Decadal trends in phytoplankton communities along a rapidly changing West Antarctic Peninsula

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***Abstract*— The West Antarctic Peninsula (WAP) is associated with large phytoplankton blooms that are dominated by large (>20 microns) diatoms however, nanoplankton (<20 microns) are also an important component in the phytoplankton community. The dominant nanoflagellate in the WAP has been suggested to be cryptomonad algae. Using a twenty-year time series collected by the Palmer Long Term Ecological Research (Pal LTER) program, we assessed long-term patterns and stability in the coastal phytoplankton communities in the WAP. There was significant interannual variability in the integrated water column chlorophyll *a* (chl-*a*) concentrations, which varied by a factor of 5 over the 20-year time series. Within the time series the dominant phytoplankton taxa were diatoms, with the second most abundant phytoplankton taxa present being cryptophyes. While diatoms were observed over the full range of observed salinities (34.5 to 32) as well as over the full range of *in situ* temperatures (-1.5 to 2.5° C), the cryptophyte populations were observed in lower salinity (33.75 to 32.5) and colder water (-1 to 1° C) for the local time series at Palmer Station. This pattern was not observed for the ship spatial time series data, which might reflect the species diversity in the cryptophyte species between northern and southern waters of the WAP. Regardless, diatoms and cryptophytes were inversely related to each other across the entire WAP. Years when environmental factors favor water column stability, there are anomalously large summer diatom blooms. Consistent with modeling studies this suggests a potential shift to multivorous food web, which has significant ecological and biogeochemical implications, such as decreased efficiency of atmospheric carbon sequesteration.**

Keywords— polar science, phytoplankton

I. Introduction

The West Antarctic Peninsula (WAP) is experiencing some of the fastest rates of regional change on Earth [1][2]. The changes in the WAP are profound with mid-winter surface atmospheric temperatures increasing by 6°C (>5x the global average) over the last 50 years[3][4][5]. Eighty-seven percent of the WAP glaciers are in retreat, the annual sea ice season has shortened by 90 days, and perennial ice is no longer a feature of the northern WAP [6][7]. These changes appear to be accelerating [8]. Ocean warming has been implicated as a major driver for the deglaciation [9] through the upwelling of the heat delivered by relatively warm (~2° C) Upper Circumpolar Deep Water (UCDW). The UCDW is derived from the Antarctic Circumpolar. The net change in sea-ice cover has been hypothesized to underlie observed changes in the coastal ecosystems of the WAP [10][11].

The coastal waters of the WAP are associated with large phytoplankton blooms that are dominated by diatoms [11][12]. The high phytoplankton productivity is fueled by an ample supply of nutrients and the availability of light when the mixed layer depths (MLD) are shallow allowing cells to overcome light limitation. Macronutrients are highly abundant throughout the WAP [13][14] and although they show marked seasonality [15], in most cases they do not appear to limit phytoplankton growth [16][17] except during very large blooms. The high productivity supports a productive food web that is tightly coupled to the seasonal phytoplankton dynamics suggesting strong bottom-up control of the system [18]. Over the past 30 years, there is evidence that the magnitude of phytoplankton blooms in the WAP have changed [19]. The changes have been particularly dramatic in the northern WAP, with a decline in chlorophyll *a* associated with an increase in cloudy days, deepening upper mixed layer depth, stronger intensity winds, and shorter sea ice seasons along the marginal ice zone [19]. In contrast to the northern sectors of the WAP, the southern areas have experienced increasing phytoplankton biomass over time. They argued these increases reflected an increase in the duration and area of ice free water during the summer season [19].

Phytoplankton blooms in the WAP are dominated by large (>20 micron) diatoms; however over the last three decades the traditional paradigm has been revised recognizing that nano- (<20 micron) and picoplankton (<2 micron) are a critically important component to the WAP phytoplankton community [20][21]. The dominant nano-flagellates in the WAP appear to be cryptophytes [21]. Numerous field programs have documented that cryptophytes are often spatially and temporally segregated from the diatom communities [22][23][24]. Cryptophyte populations are often associated with either mid-shelf fronts [25] or low salinity surface plumes [24][25]. This has led to the hypothesis that cryptophyte communities will grow in importance in the WAP food web as

978-0-692-94690-9/$31.00 ©2017 MTS

sea and glacial ice melt will increase the spatial extent of low salinity water [24].

