale tracks and sightings (circles sizes are scaled from 1 to 30 individuals) from 2018-19. **(C)** Detailed map of the Palmer Station region within the small boating limit (gray line, also shown in B), showing the locations of active and extinct penguin colonies and long-term sampling stations B and E (triangles).

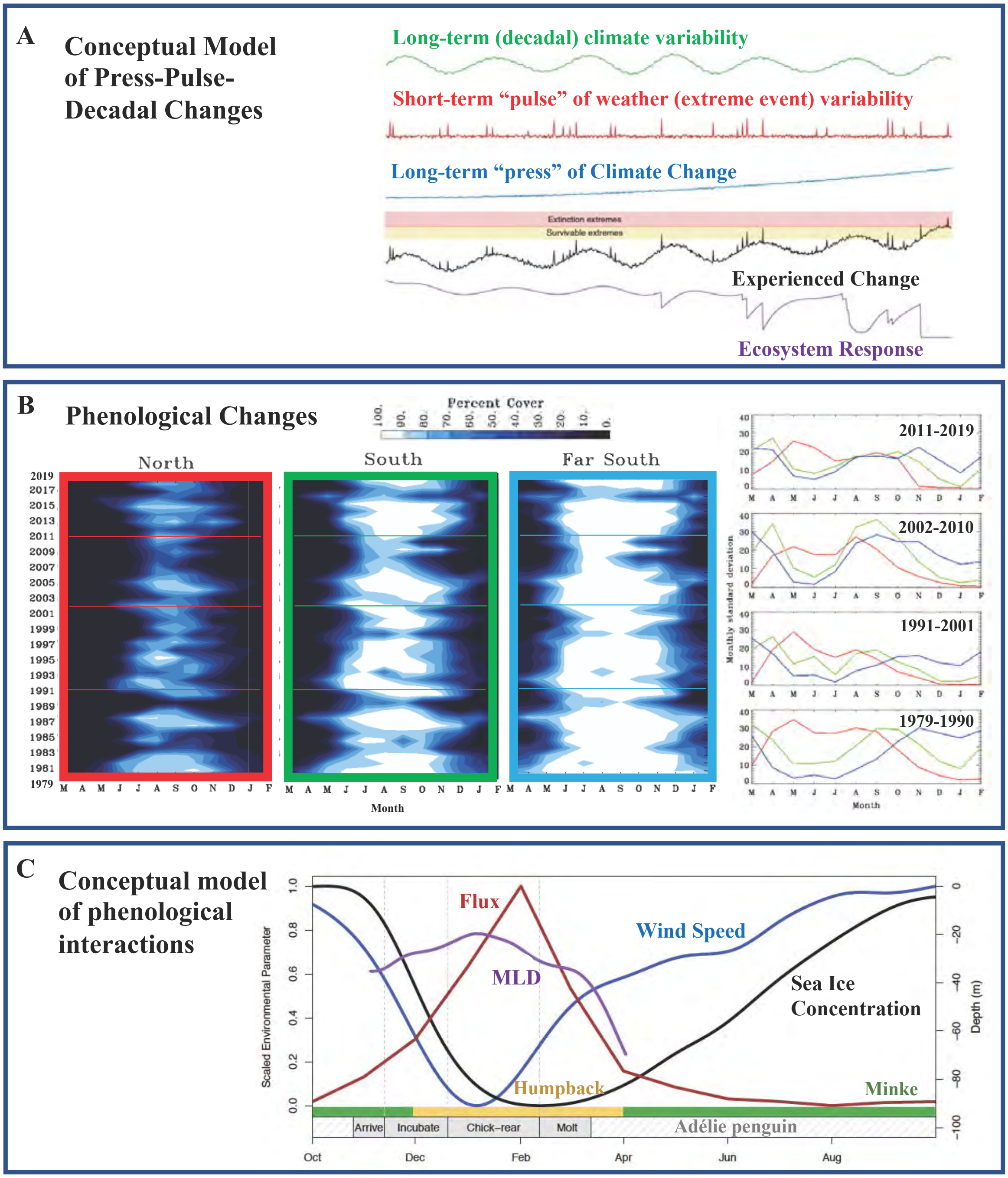

Figure 4. **Research Theme A: Ecological Response to Press-Pulse-Decadal and Seasonal Variability. (A)** Conceptual model for press-pulse framework (Harris et al, 2018); with ongoing climate change and increased pulse events, the threshold between survivable pulse events (yellow) and extinction extremes (pink) is crossed more frequently, preventing recovery. **(B)** Phenological seasonal sea ice changes (1979-2019) for the North (red), South (green) and Far South (blue) coastal regions, and changes in monthly standard deviation (% ice cover) for same regions over the last 4 decades (far right). Illustrative of the WAP 'climate gradient'. **(C)** Conceptual model of seasonal phenological interactions from environmental features (colored lines) to Adélie penguin life cycle events (bottom gray bars), to the presence of minke (bottom green bar) and humpback (bottom yellow bar) whales near Palmer Station.

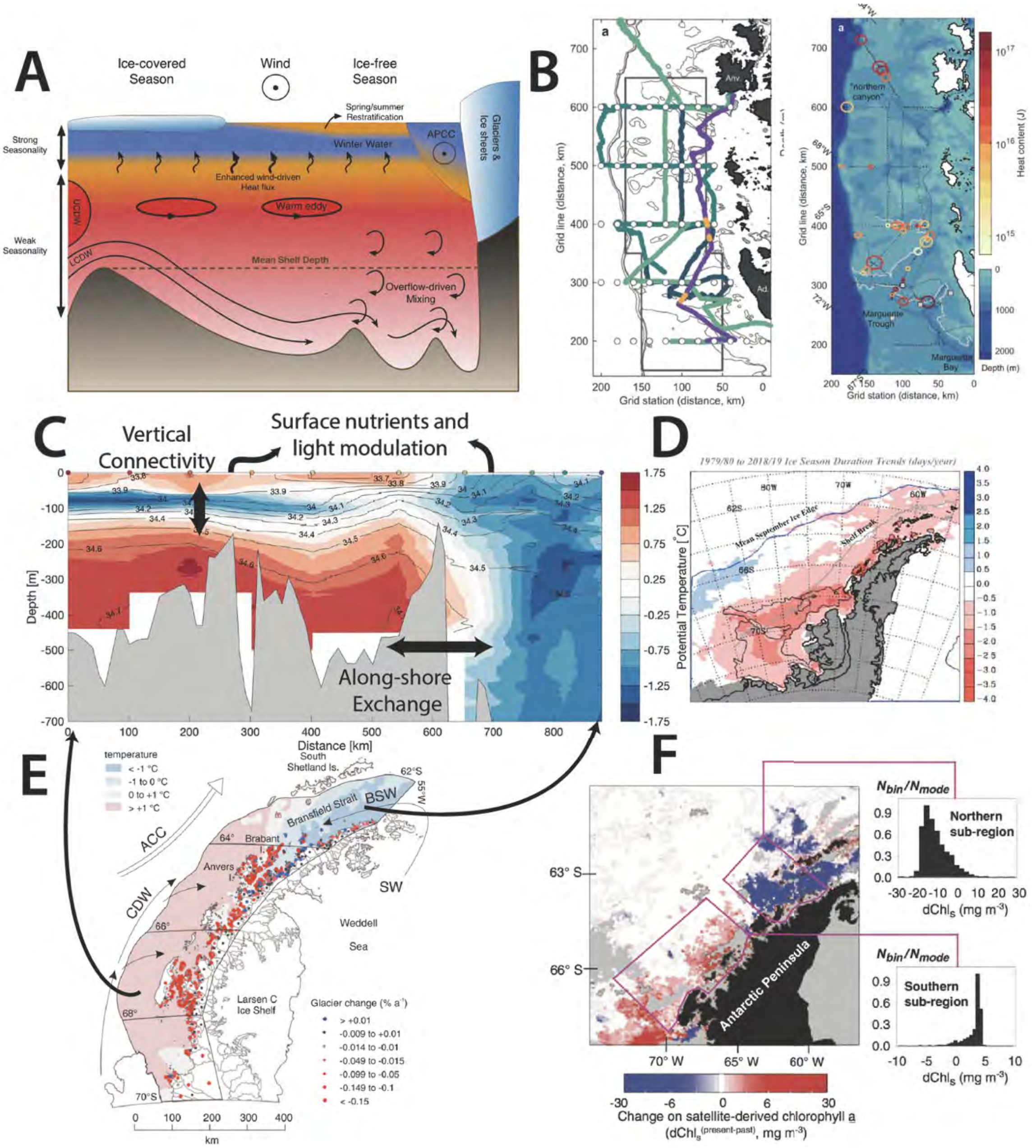

Figure 5. Research Theme B: Vertical & alongshore connectivity processes for physics and biology. **(A)** Two-dimensional circulation and property budget diagram showing key processes studied during PAL-5 (Moffat & Meredith 2018). **(B)** Survey of warm ocean eddies found on submarine canyons on the WAP (Couto et al. 2017). **(C)** Distribution of summer ocean temperature and salinity, showing large changes in hydrographic properties vertically and horizontally along the shelf (modified from Moffat & Meredith 2018). **(D)** Trend in sea-ice season duration, showing larger changes in the southern part of the WAP shelf (Stammerjohn et al. 2015). **(E)** Glacier retreat, where glaciers in the southern WAP shelf are retreating faster (red dots) compared to those in Bransfield Strait, following the ocean temperature (Cook et al. 2009). **(F)** Significant along-shore variation in chlorophyll concentration changes on decadal time-scales, indicating a decrease in the northern Peninsula and an increase in the south; the latter encompasses the current PAL sampling region (Montes-Hugo et al. 2009).

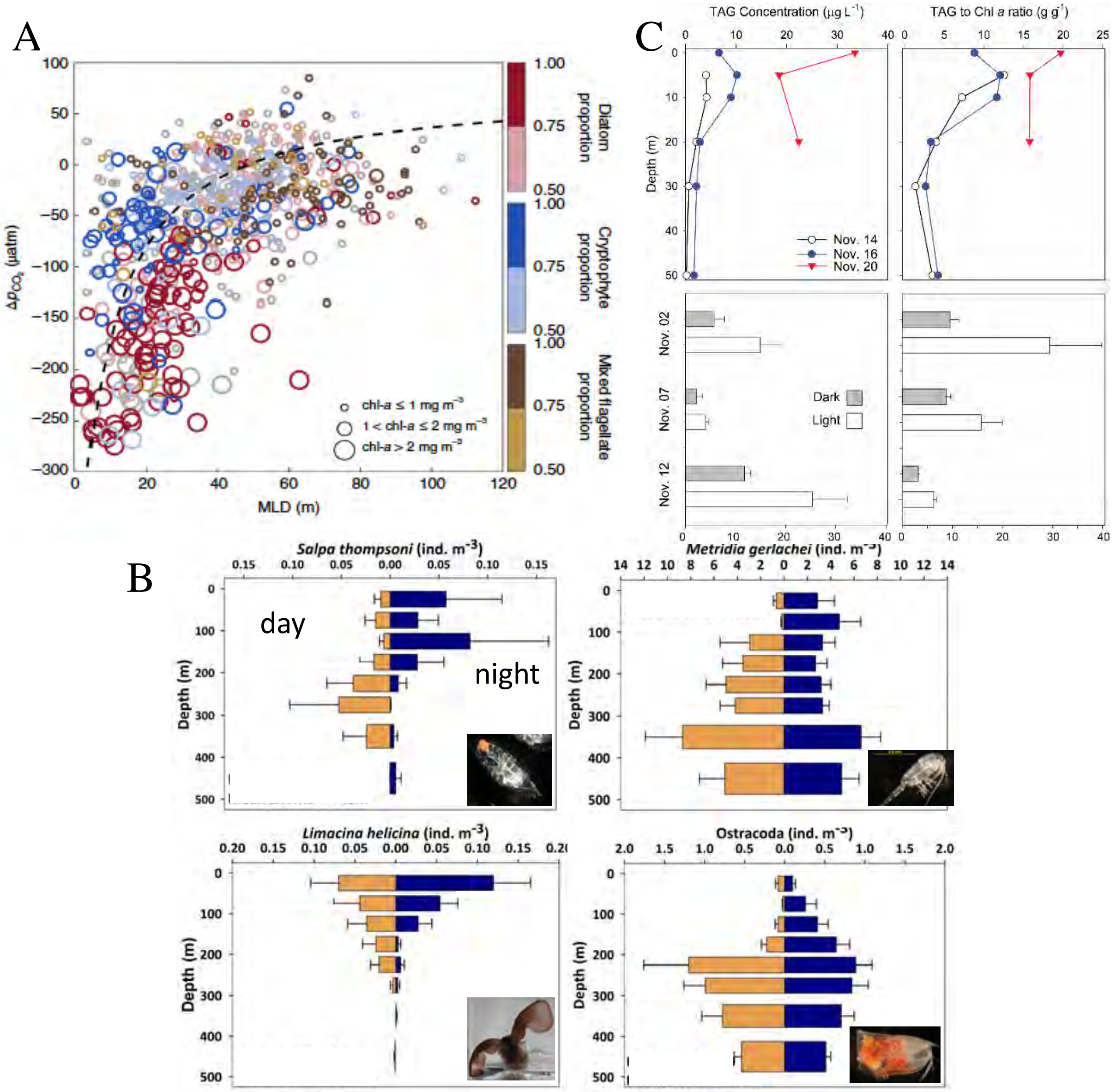

Figure 6. Research Theme C: Food webs and carbon cycling. **(A)** Relationship between PAL summer grid-wide averages of mixed layer depth (MLD) and the air-sea pCO$_2$ difference where negative values indicate undersaturation that drives the transfer of CO$_2$ from the atmosphere to the ocean; phytoplankton community structure marked by symbol color and chlorophyll by symbol size (Brown et al. 2019). **(B)** Diel vertical migration of common zooplankton along the WAP continental shelf (Conroy et al. submitted-b). 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). **(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 rapid production of TAGs in sunlight and consumption in the dark.

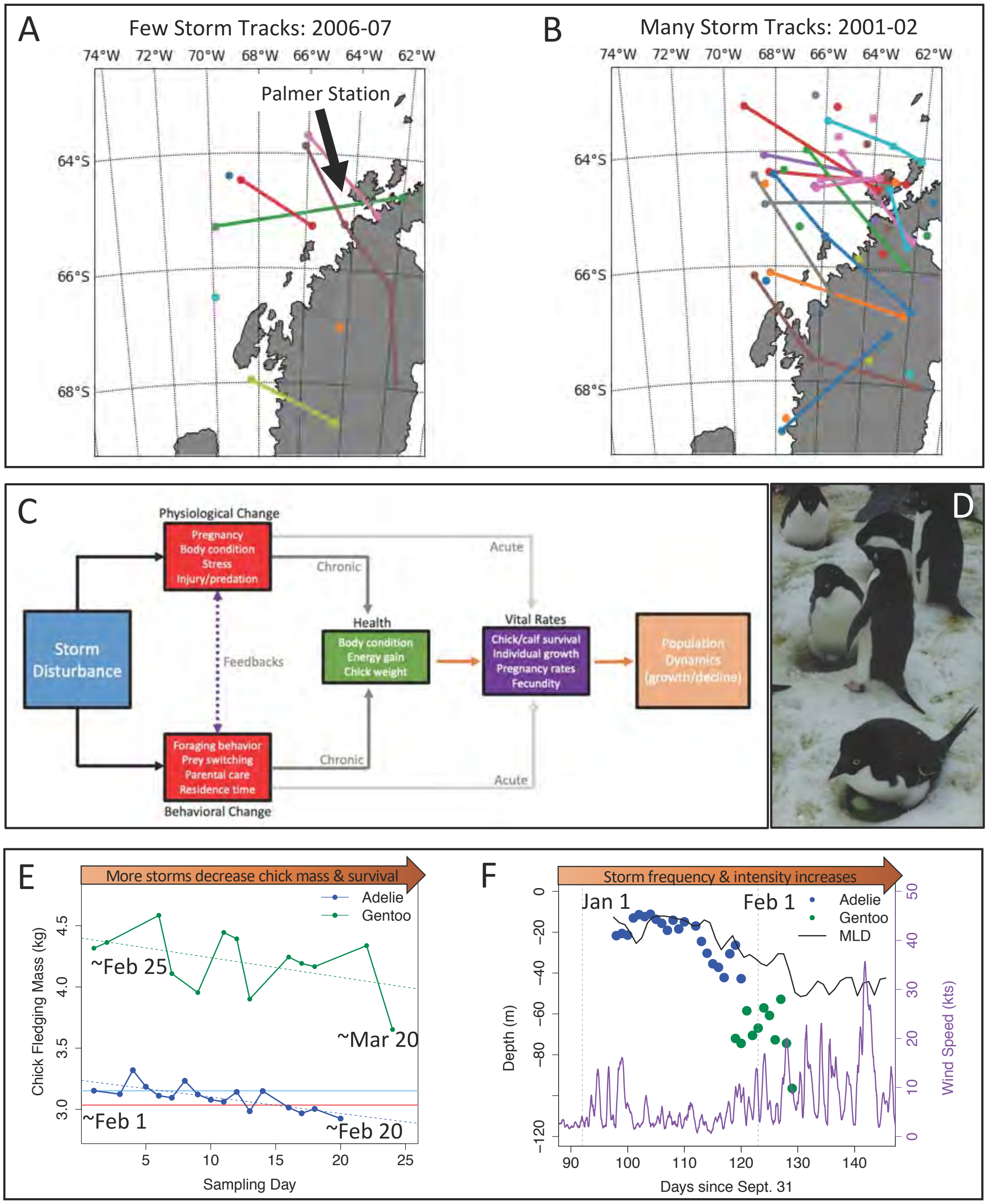

Figure 7. Research Theme D: Disturbance from storms as a control on ecosystem structure. (A,B) Storm tracks along the WAP during austral spring/summer seasons (Oct-Apr) with low (2006-07, A) and high storm intensity (2001-02, B). **(C)** A framework for population consequences of disturbance describing how storms affect the behavior and physiology of krill predators. **(D)** An example of the devasting impact of snow accumulation and meltwater pools on poor egg survival. Near Palmer Station, **(E)** decreasing mean penguin chick fledging mass by day relative to thresholds for surviving (above blue line) and non-surviving (below red line) Adélie chicks, and **(F)** the correspondence of mean glider-derived mixed layer depth (MLD) and penguin dive depth with wind speed by day. We hypothesize that increased storminess from January to March leads to lower chick mass, and thus, survival.

REFERENCES CITED

Bold indicates 10 highlighted LTER publications in the last 6 years, *Italics indicates a LTER publication*, * lead author that is a LTER graduate student or postdoctoral research

Aguiar-Gonzalez B, Moffat C, Sutherland D (in prep) Hydrography of the shelf ocean west of the Antarctic Peninsula: Seasonal and Interannual Variability.