To date, the majority of the studies have been based on ship and/or field station efforts conducted for a limited duration (1-3 field seasons) thus providing snapshots of the ecosystem at any given time. For this study we analyzed a twenty-year time series collected by the Palmer Long Term Ecosystem research (Pal LTER) program at the United States Palmer Research Station to assess long-term ecological patterns and stability in the coastal phytoplankton communities in the WAP. Our results confirm that diatoms and cryptophytes are the dominant phytoplankton groups and are inversely related to each other; however mixed flagellates are also a significant fraction of the phytoplankton community. At Palmer Station the presence of the cryptophytes is associated with lower temperature and lower salinity water associated with the sea ice and glacial melt. We observe, since 2009, increasing sea ice at Palmer Station along with increased seasonal concentrations of chlorophyll. These increases are associated with an increasing proportion of diatoms with the phytoplankton community, which should be favorable for the Antarctic krill.

II. The Palmer LTER Program

Data was collected as part of the Palmer Long Term Ecological Research (LTER) project, which was initiated in 1991 to study how annual sea ice variability structures the ecology and biogeochemistry of the West Antarctic Peninsula (WAP). The project was established before it was appreciated that this region was undergoing significant change associated with a warming atmosphere. The data is publicly available through the Palmer LTER data system (http://pal.lternet.edu/data).

The Palmer LTER program has carried out sampling at Palmer Station (-64.8° South, -64.1° West) in the austral spring-summer annually since December of 1991 (Figure 1). The sampling locations at Palmer Station are an inshore station B (bottom depth ≈ 75 m) and an offshore station E (bottom depth ≈ 200 m) (Figure 1), both of which are within Adélie penguin foraging areas [26], which is a central focus for the LTER [27]. Station E is located offshore at the edge of the Palmer Station boating limit and has a distinct marine signature associated with Palmer Deep Canyon, which is a seafloor conduit hypothesized to allow the inputs of modified UCDW [27][28]. Station B is adjacent to the Marr Glacier. Despite these differences, phytoplankton biomass and community composition from Stations B and E are highly correlated. The one difference is that overall phytoplankton concentrations were consistently higher in the nearshore waters at Station B.

The goal of the Palmer LTER is to sample stations B and E twice per week from mid-/end of October to mid-/end March. Sampling at each station is conducted via Zodiac where a CTD is lowered manually for a vertical profile of water column physics, and is immediately followed by a Go-Flo bottle cast to collect seawater at selected depths for phytoplankton (i.e., chlorophyll *a* [chl-*a*], phytoplankton pigments, primary productivity). Seawater from each depth is stored in dark amber Nalgene bottles and processed immediately upon returning to the laboratory at Palmer Station. Zodiac sampling in this region is heavily dependent on weather, sea ice, time, and personnel availability. Thus, data gaps exist within the time series, as some seasons had limited or irregular sampling as well instrument issues in the early years. Data exist for all years except 2007-08. Nonetheless, the summer months of December, January, and February (DJF) were the most consistently sampled.

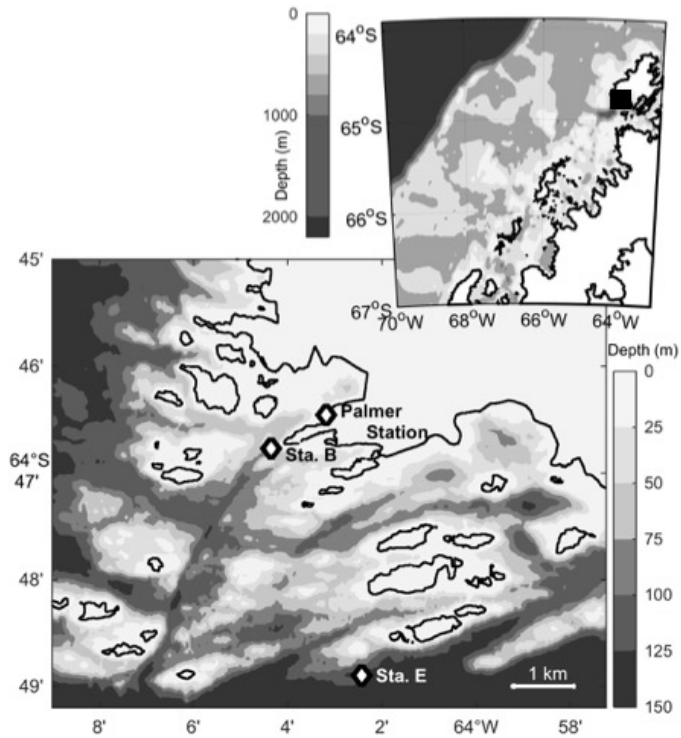

Figure 1. Study site for LTER research at Palmer Station, which is located on the West Antarctic Peninsula. Data for this study was collected at Stations B and E.