Ainley D, Pauly D (2013) Fishing down the food web of the Antarctic continental shelf and slope. Polar Record 50:92-107

Albertson GR, Friedlaender AS, Steel DJ, Aguayo-Lobo A, Bonatto SL, Caballero S, Flórez-González L (2018) Temporal stability and mixed-stock analyses of humpback whales (Megaptera novaeangliae) in the nearshore waters of the Western Antarctic Peninsula. Polar Biology 41:323-340

Annett AL, Henley SF, Venables HJ, Meredith MP, Clarke A, Ganeshram RS (2017) Silica cycling and isotopic composition in northern Marguerite Bay on the rapidly-warming western Antarctic Peninsula. Deep-Sea Research Part II - Topical Studies in Oceanography 139:132-142

Archibald KM, Siegel DA, Doney SC (2019) Modeling the Impact of Zooplankton Diel Vertical Migration on the Carbon Export Flux of the Biological Pump. Global Biogeochemical Cycles 33:181-199

Atkinson A, Hill SL, Pakhomov EA, Siegel V, Reiss CS, Loeb VJ, Steinberg DK, Schmidt K, Tarling GA, Gerrish L, Sailley SF (2019) Krill (Euphausia superba) distribution contracts southward during rapid regional warming. Nature Climate Change 9:142-147

Avila IC, Dormann CF, García C, Payán LF, Zorrilla MX (2019) Humpback whales extend their stay in a breeding ground in the Tropical Eastern Pacific. ICES Journal of Marine Science 77:109-118

Ballance LT, Pitman RL, Hewitt RP, Siniff DB, Trivelpiece WZ, Clapham PJ, Brownell RL (2006) The Removal of Large Whales from the Southern Ocean: Evidence for Long-Term Ecosystem Effects? In: Brownell RL, Estes JA, Demaster DP, Doak DF, Williams TM (eds) Whales, Whaling, and Ocean Ecosystems. University of California Press, p 215-230

Becker KW, Collins JR, Durham BP, Groussman RD, White AE, Fredricks HF, Ossolinski JE, Repeta DJ, Carini P, Armbrust EV, Van Mooy BAS (2018) Daily changes in phytoplankton lipidomes reveal mechanisms of energy storage in the open ocean. Nature Communications 9:5179

Beirlich K, Dale J, Larsen G, Friedlaender AS, Johnston D (in prep) Seasonal growth rates for individual humpback whales around the Antarctic peninsula.

Bejder M, Johnston DW, Smith J, Friedlaender A, Bejder L (2016) Embracing conservation success of recovering humpback whale populations: Evaluating the case for downlisting their conservation status in Australia. Marine Policy 66:137-141

Bernard KS, Steinberg DK (2013) Krill biomass and aggregation structure in relation to tidal cycle in a penguin foraging region off the Western Antarctic Peninsula. ICES Journal of Marine Science 70:834-849

Bestelmeyer BT, Ellison AM, Fraser WR, Gorman KB, Holbrook SJ, Laney CM, Ohman MD, Peters DPC, Pillsbury FC, Rassweiler A, Schmitt RJ, Sharma S (2011) Analysis of abrupt transitions in ecological systems. Ecosphere 2:art129

Boersma PD, Rebstock GA (2014) Climate change increases reproductive failure in Magellanic penguins. PLoS One 9:e85602-e85602

Bonan GB, Doney SC (2018) Climate, ecosystems, and planetary futures: The challenge to predict life in Earth system models. Science 359:eaam8328

Bottino NR (1974) The fatty acids of antarctic phytoplankton and euphausiids. Fatty acid exchange among trophic levels of the Ross Sea. Marine Biology 27:197-204

Boucek RE, Rehage JS (2014) Climate extremes drive changes in functional community structure. Global Change Biology 20:1821-1831

**Bowman JS, Kavanaugh MT, Doney SC, Ducklow HW (2018) Recurrent seascape units identify key ecological processes along the western Antarctic Peninsula. Global Change Biology 24:3065-3078*

Boyd PW, Lennartz ST, Glover DM, Doney SC (2015) Biological ramifications of climate-change-mediated oceanic multi-stressors. Nature Climate Change 5:71-79

Boyd PW, Cornwall CE, Davison A, Doney SC, Fourquez M, Hurd CL, Lima ID, McMinn A (2016) Biological responses to environmental heterogeneity under future ocean conditions. Global Change Biology 22:2633-2650

Brearley JA, Moffat C, Venables HJ, Meredith MP, Dinniman MS (2019) The Role of Eddies and Topography in the Export of Shelf Waters From the West Antarctic Peninsula Shelf. Journal of Geophysical Research: Oceans 124:7718-7742

****Brown MS, Munro DR, Feehan CJ, Sweeney C, Ducklow HW, Schofield OM (2019) Enhanced oceanic CO2 uptake along the rapidly changing West Antarctic Peninsula. Nature Climate Change 9:678-683***

Brown ZW, Arrigo KR (2012) Contrasting trends in sea ice and primary production in the Bering Sea and Arctic Ocean. ICES Journal of Marine Science 69:1180-1193

**Brum JR, Hurwitz BL, Schofield O, Ducklow HW, Sullivan MB (2016) Seasonal time bombs: dominant temperate viruses affect Southern Ocean microbial dynamics. The ISME Journal 10:437-449*

**Carvalho F, Kohut J, Oliver MJ, Sherrell RM, Schofield O (2016) Mixing and phytoplankton dynamics in a submarine canyon in the West Antarctic Peninsula. Journal of Geophysical Research: Oceans 121:5069-5083*

**Carvalho F, Fitzsimmons JN, Couto N, Waite N, Gorbunov M, Kohut J, Oliver MJ, Sherrell RM, Schofield O (2019) Testing the Canyon Hypothesis: Evaluating light and nutrient controls of phytoplankton growth in penguin foraging hotspots along the West Antarctic Peninsula. Limnology and Oceanography*

Cavan EL, Belcher A, Atkinson A, Hill SL, Kawaguchi S, McCormack S, Meyer B, Nicol S, Ratnarajah L, Schmidt K, Steinberg DK, Tarling GA, Boyd PW (2019) The importance of Antarctic krill in biogeochemical cycles. Nat Commun 10:4742

Chapin III FS, Berman M, Callaghan TV, Convey P, Crepin A-S, Danell K, Ducklow H, Forbes B, Kofinas GP, McGuire AD, Nuttall M, Virginia RA, Young O, Zimov SA (2005) Polar Systems. In: Hassan R, Scholes R, Ash N (eds) Ecosystems and Human Well-being: Current State and Trends. Island Press, Washington, DC

Chapman EW, Hofmann EE, Patterson DL, Fraser WR (2010) The effects of variability in Antarctic krill (Euphausia superba) spawning behavior and sex/maturity stage distribution on Adélie penguin (Pygoscelis adeliae) chick growth: A modeling study. Deep Sea Research Part II: Topical Studies in Oceanography 57:543-558

Chapman EW, Hofmann EE, Patterson DL, Ribic CA, Fraser WR (2011) Marine and terrestrial factors affecting Adélie -penguin Pygoscelis adeliae chick growth and recruitment off the western Antarctic Peninsula. Marine Ecology Progress Series 436:273-289

Chappell MA, Morgan KR, Souza SL, Bucher TL (1989) Convection and thermoregulation in two Antarctic seabirds. Journal of Comparative Physiology B 159:313-322

****Cimino MA, Fraser WR, Patterson-Fraser DL, Saba VS, Oliver MJ (2014) Large-scale climate and local weather drive interannual variability in Adélie penguin chick fledging mass. Marine Ecology Progress Series 513:253-268***

**Cimino MA, Lynch HJ, Saba VS, Oliver MJ (2016a) Projected asymmetric response of Adélie penguins to Antarctic climate change. Scientific Reports 6:28785*

**Cimino MA, Moline MA, Fraser WR, Patterson-Fraser DL, Oliver MJ (2016b) Climate-driven sympatry may not lead to foraging competition between congeneric top-predators. Scientific Reports 6:18820*

Cimino MA, Patterson-Fraser DL, Stammerjohn S, Fraser WR (2019) The interaction between island geomorphology and environmental parameters drives Adélie penguin breeding phenology on neighboring islands near Palmer Station, Antarctica. Ecology and Evolution 9:9334-9349

Cimino MA, Friedlaender AS, Nichols R, Patterson-Fraser DL, Fraser W (in prep) Debunking the competitive exclusion hypotheses between penguins and whales on the West Antarctic Peninsula.