Over the course of the program, physical oceanographic data (temperature and conductivity as a function of pressure) was collected using several instruments. From 1991 to 2007, a SeaBird Elecronics (www.seabird.com) Seacat SBE 19 was used. From 2007 onward a SeaBird Elecronics Seacat SBE 19plus was used, though not in field season 2008-2009. We accounted for sensor drift using calibrations made before and after each field season, following methods recommended by SeaBird, assuming linear drift for sensors. We used SeaBird's standard software functions to process the data, removing effects for zodiac heave (pressure reversals), and to ensure that the temperature, conductivity and pressure were measured on the same water parcel. Data was averaged into 2 db pressure bins for the older SBE19 data and 1 db bins for the newer instrument, which samples at twice the frequency. Conductivity data was then converted to salinity. From 2008 until 2011, a Falmouth Scientific Inc. FSI MCTD-3 and a Satlantic HyperPro-II (which includes temperature, conductivity and pressure ancillary sensors) were also used to collect physical oceanographic data. As much as possible, we followed the same methods to process this data. The three

instruments combined provided full data coverage every time water samples were collected. Plots of each cast were inspected visually and in relation to other casts to look for any issues with the data (eg, bad surface values due to sea-state). These values were removed from the data set. In order to define an ecologically relevant seasonal mixed layer (MLD), we used the approach described in Carvalho et al. [29].

III. Results form the Time Series

It is well documented that the West Antarctic Peninsula (WAP) has been experiencing changes in the sea ice duration and extent (Stammerjohn et al. 2008) which is also true for the Palmer Station region (Figure 2). Despite significant interannual variability, the timing of sea ice retreat in the Palmer region has been occurring earlier over time (Figure 2A). Sea ice retreat in the early nineties often occurred in the month of December, but after declines from 2006 through 2009, sea ice retreat occurred as early as mid-September. Since 2009, the timing of sea ice retreat has rebounded and now most often occurs in mid-November. Sea ice advance also has exhibited significant change with sea ice advance occurring later by almost 2 months during the year (Figure 2B). Sea ice retreat shows larger interannual variability than sea ice advance. The net result is that over the last two decades the number of days between sea ice advance and retreat (Figure 2C) and total of sea ice days (Figure 2D) have shown significant ($p<0.05$) declines. The coastal waters around Palmer Station exhibit significant interannual variability in phytoplankton biomass. Integrated water column chl-*a* concentrations varied by a factor of 5 over the 20-year time series at Palmer (Figure 3A). Values ranged from ~100 to over 500 mg chl-*a* m^{-2}. Seasonally integrated chl-*a* anomalies show an increasing trend (Station B: $R^2 = 0.38$, $p=0.01$; Station E- $R^2 = 0.24$, $p=0.01$) over the last two decades (Figure 3B). In recent years there were two years 2009/2010 and 2012/2013 that exhibited large week-long chl-*a* blooms during the summer that resulted in a 2-3 fold higher seasonal variance in the chlorophyll biomass (Figure 3C). The shifts from generally lower chl-*a* biomass in the 1990's and early 2000's to higher chl-*a* values in the later years of the time series were associated with a shallower seasonal mixed layer depth (SMLD) (Figure 3B). These was a significant inverse correlation ($p = 0.04$) between the seasonal averaged sum- mer mixed layer depth and the integrated summer chl-*a* (Figure 4). The SMLD could account for 27% of the variance in the integrated chl-*a* (Figure 4).

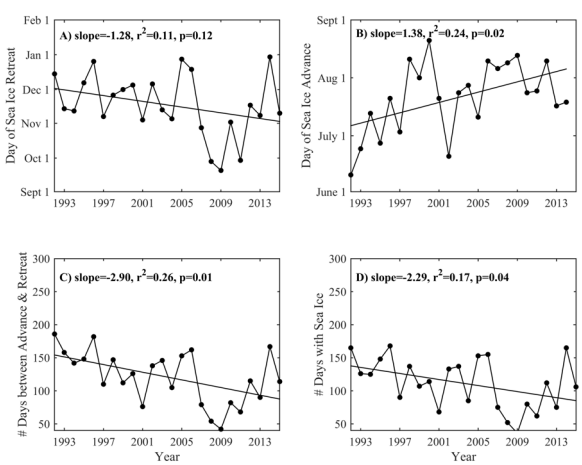

Figure 2. Changes in annual sea ice dynamics near Palmer Station. A) Time series of the day of sea ice retreat. B) Time series of the number of days of sea ice advance. There was a significant (p = 0.02) postive trend over time. C) The time series variability of the days between of sea ice advance and retreat. There has been a significant decrease (p = 0.02) in the day of sea ice advance in the Palmer Station station region. D) The interannual variability in the number of sea days. The number of sea ice days has significantly (p = 0.04) decreased over the last 2 decades.

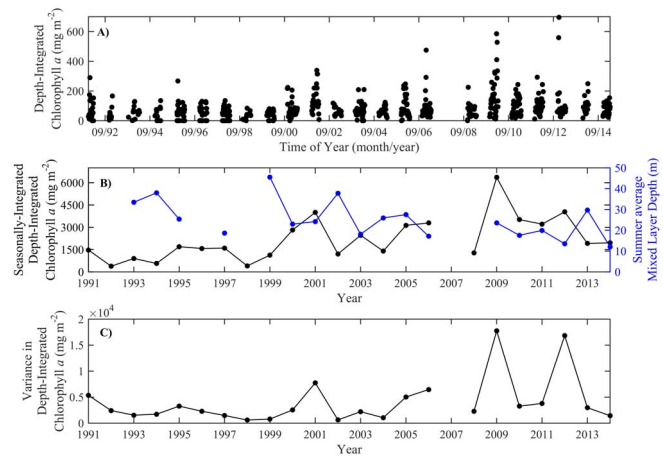

Figure 3. The interannual variability chlorophyll a at Station E. A) The internanual variability in the water column integrated water column chlorophyll a (mg chl a m^{-2}). Data was only collected during the austral summer months. B) The inter-annual seasonally-integrated water column chl a from Station E. The seasonally integrated data shows a positive trend over the last two decades (p = 0.004). Overlaid in blue are the summer season average mixed layer depth. Missing years in the mixed layer were when there were fewer the 6 profiles for that season. C) The time series of the variance in depth and seasonally integrated chl-a. The relationship was positive and heavily weighted by the later years in the time series but was not significant (p = 0.09).

Combining the CHEMTAX outputs with measured chl-*a* allowed estimation of the amount of chl-*a* for the major phytoplankton taxa to be estimated. The most dominant phytoplankton taxa present in the waters near Palmer Station were diatoms, which each year accounted for over 90% of the chl-*a* at both Stations B and E. Water column integrated chl-*a* associated with diatoms often exceeded 200 mg m^{-2}, which was significantly higher than the chl-*a* associated with other major phytoplankton taxa. This was consistent with the observation that the concentration of accessory pigment fucoxanthin, associated with diatoms, could account for up to 60% of the variability in the concentration of chl-*a* ($p = 0.005$). The next

most abundant phytoplankton taxa were the cryptophytes and mixed flagellates. Cryptophyte populations peaked at ≥50% of the chl-*a* in 8 of the 20 years. Six of the years had >50 mg chl-*a* m^{-2} associated with cryptophytes. Mixed flagellates were also a significant component to the phytoplankton community consistently accounting for ~50 mg chl-*a* m^{-2}. Prasinophytes were present throughout the time series consistently accounting for <10 mg chl-*a* m^{-2} except for 2001 and 2008. Similar to the prasinophytes, the type-4 haptophytes concentrations were consistently 10-20 mg chl-*a* m^{-2}. Despite significant interannual changes in phytoplankton communities, the chlorophyll-normalized ^{14}C productivity was relatively consistent over the time series.

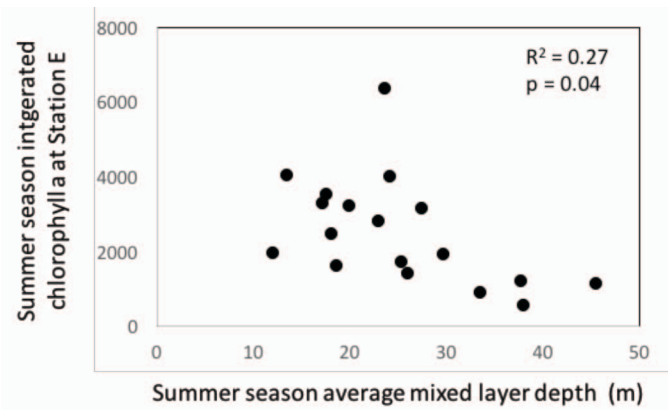

Figure 4. The correlation between summer integrated chlorophyll a at Station E with the summer averaged mixed layer depth. There was a significant inverse relationship between the chl-a and mixed layer depth (p = 0.04).