Clark EB, Branch A, Chien S, Mirza F, Farrara JD, Chao Y, Fratantoni D, Aragon D, Schofield O, Flexas MM, Thompson A (2019) Station-Keeping Underwater Gliders Using a Predictive Ocean Circulation Model and Applications to SWOT Calibration and Validation. IEEE Journal of Oceanic Engineering:1-14

Clarke A, Murphy EJ, Meredith MP, King JC, Peck LS, Barnes DKA, Smith RC (2007) Climate change and the marine ecosystem of the western Antarctic Peninsula. Philosophical transactions of the Royal Society of London Series B, Biological sciences 362:149-166

Clarke A, Meredith MP, Wallace MI, Brandon MA, Thomas DN (2008) Seasonal and interannual variability in temperature, chlorophyll and macronutrients in northern Marguerite Bay, Antarctica. Deep Sea Research Part II: Topical Studies in Oceanography 55:1988-2006

Clarke A, Barnes DKA, Bracegirdle TJ, Ducklow H, King JC, Meredith M, Murphy E, Peck LS (2012) The impact of regional climate change on the marine ecosystem of the western Antarctic Peninsula. In: Rogers AD, Johnston NM, Murphy E, Clarke A (eds) Antarctic ecosystems: an extreme environment in a changing world. Wiley-Blackwell, Oxford, p 91-120

Collins JR, Edwards BR, Fredricks HF, Van Mooy BAS (2016) LOBSTAHS: An Adduct-Based Lipidomics Strategy for Discovery and Identification of Oxidative Stress Biomarkers. Analytical Chemistry 88:7154-7162

Collins JR, Fredricks HF, Bowman JS, Ward CP, Moreno C, Longnecker K, Marchetti A, Hansel CM, Ducklow HW, Van Mooy BAS (2018) The molecular products and biogeochemical significance of lipid photooxidation in West Antarctic surface waters. Geochimica et Cosmochimica Acta 232:244-264

Collins SL, Carpenter SR, Swinton SM, Orenstein DE, Childers DL, Gragson TL, Grimm NB, Grove JM, Harlan SL, Kaye JP, Knapp AK, Kofinas GP, Magnuson JJ, McDowell WH, Melack JM, Ogden LA, Robertson GP, Smith MD, Whitmer AC (2011) An integrated conceptual framework for long-term social–ecological research. Frontiers in Ecology and the Environment 9:351-357

**Conroy JA, Reiss CS, Gleiber MR, Steinberg DK (submitted-a) Krill larval production and recruitment along the Antarctic Peninsula. Integrative and Comparative Biology*

**Conroy JA, Steinberg DK, Thibodeau PS, Schofield O (submitted-b) Zooplankton diel vertical migration during Antarctic summer. Deep Sea Research Part I: Oceanographic Research Papers*

Convey P, Chown SL, Clarke A, Barnes DKA, Bokhorst S, Cummings V, Ducklow H, Frati F, Green TGA, Gordon S, Griffiths HJ, Howard-Williams C, Huiskes AHL, Laybourn-Parry J, Lyons WB, McMinn A, Morley SA, Peck LS, Quesada A, Robinson SA, Shiaparelli S, Wall DH (2014) The spatial structure of Antarctic biodiversity. Ecological Monographs 84:203-244

Cook AJ, Holland PR, Meredith MP, Murray T, Luckman A, Vaughan DG (2016) Ocean forcing of glacier retreat in the western Antarctic Peninsula. Science 353:283-286

****Couto N, Martinson DG, Kohut J, Schofield O (2017a) Distribution of Upper Circumpolar Deep Water on the warming continental shelf of the West Antarctic Peninsula. Journal of Geophysical Research: Oceans 122:5306-5315***

**Couto N, Kohut J, Schofield O, Dinniman MS, Graham J (2017b) Pathways and retention times in a biologically productive canyon system on the West Antarctic Peninsula MTS/IEEE OCEANS - 2017, Anchorage, AK*

Croll DA, Marinovic B, Benson S, Chavez FP, Black N, Ternullo R, Tershy BR (2005) From wind to whales: trophic links in a coastal upwelling system. Marine Ecology Progress Series 289:117-130

Curtice C, Johnston DW, Ducklow H, Gales N, Halpin PN, Friedlaender AS (2015) Modeling the spatial and temporal dynamics of foraging movements of humpback whales (Megaptera novaeangliae) in the Western Antarctic Peninsula. Movement Ecology 3:13

Dee DP, Uppala SM, Simmons AJ, Berrisford P, Poli P, Kobayashi S, Andrae U, Balmaseda MA, Balsamo G, Bauer P, Bechtold P, Beljaars ACM, van de Berg L, Bidlot J, Bormann N, Delsol C, Dragani R, Fuentes M, Geer AJ, Haimberger L, Healy SB, Hersbach H, Hólm EV, Isaksen L, Kållberg P, Köhler M, Matricardi M, McNally AP, Monge-Sanz BM, Morcrette J-J, Park B-K, Peubey C, de Rosnay P, Tavolato C, Thépaut J-N, Vitart F (2011) The ERA-Interim reanalysis: configuration and performance of the data assimilation system. Quarterly Journal of the Royal Meteorological Society 137:553-597

Dietze MC (2017) Ecological Forecasting, Vol. Princeton University Press

Dinniman MS, Klinck JM (2004) A model study of circulation and cross-shelf exchange on the west Antarctic Peninsula continental shelf. Deep Sea Research Part II: Topical Studies in Oceanography 51:2003-2022

Dinniman MS, Klinck JM, Hofmann EE (2012) Sensitivity of Circumpolar Deep Water Transport and Ice Shelf Basal Melt along the West Antarctic Peninsula to Changes in the Winds. Journal of Climate 25:4799-4816

Djurhuus A, Pitz K, Sawaya NA, Rojas-Márquez J, Michaud B, Montes E, Muller-Karger F, Breitbart M (2018) Evaluation of marine zooplankton community structure through environmental DNA metabarcoding. Limnology and Oceanography: Methods 16:209-221

Ducklow H, Steinberg DK, Buesseler KO (2001) Upper ocean carbon export and the biological pump. Oceanography 14:50-58

Ducklow H, Clarke A, Dickhut R, Doney SC, Geisz H, Huang K, Martinson D, Meredith MP, Moeller HV, Montes-Hugo M, Schofield O, Stammerjohn S, Steinberg DK, Fraser W (2012a) The Marine Ecosystem of the West Antarctic Peninsula. In: Rogers A, Johnston N, Clarke A, Murphy E (eds) Antarctica: An Extreme Environment in a Changing World. Blackwell, London

Ducklow H, Doney SC, Sailley SF (2015) Ecological controls on biogeochemical fluxes in the western Antarctic Peninsula studied with an inverse food-web model. Advances in Polar Science 26:122-139

Ducklow HW, Fraser W, Karl DM, Quetin LB, Ross RM, Smith RC, Stammerjohn SE, Vernet M, Daniels RM (2006) Water-column processes in the West Antarctic Peninsula and the Ross Sea: Interannual variations and foodweb structure. Deep Sea Research Part II: Topical Studies in Oceanography 53:834-852

Ducklow HW, Baker K, Martinson DG, Quetin LB, Ross RM, Smith RC, Stammerjohn SE, Vernet M, Fraser W (2007) Marine pelagic ecosystems: the West Antarctic Peninsula. Philosophical Transactions of the Royal Society B: Biological Sciences 362:67-94

Ducklow HW, Erickson M, Kelly J, Montes-Hugo M, Ribic CA, Smith RC, Stammerjohn SE, Karl DM (2008) Particle export from the upper ocean over the continental shelf of the west Antarctic Peninsula: A long-term record, 1992–2007. Deep Sea Research Part II: Topical Studies in Oceanography 55:2118-2131

Ducklow HW, Schofield O, Vernet M, Stammerjohn S, Erickson M (2012b) Multiscale control of bacterial production by phytoplankton dynamics and sea ice along the western Antarctic Peninsula: A regional and decadal investigation. Journal of Marine Systems 98-99:26-39

Ducklow HW, Fraser WR, Meredith MP, Stammerjohn SE, Doney SC, Martinson DG, Sailley SF, Schofield OM, Steinberg DK, Venables HJ, Amsler CD (2013) West Antarctic Peninsula: An Ice-Dependent Coastal Marine Ecosystem in Transition. Oceanography 26:190-203

Ducklow HW, Stukel MR, Eveleth R, Doney SC, Jickells T, Schofield O, Baker AR, Brindle J, Chance R, Cassar N (2018) Spring-summer net community production, new production, particle export and related water column biogeochemical processes in the marginal sea ice zone of the Western Antarctic Peninsula 2012-2014. Philosophical Transactions of the Royal Society A: Mathematical, Physical and Engineering Sciences 376:20170177

**Eveleth R, Cassar N, Doney SC, Munro DR, Sweeney C (2017) Biological and physical controls on O2/Ar, Ar and pCO2 variability at the Western Antarctic Peninsula and in the Drake Passage. Deep Sea Research Part II: Topical Studies in Oceanography 139:77-88*

Falkowski PG, Lin H, Gorbunov MY (2017) What limits photosynthetic energy conversion efficiency in nature? Lessons from the oceans. Philosophical transactions of the Royal Society of London Series B, Biological sciences 372

Forster M, Bestelmeyer S, Baez-Rodriguez N, Berkowitz A, Caplan B, Esposito E, McGee S (2018) Data Jams. The Science Teacher 86:48-53

Fountain AG, Saba G, Adams B, Doran P, Fraser W, Gooseff M, Obryk M, Priscu JC, Stammerjohn S, Virginia RA (2016) The Impact of a Large-Scale Climate Event on Antarctic Ecosystem Processes. BioScience 66:848-863

Fraser W, Trivelpiece W (1996) Factors Controlling the Distribution of Seabirds: Winter-Summer Heterogeneity in the Distribution of AdéLie Penguin Populations. In: Foundations for Ecological Research West of the Antarctic Peninsula, Vol 70, p 257-272

Fraser W, Hofmann EE (2003) A predator's perspective on causal links between climate change, physical forcing and ecosystem response. Marine Ecology Progress Series 265:1-15

Fraser WR, Trivelpiece WZ, Ainley DG, Trivelpiece SG (1992) Increases in Antarctic penguin populations: reduced competition with whales or a loss of sea ice due to environmental warming? Polar Biology 11:525-531

Fraser WR, Patterson-Fraser DL, Ribic CA, Schofield O, Ducklow H (2013) A Nonmarine Source of Variability in Adélie Penguin Demography. Oceanography 26:207-209

Friedlaender AS, Tyson RB, Stimpert AK, Read AJ, Nowacek DP (2013) Extreme diel variation in the feeding behavior of humpback whales along the western Antarctic Peninsula during autumn. Marine Ecology Progress Series 494:281-289

Friedlaender AS, Johnston DW, Tyson RB, Kaltenberg A, Goldbogen JA, Stimpert AK, Curtice C, Hazen EL, Halpin PN, Read AJ, Nowacek DP (2016) Multiple-stage decisions in a marine central-place forager. Royal Society Open Science 3:160043

Friedlaender AS, Cade D, Johnston D, Nowacek DP, Nichols R, Goldbogen JA (in prep) Foraging ecology of Antarctic baleen whales: sympathy and niche separation.