Histograms of the frequency of the occurrence for the major phytoplankton groups (diatoms, cryptophytes and mixed flagellates) against air temperature, water depth, and mixed layer depth are presented in Figure 5. The three taxa were found at distinct air temperature, water depths. All three of the phytoplankton taxa were skewed to air temperatures above the 0° C. Peak diatom abundance was found at the lowest mean air temperature of 1.20° C (Figure 5A). Peak mixed flagellates were on average associated with an air temperatures of 1.39° C and the cryptophytes were associated with the warmest air temperature at 2.32° C (Figure 5A). Peak cryptophyte abundance was associated with the shallowest mean water depth of 10.23 meters (Figure 5B). The diatoms were on average associated with a mean water depth of 15.09 meters (Figure 5B). Mixed flagellate abundance was associated with the deepest depth of 17.60 (Figure 5B). Mixed flagellates were found at the deepest MLD (17.55 m) consistent with what appeared as a consistent background population throughout the time series. Diatoms were found in greatest number at a MILD of 15.14 m, with cryptophytes found most often at the shallowest MLD of 14.11 m. This is consistent with the cryptophytes associated with shallow, lower salinity waters. Overall the results suggest evidence of niche segregation between the diatoms, cryptophytes, and mixed flagellates.

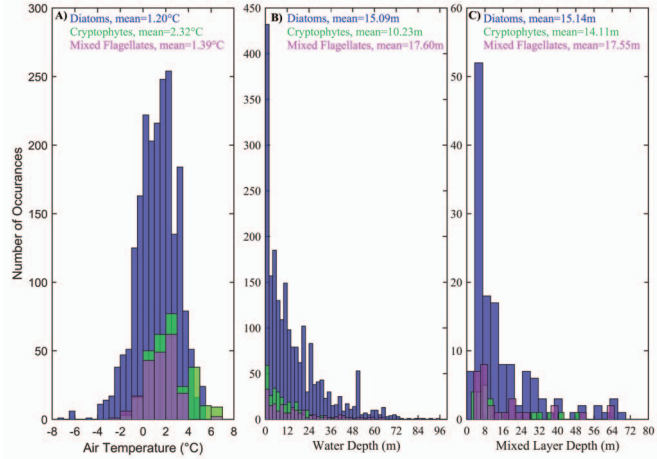

Figure 5. Frequency of observations of specific taxa when greater than 50% of the chl-a against atmospheric air temperature, water depth and mixed layer depth. A) The frequency of observations where water column chl-a concentrations were dominated by either diatoms, cryptophytes, and mixed flagellates. B) The frequency of observations where chl-a concentrations were dominated by either diatoms, cryptophytes, and mixed flagellates as a function of water column depth. C) The frequency of observations where chl-a concentrations were dominated by either diatoms, cryptophytes, and mixed flagellates as a function of mixed layer depth. Data does not include depth when no stratification was observed.

During the time series (1991–2012), peaks in depth-integrated (0–50m) summer chl-*a* concentration occurred, on average, every 4–6 years (Fig. 6, Saba et al. 2014). The relative phytoplankton composition (as determined by phytoplankton pigments) during peak chl-*a* years was dominated by diatoms, whereas the proportion of cryptophytes increased in low chl-*a* years (Figure 6) (one-way analysis of variance, P<0.001). The relative concentrations of the other phytoplankton taxa did not show significant changes during the high and low chl-*a* years (Figure 6). Summers with high chlorophyll concentrations were associated with years of high abundances of diatoms and crptophytes. We observed significant correlations between the SMLD and integrated summer chl-*a*. While high chorophyll years were associated with a relative increase in the diatoms over other phytoplankton groups (Figure 6).

IV. CONCLUSIONS

The WAP has been exhibiting significant change over the last decade [7] [15][19]; however the relative change in the physics, chemistry, and the biology varies latitudinally [15]. Based on a satellite analysis Palmer station is located in the transition zone between the warmer maritime conditions associated with declining chl-*a* in the northern WAP and the more polar continental conditions associated with increasing chl-*a* in the south [19]. Increasing chl-*a* in the southern waters of the WAP have been hypothesized to reflect the increased

periods of open water due to reduced sea ice coverage in the spring and summer. Our results suggest the same is true at Palmer Station where the number of sea ice days are inversely related to the amount of summer chl-*a*. While for much of the time series at Palmer there was a decline in the numbers of days of sea ice each year, there recently has been a change with a significant increase in sea ice. Associated with the increasing sea ice has been the increase in the amount of summer chl-*a* at Palmer. The analysis [19] did not include recent changes as it compared the changes between 1978-1986 and 1998-2006, well before the recent increases in chl-*a* and sea ice began after 2009. While there was an increase in sea ice, the summer months at Palmer still remain relatively ice free and the primary factor influencing the bloom is depth of the summer mixed layer depth which is most likely regulated to local wind forcing and circulation patterns.

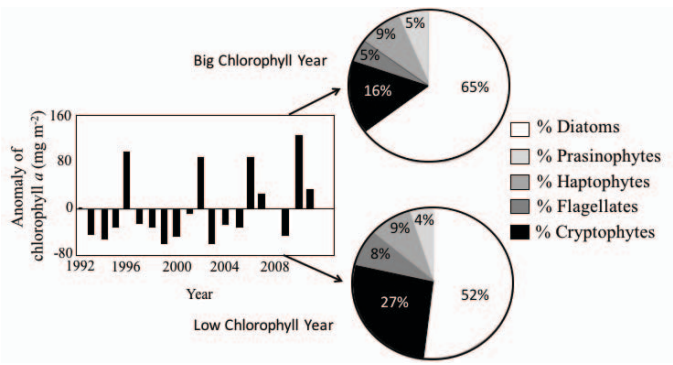

Figure 6. The dynamics associated with years of high and low phytoplankton biomass as indicated by chl-a anomalies (calculated as described in Saba et al. 2014) and the relative abundance, calculated from CHEMTAX, for the major phytoplankton taxa over the full summer season.

Highest concentrations and the inter-annual variability in chl-*a* were associated with the dynamics in diatoms and cryptophytes (Figure 11). Mixed flagellates showed limited interannual variability but were a consistent component to the overall phytoplankton population. Diatom blooms accounted for the largest phytoplankton blooms in the region and the highest chl-*a* concentrations were associated with shoaling seasonal mixed layer depths in the summer [28], , while cryptophytes blooms occurred during the summer and were associated with glacial melt-water after sea ice retreat.

Antarctic coastal waters are highly productive with a short summer growing season initiated when light levels are sufficiently high to support photosynthesis [30][31]. The phytoplankton productivity supports an extensive food web with krill as a keystone trophic link between primary producers and top predators [32][33]. The interannual variability in the summer diatom productivity in the WAP [15] is associated with krill recruitment [20], which is consistent with the Antarctic paradigm of a short diatom−krill−top predator food chain. In summer seasons with lower phytoplankton biomass there is an enhanced proportion of the chl-*a* being associated with cryptophytes, which represents a shift in the overall size spectrum of the primary producers. Bloom-forming diatoms range in size from 15 to 270 μm [34][35], while the Antarctic cryptophytes have been measured microscopically to be 8 $\pm$ 2 μm [36]. The shift in the nature of the phytoplankton community suggests the importance of regenerated communities in the WAP, which is consistent with other studies that have stressed the importance of microzooplankton grazing on smaller size phytoplankton [37][38][39].

The results of Saba et al [20] and this study support an ecosystem view, where periodic high productivity diatom-dominated years are associated with specific environmental conditions eliciting an immediate response in krill recruitment followed by a series of lower productivity years associated with lower krill recruitment. The switch to a multivorous community provides sufficient food for the krill population to mature [20] despite lower biomass and an overall smaller sized phytoplankton communities. Ensuring a stable community over time would require periodic high productivity diatom summers to ensure high krill fecundity to replenish the aging populations.

V. ACKNOWLEDGMENTS

The research was supported by the LTER Program of the US National Science Foundation (ANT-0823101). Data from the PAL-LTER data repository were supported by Office of Polar Programs, NSF Grants OPP-9011927, OPP-9632763 and OPP-0217282. We also are grateful from funding provided by NASA Award NNX14AL86G.

IV. REFERENCES

[1] Clarke A., Murphy, E.J., Meredith, M.P., King, J.C., Peck, L.S., Barnes, D.K.A., Smith, R.C. 2007. Climate change and the marine ecosystem of the western Antarctic Peninsula. *Philosphical Transactions of the Royal Society of London B* 362, 149–166. doi:10.1098/rstb.2006.1958

[2] Schofield, O., Ducklow, H.W., Martinson, D.G., Meredith, M.P., Moline, M. A., Fraser, W. R. 2010. How do polar marine ecosystems respond to rapid climate change? *Science* 328, 1520 DOI: 10.1126/science.1185779

[3] Skvarca, P., Rack, W., Rott, H. 1999. Climatic trend and the retreat and disintegration of ice shelves on the Antarctic Peninsula: an overview. *Polar Research* 18, 151–157.

[4] Vaughan, D. G., Marshall, G. J., Connolley, W. M., Parkinson, C., Mulvaney, R., Hodgson, D. A., King, J. C., Pudsey, C. J., Turner, J. 2003 Recent rapid regional climate warming on the Antarctic Peninsula. Climatic Change 60, 243-274.