Fulton JM, Fredricks HF, Van Mooy BAS (2017) Intact polar lipid export in the temperate western North Atlantic and Sargasso Sea. Organic Geochemistry 114:45-56

Gaiser EE, Bell DM, Castorani MCN, Childers DL, Groffman PM, Jackson CR, Kominoski JS, Peters DPC, Pickett STA, Ripplinger J, Zinnert JC (2020) Long-Term Ecological Research and Evolving Frameworks of Disturbance Ecology. BioScience 70:141-156

**Garzio LM, Steinberg DK, Erickson M, Ducklow HW (2013) Microzooplankton grazing along the Western Antarctic Peninsula. Aquatic Microbial Ecology 70:215-232*

**Gleiber MR, Steinberg DK, Ducklow HW (2012) Time series of vertical flux of zooplankton fecal pellets on the continental shelf of the western Antarctic Peninsula. Marine Ecology Progress Series 471:23-36*

Graham JA, Dinniman MS, Klinck JM (2016) Impact of model resolution for on-shelf heat transport along the West Antarctic Peninsula. Journal of Geophysical Research: Oceans 121:7880-7897

Grise KM, Son S-W, Gyakum JR (2013) Intraseasonal and Interannual Variability in North American Storm Tracks and Its Relationship to Equatorial Pacific Variability. Monthly Weather Review 141:3610-3625

*Gruber N, Clement D, Carter BR, Feely RA, van Heuven S, Hoppema M, Ishii M, Key RM, Kozyr A, Lauvset SK, Lo Monaco C, Mathis JT, Murata A, Olsen A, Perez FF, Sabine CL, Tanhua T, Wanninkhof R (2019) The oceanic sink for anthropogenic CO₂ from 1994 to 2007. Science 363:1193-1199

Gunderson LH (2000) Ecological Resilience—In Theory and Application. Annual Review of Ecology and Systematics 31:425-439

Hagen W, Schnack-Schiel SB (1996) Seasonal lipid dynamics in dominant Antarctic copepods: Energy for overwintering or reproduction? Deep Sea Research Part I: Oceanographic Research Papers 43:139-158

Harris RMB, Beaumont LJ, Vance TR, Tozer CR, Remenyi TA, Perkins-Kirkpatrick SE, Mitchell PJ, Nicotra AB, McGregor S, Andrew NR, Letnic M, Kearney MR, Wernberg T, Hutley LB, Chambers LE, Fletcher MS, Keatley MR, Woodward CA, Williamson G, Duke NC, Bowman DMJS (2018) Biological responses to the press and pulse of climate trends and extreme events. Nature Climate Change 8:579-587

Hart T (1942) Phytoplankton periodicity in Antarctic surface waters. Discovery Reports 21:261-356

Hauck J, Völker C, Wolf-Gladrow DA, Laufkötter C, Vogt M, Aumont O, Bopp L, Buitenhuis ET, Doney SC, Dunne J, Gruber N, Hashioka T, John J, Quéré CL, Lima ID, Nakano H, Séférian R, Totterdell I (2015) On the Southern Ocean CO2 uptake and the role of the biological carbon pump in the 21st century. Global Biogeochemical Cycles 29:1451-1470

Hauri C, Doney SC, Takahashi T, Erickson M, Jiang G, Ducklow HW (2015) Two decades of inorganic carbon dynamics along the West Antarctic Peninsula. Biogeosciences 12:6761-6779

Henley SF, Schofield OM, Hendry KR, Schloss IR, Steinberg DK, Moffat C, Peck LS, Costa DP, Bakker DCE, Hughes C, Rozema PD, Ducklow HW, Abele D, Stefels J, Van Leeuwe MA, Brussaard CPD, Buma AGJ, Kohut J, Sahade R, Friedlaender AS, Stammerjohn SE, Venables HJ, Meredith MP (2019) Variability and change in the west Antarctic Peninsula marine system: Research priorities and opportunities. Progress in Oceanography 173:208-237

Hobbs WR, Massom R, Stammerjohn S, Reid P, Williams G, Meier W (2016) A review of recent changes in Southern Ocean sea ice, their drivers and forcings. Global and Planetary Change 143:228-250

Holland PR, Bracegirdle TJ, Dutrieux P, Jenkins A, Steig EJ (2019) West Antarctic ice loss influenced by internal climate variability and anthropogenic forcing. Nature Geoscience 12:718-724

Holm HC, Collins JR, Lowenstein DP, Schrage K, Van Mooy BAS (in prep-a) Energy storage lipids off the West Antarctica Peninsula.

Holm HC, Conroy J, Collins JR, Schrage K, Lowenstein DP, Steinberg DK, Van Mooy BAS (in prep-b) The nexus of UV light, lipid peroxidation, and krill off the West Antarctic Peninsula.

Hoskins BJ, Hodges KI (2005) A New Perspective on Southern Hemisphere Storm Tracks. Journal of Climate 18:4108-4129

Hughes TP, Kerry JT, Álvarez-Noriega M, Álvarez-Romero JG, Anderson KD, Baird AH, Babcock RC, Beger M, Bellwood DR, Berkelmans R, Bridge TC, Butler IR, Byrne M, Cantin NE, Comeau S, Connolly SR, Cumming GS, Dalton SJ, Diaz-Pulido G, Eakin CM, Figueira WF, Gilmour JP, Harrison HB, Heron SF, Hoey AS, Hobbs J-PA, Hoogenboom MO, Kennedy EV, Kuo C-y, Lough JM, Lowe RJ, Liu G, McCulloch MT, Malcolm HA, McWilliam MJ, Pandolfi JM, Pears RJ, Pratchett MS, Schoepf V, Simpson T, Skirving WJ, Sommer B, Torda G, Wachenfeld DR, Willis BL, Wilson SK (2017) Global warming and recurrent mass bleaching of corals. Nature 543:373-377

Jentsch A, White P (2019) A theory of pulse dynamics and disturbance in ecology. Ecology 100:e02734

Johnson JM, Moore LJ, Ells K, Murray AB, Adams PN, MacKenzie III RA, Jaeger JM (2015) Recent shifts in coastline change and shoreline stabilization linked to storm climate change. Earth Surface Processes and Landforms 40:569-585

Jónasdóttir SH, Visser AW, Richardson K, Heath MR (2015) Seasonal copepod lipid pump promotes carbon sequestration in the deep North Atlantic. Proceedings of the National Academy of Sciences 112:12122-12126

**Kahl LA, Schofield O, Fraser WR (2010) Autonomous Gliders Reveal Features of the Water Column Associated with Foraging by Adélie Penguins. Integrative and Comparative Biology 50:1041-1050*

Karp-Boss L, Azevedo L, Boss E (2007) LISST-100 measurements of phytoplankton size distribution: evaluation of the effects of cell shape. Limnology and Oceanography: Methods 5:396-406

Kattner G, Graeve M, Hagen W (2012) Energy reserves of Southern Ocean copepods: Triacylglycerols with unusually long-chain monounsaturated fatty acids. Marine Chemistry 138-139:7-12

****Kavanaugh MT, Abdala FN, Ducklow H, Glover D, Fraser W, Martinson D, Stammerjohn S, Schofield O, Doney SC (2015) Effect of continental shelf canyons on phytoplankton biomass and community composition along the western Antarctic Peninsula. Marine Ecology Progress Series 524:11-26***

Kearney WS, Fernandes A, Fagherazzi S (2019) Sea-level rise and storm surges structure coastal forests into persistence and regeneration niches. PLoS One 14:1-14

**Kim H, Doney SC, Iannuzzi RA, Meredith MP, Martinson DG, Ducklow HW (2016) Climate forcing for dynamics of dissolved inorganic nutrients at Palmer Station, Antarctica: An interdecadal (1993–2013) analysis. Journal of Geophysical Research: Biogeosciences 121:2369-2389*

***Kim H, Ducklow HW, Abele D, Barlett EMR, Buma AGJ, Meredith MP, Rozema PD, Schofield OM, Venables HJ, Schloss IR (2018) Inter-decadal variability of phytoplankton biomass along the coastal West Antarctic Peninsula. Philosophical Transactions of the Royal Society A: Mathematical, Physical and Engineering Sciences 376:20170174**

**Kim H, Luo YW, Ducklow H, Schofield O, Steinberg DK, Doney SC (in prep) Quantifying microbial control of marine planktonic carbon and biogeochemical cycling in a warming coastal Antarctic ecosystem by data assimilation modeling.*

Klinck JM (1998) Heat and salt changes on the continental shelf west of the Antarctic Peninsula between January 1993 and January 1994. Journal of Geophysical Research: Oceans 103:7617-7636