[5] Turner, J., and others. 2005. Antarctic climate change during the last 50 years. *International Journal of Climatology* 25: 279–294, doi:10.1002/joc.1130

[6] Cook A.J. Fox, A.J., Vaughan, D.G., Ferrigno, J.G. 2005. Retreating glacier fronts on the antarctic Peninsula over the past half-century. *Science* 308, 541–544.

[7] Stammerjohn, S.E., Martinson, D.G., Smith, R.C., Iannuzzi, R.A. 2008. Sea ice in the western Antarctic Peninsula region: Spatio-temporal variability from ecological and climate change perspectives. *Deep Sea Research II* 55, 2041-2058.

[8] Rignot, E., Bamber, J.L., Van den Broeke. 2008. Recent Antarctic ice mass loss from radar interferometry and regional climate modeling. *Nature Geoscience*. 1: 106-110.

[9] Vaughan, D. G., Marshall, G. J., Connolley, W. M., Parkinson, C., Mulvaney, R., Hodgson, D. A., King, J. C., Pudsey, C. J., Turner, J. 2003 Recent rapid regional climate warming on the Antarctic Peninsula. *Climatic Change* 60, 243-274.

[10] Smith, R.C., Ainley, D., Baker, K., Domack, E., Emslie, S., Fraser, B., Kennet, J., Leventer, A., Mosley-Thompson, E., Stammerjohn, S., Vernet,

M. 1999. Marine ecosystem sensitivity to climate change. *Bioscience* 49(5): 393-404.

[11] Ducklow, H.W., Baker, K., Martinson, D.G., Quetin, L.B., Ross, R.M., Smith, R.C., Stammerjohn, S.E., Vernet, M., Fraser, W. 2007. Marine ecosystems: The West Antarctic Peninsula. *Philosophical Transactions of the Royal Society of London B* 362, 67-94.

[12] Prézelin B.B., Hofmann E.E., Mengelt C., Klinck, J. M. 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.

[13] Smith, R.C., Martinson, D.G., Stammerjohn, S.E., Iannuzzi, R.A., Ireson, K., 2008. Bellingshausen and Western Antarctic Peninsula region: pigment biomass and sea ice spatial/temporal distributions and interannual variability. *Deep-Sea Research II*, 55 doi:10.1016/j.dsr2.2008.04.027

[14] Serebrennikova, Y.M., Fanning, K.A. 2004. Nutrients in the Southern Ocean GLOBEC region: variations, water circulation, and cycling. Deep-Sea Research II 51, 1981–2002. (doi:10.1016/j.dsr2.2004.07.023)

[15] Ducklow, H., Clarke, A., Dickhut, R., Doney, S.C., Geisz, H., Huang, K., Martinson, D.G., Meredith, M.P., Moeller, H.V., Montes-Hugo, M., Schofield, O., Stammerjohn, S.E., Steinberg, D., Fraser, W. 2012. Marine pelagic ecosystems: the West Antarctic Peninsula, in Antarctica: An Extreme Environment in a Changing World, ed. A.D. Rogers, Wiley.

[16] Clarke, A., Meredith, M. P. M., Wallace, M. I., Brandon, A., Thomas, D. N. 2008. Seasonal and interannual variability in temperature, chlorophyll, and macronutrients in thenortherm Marguerite Bay, Antarctica. *Deep-Sea Res. Part I*I. 55: 1988-2006. Doi:10.1016/j.dsr2.2008.04.035

[17] Holm-Hansen, O., Mitchell, B.G. 1991. Spatial and temporal distribution of phytoplankton and primary production in the western Bransfield Strait region. *Deep-Sea Research* 38, 961–980. doi:10.1016/0198-0149(91)90092-T

[18] Kim, H., Doney, S. C., Iannuzzi, R. A., Meredith, M. P., Martininson, D. G., Ducklow, H. W. 2016. Climate forcing for dynamics of dissolved inorganic nutrients at Palmer Station, Antarctica: An interdecadal (1993-2013) analysis. *Journal of Geophysical Research: Biogeosciences* 12, doi: 10.1002/2015JG003311

[19] Montes-Hugo, M., Doney, S.C., Ducklow, H.W., Fraser, W., Martinson, D., Stammerjohn, S.E., Schofield, O. 2009 Recent Changes in Phytoplankton Communities Associated with Rapid Regional Climate Change Along the Western Antarctic Peninsula. *Science* 323, 1470-1473.

[20] Saba, G.K., Fraser, W.R., Saba, V.S., Iannuzzi, R.A., Coleman, K.E., Doney, S.C., Ducklow, H.W., Martinson, D.G., Miles, T.N., Patterson-Fraser, D.L., Stammerjohn, S.E., Steinberg, D.K., Schofield, O. 2014. Winter and spring controls on the summer food web of the coastal West Antarctic Peninsula. *Nature Communications* 5: 4318 doi: 10.1038/ncomms5318

[21] Whitaker, T.M. 1982. Primary production of phytoplankton off Signy Island, South Orkneys, the Antarctic. *Proceedings of the Royal Society of London*, 214, 169–189.

[22] Krebs, W.N. 1983. Ecology of neritic marine diatoms, Arthur Harbor, Antarctica. *Micropaleontology* 29: 267-297.

[23] Garibotti, I.A., Vernet, M., Ferrario, M.E., Smith, R.C., Ross, R.M., Quetin, L.B. 2003. Phytoplankton spatial distribution patterns along the Western Antarctic Peninsula (Southern Ocean). *Marine Ecology Progress Series* 261, 21-39. [24] Rodriguez, F., Varela, M., Zapata, M. 2002a. Phytoplankton assemblages in the Gerlache and Bransfield Straits (Antarctic Peninsula) determined by light microscopy and CHEMTAX analysis of HPLC pigment data. *Deep Sea Research Part II*. 49: 723-747.

[25] Moline, M.A., Claustre, H., Frazer, T.K., 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.

[26] Oliver, M. A., Irwin, A., Moline, M. A., Fraser, W., Patterson, D., Schofield, O., Kohut, J. 2013. Adelie penguin foraging location correlated with local tides. *Plos ONE*. E55163 doi:10.1371/journal.pone.0055163.

[27] Schofield, O., Duclow, H., Bernard, K., Doney, S., Fraser-Patterson, D., Gorman, K., Martinson, D., Meredith, M., Saba, G., Stammerjohn, S., Steinberg, D., Fraser, W. 2013. Penguin biogeography along the West Antarctic Peninsula: Testing the canyon hypothesis with Palmer LTER observations. *Oceanography* 26: 78-80.

[28] Carvalho, F., Kohut, J., Oliver, M. J., Sherrell, R. M., Schofield, O. 2016. Mixing and phytoplankton dynamics in a submarine canyon in the West Antarctic Peninsula. *Journal of Geophysical Research* doi: 10.1002/2016JC011650

[29] Carvalho, F., Kohut, J., Oliver, M. J., Schofield, O. 2017. Defining the ecologically relevant mixed-layer depth for Antarctica's coastal seas. *Geophysical Research Letters* 44 doi:10.1002/2016GL071205.

[30] Smith R.C., Dierssen H., Vernet M. 1996. Phytoplankton biomass and productivity in the western Antarctic Peninsula region. In: Ross R., Hofmann E., Quetin L. (eds) Foundation for ecological research west of the Antarctic Peninsula. American Geophysical Union, Washington, DC, p 333−356

[31] Vernet M., Martinson D., Ianuzzi R., Stammerjohn S., Kozlowski, S., Sines, K., Smith, R. C., Garibotti. 2008. Primary production within the sea-ice zone west of the Antarctic Peninsula. I. Sea ice, summer mixed layer, and irradiance. *Deep-Sea Research II* 55: 2068−2085.

[32] McWhinnie M.A., Denys C.J. 1980. The high importance of the lowly krill. *Natural History* 89: 66−73.

[33] Valiela I. 1995. Marine Ecological Processes. Springer, New York, NY

[34] Kopczynska E.E. 1992. Dominance of microflagellates over diatoms in the Antarctic areas of deep vertical mixing and krill concentrations. *Journal of Plankton Research*, 14, 1031–1054.

[35] Moline M.A., Prézelin B.B. 1996. Palmer LTER 1991–1994: 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.

[36] McMinn A. Hodgson D. 1993 Summer phytoplankton succession in Ellis Fjord, eastern Antarctica. *Journal of Plankton Research*. 15, 925–938.

[37] Hewes C., Sakshaug E., Holm-Hansen O. 1985. Alternative pathways at lower trophic levels in the Antarctic food web. In: Siegfried W, Condy P, Laws R (eds) Antarctic Nutrient Cycles and Food Webs. Springer, Berlin, p 277–283

[38] El-Sayed S. 1988. Productivity of the southern ocean: a closer look. *Comparative Biochemistry and Physiology B* 90: 489−498

[39] Garzio, L. M., Steinberg, D. K. 2013. Microzooplankton community composition along the Western Antarctic Peninsula. *Deep Sea Research I* 77: 36-49. doi.org/10.1016/j.dsr.2013.03.001