Kohout AL, Williams MJM, Dean SM, Meylan MH (2014) Storm-induced sea-ice breakup and the implications for ice extent. Nature 509:604-607

Kohut JT, Winsor P, Statscewich H, Oliver MJ, Fredj E, Couto N, Bernard K, Fraser W (2018) Variability in summer surface residence time within a West Antarctic Peninsula biological hotspot. Philosophical Transactions of the Royal Society A: Mathematical, Physical and Engineering Sciences 376:20170165

Kuzminov FI, Gorbunov MY (2016) Energy dissipation pathways in Photosystem 2 of the diatom, Phaeodactylum tricornutum, under high-light conditions. Photosynthesis Research 127:219-235

Large WG, McWilliams JC, Doney SC (1994) Oceanic vertical mixing: A review and a model with a nonlocal boundary layer parameterization. Reviews of Geophysics 32:363-403

Lascara CM, Hofmann EE, Ross RM, Quetin LB (1999) Seasonal variability in the distribution of Antarctic krill, Euphausia superba, west of the Antarctic Peninsula. Deep Sea Research Part I: Oceanographic Research Papers 46:951-984

Laws RM, Fuchs VE (1977) Seals and whales of the Southern Ocean. Philosophical Transactions of the Royal Society of London B, Biological Sciences 279:81-96

LeResche RE, Sladen WJL (1970) Establishment of pair and breeding site bonds by young known-age adelie penguins (Pygoscelis adeliae). Animal Behaviour 18:517-526

Levin SA (1992) The problem of pattern and scale in ecology. Ecology 73:1943-1967

Li X, Holland DM, Gerber EP, Yoo C (2014) Impacts of the north and tropical Atlantic Ocean on the Antarctic Peninsula and sea ice. Nature 505:538-542

**Li Z, Cassar N, Huang K, Ducklow H, Schofield O (2016) Interannual variability in net community production at the Western Antarctic Peninsula region (1997–2014). Journal of Geophysical Research: Oceans 121:4748-4762*

Lin H, Kuzminov FI, Park J, Lee S, Falkowski PG, Gorbunov MY (2016) The fate of photons absorbed by phytoplankton in the global ocean. Science:aab2213

Liszka CM, Manno C, Stowasser G, Robinson C, Tarling GA (2019) Mesozooplankton Community Composition Controls Fecal Pellet Flux and Remineralization Depth in the Southern Ocean. Frontiers in Marine Science 6

Luo YW, Friedrichs MAM, Doney SC, Church MJ, Ducklow HW (2010) Oceanic heterotrophic bacterial nutrition by semilabile DOM as revealed by data assimilative modeling. Aquatic Microbial Ecology 60:273-287

Luria CM, Amaral-Zettler LA, Ducklow HW, Repeta DJ, Rhyne AL, Rich JJ (2017) Seasonal Shifts in Bacterial Community Responses to Phytoplankton-Derived Dissolved Organic Matter in the Western Antarctic Peninsula. Frontiers in Microbiology 8:2117

Lyon BE, Chaine AS, Winkler DW (2008) A Matter of Timing. Science 321:1051-1052

Martinson DG, Stammerjohn SE, Iannuzzi RA, Smith RC, Vernet M (2008) Western Antarctic Peninsula physical oceanography and spatio–temporal variability. Deep Sea Research Part II: Topical Studies in Oceanography 55:1964-1987

Martinson DG, McKee DC (2012) Transport of warm Upper Circumpolar Deep Water onto the western Antarctic Peninsula continental shelf. Ocean Sci 8:433-442

Massom RA, Stammerjohn SE, Lefebvre W, Harangozo SA, Adams N, Scambos TA, Pook MJ, Fowler C (2008) West Antarctic Peninsula sea ice in 2005: Extreme ice compaction and ice edge retreat due to strong anomaly with respect to climate. Journal of Geophysical Research: Oceans 113

McClintock J, Ducklow H, Fraser W (2008) Ecological Responses to Climate Change on the Antarctic Peninsula: The Peninsula is an icy world that's warming faster than anywhere else on Earth, threatening a rich but delicate biological community. American Scientist 96:302-310

McDonnell J, Kohut J, Schofield O, Hunter-Thomson K, Ferraro C, Hotaling L, Van Dyk P (2017) Polar ICE: Bringing the poles to classrooms Oceans 2017 Anchorage, Anchorage, AK, p 1-7

McDonnell J, Hotaling L, Schofield O, Kohut J (2020a) Key Concepts in Polar Science: Coming to Consensus on the Essential Polar Literacy Principles. Currents Journal of Marine Education 34:2-8

McDonnell J, Schofield O, Bean C (2020b) Bringing Long-term Ecological Research (LTER) at Palmer Station, Antarctica to your classroom. Currents Journal of Marine Education 34:15-17

****McKee DC, Martinson DG, Schofield O (2019) Origin and Attenuation of Mesoscale Structure in Circumpolar Deep Water Intrusions to an Antarctic Shelf. Journal of Physical Oceanography 49:1293-1318***

Meehl GA, Arblaster JM, Chung CTY, Holland MM, DuVivier A, Thompson L, Yang D, Bitz CM (2019) Sustained ocean changes contributed to sudden Antarctic sea ice retreat in late 2016. Nature Communications 10:14

Moffat C, Owens B, Beardsley RC (2009) On the characteristics of Circumpolar Deep Water intrusions to the west Antarctic Peninsula Continental Shelf. Journal of Geophysical Research: Oceans 114

Moffat C, Meredith M (2018) Shelf-ocean exchange and hydrography west of the Antarctic Peninsula: a review. Philosophical Transactions of the Royal Society A: Mathematical, Physical and Engineering Sciences 376:20170164

**Moline MA, Prézelin BB (1996) Long-term monitoring and analyses of physical factors regulating variability in coastal Antarctic phytoplankton biomass, in situ productivity and taxonomic* *composition over subseasonal, seasonal and interannual time scales. Marine Ecology Progress Series 145:143-160*

**Moline MA, Prézelin BB (1997) High-resolution time-series data for 1991/1992 primary production and related parameters at a Palmer LTER coastal site: implications for modeling carbon fixation in the Southern Ocean. Polar Biology 17:39-53*

**Moline MA, Schofield O, Boucher NP (1998) Phoyosynthetic parameters and empirical modelling of primary production: a case study on the Antarctic Peninsula shelf. Antarctic Science 10:45-54*

Moline MA, Claustre H, Frazer TK, Schofield O, Vernet M (2004) Alteration of the food web along the Antarctic Peninsula in response to a regional warming trend. Global Change Biology 10:1973-1980

**Montes-Hugo M, Doney SC, Ducklow HW, Fraser W, Martinson D, Stammerjohn SE, Schofield O (2009) Recent Changes in Phytoplankton Communities Associated with Rapid Regional Climate Change Along the Western Antarctic Peninsula. Science 323:1470-1473*

Moore JK, Lindsay K, Doney SC, Long MC, Misumi K (2013) Marine Ecosystem Dynamics and Biogeochemical Cycling in the Community Earth System Model [CESM1(BGC)]: Comparison of the 1990s with the 2090s under the RCP4.5 and RCP8.5 Scenarios. Journal of Climate 26:9291-9312

Moore JK, Fu W, Primeau F, Britten GL, Lindsay K, Long M, Doney SC, Mahowald N, Hoffman F, Randerson JT (2018) Sustained climate warming drives declining marine biological productivity. Science 359:1139-1143

Müller F, Bergmann M, Dannowski R, Dippner JW, Gnauck A, Haase P, Jochimsen MC, Kasprzak P, Kröncke I, Kümmerlin R, Küster M, Lischeid G, Meesenburg H, Merz C, Millat G, Müller J, Padisák J, Schimming CG, Schubert H, Schult M, Selmeczy G, Shatwell T, Stoll S, Schwabe M, Soltwedel T, Straile D, Theuerkauf M (2016) Assessing resilience in long-term ecological data sets. Ecological Indicators 65:10-43

**Nardelli S, Cimino MA, Conroy J, Fraser W, Steinberg DK, Schofield O (in prep) Summer krill availability in Adélie and gentoo penguin foraging areas south of Anvers Island.*

Nelson DM, Smith Jr. W (1991) Sverdrup revisited: Critical depths, maximum chlorophyll levels, and the control of Southern Ocean productivity by the irradiance-mixing regime. Limnology and Oceanography 36:1650-1661

New LF, Hall AJ, Harcourt R, Kaufman G, Parsons ECM, Pearson HC, Cosentino AM, Schick RS (2015) The modelling and assessment of whale-watching impacts. Ocean & Coastal Management 115:10-16

Nichols PD, Palmisano AC, Rayner MS, Smith GA, White DC (1989) Changes in the lipid composition of Antarctic sea-ice diatom communities during a spring bloom: an indication of community physiological status. Antarctic Science 1:133-140

**Nichols R, Cade D, Johnston D, Nowacek DP, Goldbogen JA, Friedlaender AS (in prep) Spatiotemporal changes in humpback whale foraging behavior and links to prey patch structure.*

Nielsen UN, Wall DH, Adams BJ, Virginia RA, Ball BA, Gooseff MN, McKnight DM (2012) The ecology of pulse events: insights from an extreme climatic event in a polar desert ecosystem. Ecosphere 3:art17

Nowacek DP, Friedlaender AS, Halpin PN, Hazen EL, Johnston DW, Read AJ, Espinasse B, Zhou M, Zhu Y (2011) Super-aggregations of krill and humpback whales in Wilhelmina Bay, Antarctic Peninsula. PLoS One 6:e19173-e19173

**Oliver MJ, Moline MA, Robbins I, Fraser W, Patterson DL, Schofield O (2012) Letting Penguins Lead: Dynamic Modeling of Penguin Locations Guides Autonomous Robotic Sampling. Oceanography 25:120-121*

Oliver MJ, Kohut JT, Bernard K, Fraser W, Winsor P, Statscewich H, Fredj E, Cimino M, Patterson-Fraser D, Carvalho F (2019) Central place foragers select ocean surface convergent features despite differing foraging strategies. Scientific Reports 9:157

**Pallin L, Robbins J, Kellar N, Bérubé M, Friedlaender A (2018a) Validation of a blubber-based endocrine pregnancy test for humpback whales. Conservation Physiology 6*

****Pallin LJ, Baker CS, Steel D, Kellar NM, Robbins J, Johnston DW, Nowacek DP, Read AJ, Friedlaender AS (2018b) High pregnancy rates in humpback whales (Megaptera novaeangliae) around the Western Antarctic Peninsula, evidence of a rapidly growing population. Royal Society Open Science 5:180017***

Park J, Kuzminov FI, Bailleul B, Yang EJ, Lee S, Falkowski PG, Gorbunov MY (2017) Light availability rather than Fe controls the magnitude of massive phytoplankton bloom in the Amundsen Sea polynyas, Antarctica. Limnology and Oceanography 62:2260-2276

Patterson DL, Easter-Pilcher A, Fraser W (2003) The effects of human activity and environmental variability on long-term changes in Adelie penguin populations at Palmer Station Antarctica. In: Huiskes AHL, Gieskes WWC, Rozema J, R.M.L. S, van der vies SM, Wolff WJ (eds) Antarctic Biology in a Global Context. Backhuys Publishers, Leiden

**Pickett EP, Fraser WR, Patterson-Fraser DL, Cimino MA, Torres LG, Friedlaender AS (2018) Spatial niche partitioning may promote coexistence of Pygoscelis penguins as climate-induced sympatry occurs. Ecology and Evolution 8:9764-9778*

Piñones A, Hofmann EE, Daly KL, Dinniman MS, Klinck JM (2013) Modeling the remote and local connectivity of Antarctic krill populations along the western Antarctic Peninsula. Marine Ecology Progress Series 481:69-92

Pirotta E, Booth CG, Costa DP, Fleishman E, Kraus SD, Lusseau D, Moretti D, New LF, Schick RS, Schwarz LK, Simmons SE, Thomas L, Tyack PL, Weise MJ, Wells RS, Harwood J (2018) Understanding the population consequences of disturbance. Ecology and Evolution 8:9934-9946

Poloczanska ES, Brown CJ, Sydeman WJ, Kiessling W, Schoeman DS, Moore PJ, Brander K, Bruno JF, Buckley LB, Burrows MT, Duarte CM, Halpern BS, Holding J, Kappel CV, O’Connor MI, Pandolfi JM, Parmesan C, Schwing F, Thompson SA, Richardson AJ (2013) Global imprint of climate change on marine life. Nature Climate Change 3:919-925

Popendorf KJ, Lomas MW, Van Mooy BAS (2011) Microbial sources of intact polar diacylglycerolipids in the Western North Atlantic Ocean. Organic Geochemistry 42:803-811

Powers J, Manning KW, Bromwich DH, Cassano JJ, Cayette AM (2012) A decade of Antarctic science support through AMPS. Bulletin of the American Meteorological Society 93:1699-1712

Prézelin BB, Hofmann EE, Mengelt C, Klinck JM (2000) The linkage between Upper Circumpolar Deep Water (UCDW) and phytoplankton assemblages on the west Antarctic Peninsula continental shelf. Journal of Marine Research 58:165-202

Regan HC, Holland PR, Meredith MP, Pike J (2018) Sources, variability and fate of freshwater in the Bellingshausen Sea, Antarctica. Deep Sea Research Part I: Oceanographic Research Papers 133:59-71

Reilly SB, Bannister JL, Best PB, Brown M, Brownell Jr. RL, Butterworth DS, Clapham PJ, Cooke J, Donovan GP, Urban J, Zerbini AN (2010) Megaptera novaeangliae IUCN Red List of Threatened Species

**Rohr T, Long MC, Kavanaugh MT, Lindsay K, Doney SC (2017) Variability in the mechanisms controlling Southern Ocean phytoplankton bloom phenology in an ocean model and satellite observations. Global Biogeochemical Cycles 31:922-940*

**Rohr T, Harrison C, Long MC, Gaube P, Doney SC (submitted-a) The simulated biological response to Southern Ocean eddies via biological rate modification and physical transport. Global Biogeochemical Cycles*

**Rohr T, Harrison C, Long MC, Gaube P, Doney SC (submitted-b) Simulated eddy induced bottom up controls on phytoplankton division rates in the Southern Ocean. Global Biogeochemical Cycles*

Ross RM, Quetin LB, Martinson DG, Iannuzzi RA, Stammerjohn SE, Smith RC (2008) Palmer LTER: Patterns of distribution of five dominant zooplankton species in the epipelagic zone west of the Antarctic Peninsula, 1993–2004. Deep Sea Research Part II: Topical Studies in Oceanography 55:2086-2105

Rozema PD, Venables HJ, van de Poll WH, Clarke A, Meredith MP, Buma AGJ (2017) Interannual variability in phytoplankton biomass and species composition in northern Marguerite Bay (West Antarctic Peninsula) is governed by both winter sea ice cover and summer stratification. Limnology and Oceanography 62:235-252

**Ruck KE, Steinberg DK, Canuel EA (2014) Regional differences in quality of krill and fish as prey along the Western Antarctic Peninsula. Marine Ecology Progress Series 509:39-55*

****Saba GK, Fraser WR, Saba VS, Iannuzzi RA, Coleman KE, Doney SC, Ducklow HW, Martinson DG, Miles TN, Patterson-Fraser DL, Stammerjohn SE, Steinberg DK, Schofield OM (2014) Winter and spring controls on the summer food web of the coastal West Antarctic Peninsula. Nature Communications 5:4318***

**Saenz BT, Arrigo KR (2012) Simulation of a sea ice ecosystem using a hybrid model for slush layer desalination. Journal of Geophysical Research: Oceans 117*

**Saenz BT, McKee DC, Doney SC, Martinson D, Stammerjohn S (in prep) Influence of deep ocean heat on the sea-ice conver in the west Antarctica Peninsula.*

**Sailley SF, Ducklow HW, Moeller HV, Fraser WR, Schofield OM, Steinberg DK, Garzio LM, Doney SC (2013) Carbon fluxes and pelagic ecosystem dynamics near two western Antarctic Peninsula Adélie penguin colonies: an inverse model approach. Marine Ecology Progress Series 492:253-272*

Sanz-Lázaro C (2016) Climate extremes can drive biological assemblages to early successional stages compared to several mild disturbances. Scientific Reports 6:30607

Scambos TA, Stammerjohn S (2019) Antarctica and the Southern Ocean [in "State of the Climate in 2018"]. Bulletin of the American Meteorological Society 100:S169-S188

Scheffer M, Carpenter S, Foley JA, Folke C, Walker B (2001) Catastrophic shifts in ecosystems. Nature 413:591-596

Schneider DP, Deser C, Okumura Y (2012) An assessment and interpretation of the observed warming of West Antarctica in the austral spring. Climate Dynamics 38:323-347

Schofield O, Ducklow HW, Martinson DG, Meredith MP, Moline MA, Fraser WR (2010) How Do Polar Marine Ecosystems Respond to Rapid Climate Change? Science 328:1520-1523

Schofield O, Meredith MP, Newman L, Sparro M, Urban E (2012) Implementing a southern ocean observing system. EOS, Transactions of the American Geophysical Union 39:241-243

Schofield O, Ducklow H, Bernard K, Doney SC, Patterson-Fraser DL, Gorman KB, Martinson D, Meredith M, Saba G, Stammerjohn S, Steinberg DK, Fraser W (2013) Penguin Biogeography Along the West Anarctic Peninsula: Testing the Canyon Hypothesis with Palmer LTER Observations. Oceanography 26:204-206

Schofield O, Saba G, Coleman K, Carvalho F, Couto N, Ducklow H, Finkel Z, Irwin A, Kahl A, Miles T, Montes-Hugo M, Stammerjohn S, Waite N (2017) Decadal variability in coastal phytoplankton community composition in a changing West Antarctic Peninsula. Deep Sea Research Part I: Oceanographic Research Papers 124:42-54

Schofield O, Brown M, Kohut J, Nardelli S, Saba G, Waite N, Ducklow H (2018) Changes in the upper ocean mixed layer and phytoplankton productivity along the West Antarctic Peninsula. Philosophical Transactions of the Royal Society A: Mathematical, Physical and Engineering Sciences 376:20170173

**Schultz C (2019) A Modeling Study of the Marine Biogeochemistry, Plankton Dynamics, and Carbon Cycle on the Continental Shelf Off the West Antarctic Peninsula. Massachusetts Institute of Technology / Woods Hole Oceanographic Institution*

**Schultz C, Doney SC, Zhang WG, Regan HC, Holland PR, Meredith MP, Stammerjohn S (submitted) Modeling of the influence of sea ice cycle and Langmuir circulation on ocean surface mixed layer depth and freshwater distribution off the West Antarctic Peninsula. Journal of Geophysical Research: Oceans*

Serebrennikova YM, Fanning KA (2004) Nutrients in the Southern Ocean GLOBEC region: variations, water circulation, and cycling. Deep Sea Research Part II: Topical Studies in Oceanography 51:1981-2002

Sherman J, Gorbunov MY, Schofield O, Falkowski PG (revision resubmitted) Photosynthetic energy conversion efficiency along the West Antarctic Peninsula. Limnology and Oceanography

Sherrell RM, Annett AL, Fitzsimmons JN, Roccanova VJ, Meredith MP (2018) A "shallow bathtub ring" of local sedimentary iron input maintains the Palmer Deep biological hotspot on the West Antarctic Peninsula shelf. Philosophical Transactions of the Royal Society A: Mathematical, Physical and Engineering Sciences 376:20170171

Skerratt JH, Nichols PD, McMeekin TA, Burton H (1995) Seasonal and inter-annual changes in planktonic biomass and community structure in eastern Antarctica using signature lipids. Marine Chemistry 51:93-113

Smale DA, Wernberg T (2013) Extreme climatic event drives range contraction of a habitat-forming species. Proceedings of the Royal Society B: Biological Sciences 280:20122829

Smith MD (2011) An ecological perspective on extreme climatic events: a synthetic definition and framework to guide future research. Journal of Ecology 99:656-663

Smith RC, Baker KS, Byers ML, Stammerjohn SE (1998a) Primary productivity of the Palmer Long Term Ecological Research Area and the Southern Ocean. Journal of Marine Systems 17:245-259

Smith RC, Baker KS, Vernet M (1998b) Seasonal and interannual variability of phytoplankton biomass west of the Antarctic Peninsula. Journal of Marine Systems 17:229-243

Smith RC, Fraser W, Stammerjohn S, Vernet M (2003) Palmer Long-Term Ecological Research on the Antarctic marine ecosyste. In: Domack E, Leventer A, Burnett A, Bindschadler R, Convey P, Kirby M (eds) Antarctic Peninsula Climate Variability: Historical and Paleoenvironmental Perspective. American Geophysical Union, Washington, D.C., p 131-144

Smith RC, Martinson DG, Stammerjohn SE, Iannuzzi RA, Ireson K (2008) Bellingshausen and western Antarctic Peninsula region: Pigment biomass and sea-ice spatial/temporal distributions and interannual variabilty. Deep Sea Research Part II: Topical Studies in Oceanography 55:1949-1963

Smith WO, Nelson DM (1985) Phytoplankton Bloom Produced by a Receding Ice Edge in the Ross Sea: Spatial Coherence with the Density Field. Science 227:163-166

Sosik HM, Olson RJ (2007) Automated taxonomic classification of phytoplankton sampled with imaging-in-flow cytometry. Limnology and Oceanography: Methods 5:204-216

Stamieszkin K, Pershing AJ, Record NR, Pilskaln CH, Dam HG, Feinberg LR (2015) Size as the master trait in modeled copepod fecal pellet carbon flux. Limnology and Oceanography 60:2090-2107

Stammerjohn S, Maksym T, Heil P, Massom RA, Vancoppenolle M, Leonard KC (2011) The influence of winds, sea-surface temperature and precipitation anomalies on Antarctic regional sea-ice conditions during IPY 2007. Deep Sea Research Part II: Topical Studies in Oceanography 58:999-1018

Stammerjohn S, Massom R, Rind D, Martinson D (2012) Regions of rapid sea ice change: An inter-hemispheric seasonal comparison. Geophysical Research Letters 39

Stammerjohn S, Maksym T (2017) Gaining (and losing) Antarctic sea ice: Variability, trends and mechanisms. In: Thomas DN (ed) Sea Ice. John Wiley & Sons, Ltd, West Sussex

Stammerjohn SE, Martinson DG, Smith RC, Iannuzzi RA (2008a) Sea ice in the western Antarctic Peninsula region: Spatio-temporal variability from ecological and climate change perspectives. Deep Sea Research Part II: Topical Studies in Oceanography 55:2041-2058

Stammerjohn SE, Martinson DG, Smith RC, Yuan X, Rind D (2008b) Trends in Antarctic annual sea ice retreat and advance and their relation to El Niño–Southern Oscillation and Southern Annular Mode variability. Journal of Geophysical Research: Oceans 113

Steinberg DK, Ruck KE, Gleiber MR, Garzio LM, Cope JS, Bernard KS, Stammerjohn SE, Schofield OME, Quetin LB, Ross RM (2015) Long-term (1993–2013) changes in macrozooplankton off the Western Antarctic Peninsula. Deep Sea Research Part I: Oceanographic Research Papers 101:54-70

Steinberg DK, Landry MR (2017) Zooplankton and the Ocean Carbon Cycle. Annual Review of Marine Science 9:413-444

Steinberg DK (in prep) Relative importance of fecal pellet production by krill versus salps along the West Antarctic Peninsula.

Stommel H (1963) Varieties of oceanographic experience. Science 139:572-576

**Stukel MR, Asher E, Couto N, Schofield O, Strebel S, Tortell P, Ducklow HW (2015) The imbalance of new and export production in the western Antarctic Peninsula, a potentially "leaky" ecosystem. Global Biogeochemical Cycles 29:1400-1420*

Thibault KM, Brown JH (2008) Impact of an extreme climatic event on community assembly. Proceedings of the National Academy of Sciences 105:3410-3415

**Thibodeau PS, Steinberg DK, Stammerjohn SE, Hauri C (2019) Environmental controls on pteropod biogeography along the Western Antarctic Peninsula. Limnology and Oceanography 64:S240-S256*

**Thibodeau PS, Steinberg DK, McBride CE, Conroy JA, Keul N, Ducklow HW (submitted-a) Long-term trends in pteropod phenology along the Western Antarctic Peninsula. Deep Sea Research Part I: Oceanographic Research Papers*

**Thibodeau PS, Steinberg DK, Maas AE (submitted-b) Effects of temperature and food concentration on pteropod metabolism along the Western Antarctic Peninsula. Journal of Experimental Marine Biology and Ecology*

**Trinh R (in prep) Krill life cycle drives POC export off the western Antarctic Peninsula.*

Turner J, Lu H, White I, King JC, Phillips T, Hosking JS, Bracegirdle TJ, Marshall GJ, Mulvaney R, Deb P (2016) Absence of 21st century warming on Antarctic Peninsula consistent with natural variability. Nature 535:411-415

Tyson RB, Friedlaender AS, Nowacek DP (2016) Does optimal foraging theory predict the foraging performance of a large air-breathing marine predator? Animal Behaviour 116:223-235

Valiela I, Peckol P, Avanzo CD, Kremer J, Hersh D, Foreman K, Lajtha K, Seely B, Geyer WR, Isaji T, Crawford R (1998) Ecological Effects of Major Storms on Coastal Watersheds and Coastal Waters: Hurricane Bob on Cape Cod. Journal of Coastal Research 14:218-238

Vaughan DG, Marshall GJ, Connolley WM, King JC, Mulvaney R (2001) Devil in the Detail. Science 293:1777-1779

Vernet M, Martinson D, Iannuzzi R, Stammerjohn S, Kozlowski W, Sines K, Smith R, Garibotti I (2008) Primary production within the sea-ice zone west of the Antarctic Peninsula: I—Sea ice, summer mixed layer, and irradiance. Deep Sea Research Part II: Topical Studies in Oceanography 55:2068-2085

Wang X, Moffat C, Dinniman MS, Klinck JM, Aguiar-Gonzalez B, Sutherland D (in prep) Dynamics of along-shore exchange of the west Antarctic.

Warren JD, Santora JA, Demer DA (2009) Submesoscale distribution of Antarctic krill and its avian and pinniped predators before and after a near gale. Marine Biology 156:479-491

Waters KJ, Smith RC (1992) Palmer LTER: A sampling grid for the Palmer LTER program. Antarctic Journal of the United States 27:236-239

**Weinstein BG, Double M, Gales N, Johnston DW, Friedlaender AS (2017) Identifying overlap between humpback whale foraging grounds and the Antarctic krill fishery. Biological Conservation 210:184-191*

**Weinstein BG, Friedlaender AS (2017) Dynamic foraging of a top predator in a seasonal polar marine environment. Oecologia 185:427-435*

Wernberg T, Bennett S, Babcock RC, de Bettignies T, Cure K, Depczynski M, Dufois F, Fromont J, Fulton CJ, Hovey RK, Harvey ES, Holmes TH, Kendrick GA, Radford B, Santana-Garcon J, Saunders BJ, Smale DA, Thomsen MS, Tuckett CA, Tuya F, Vanderklift MA, Wilson S (2016) Climate-driven regime shift of a temperate marine ecosystem. Science 353:169-172

Wilson SE, Ruhl HA, Smith J, K. L. (2013) Zooplankton fecal pellet flux in the abyssal northeast Pacific: A 15 year time-series study. Limnology and Oceanography 58:881-892

Yuan X, Kaplan MR, Cane MA (2018) The Interconnected Global Climate System—A Review of Tropical–Polar Teleconnections. Journal of Climate 31:5765-5792

Zhou M, Nordhausen W, Huntley M (1994) ADCP measurements of the distribution and abundance of euphausiids near the Antarctic Peninsula in winter. Deep Sea Research Part I: Oceanographic Research Papers 41:1425-1445

Zhou M, Dorland RD (2004) Aggregation and vertical migration behavior of Euphausia superba. Deep Sea Research Part II: Topical Studies in Oceanography 51:2119-2137