PHYSICAL FORCING OF PHYTOPLANKTON COMMUNITY STRUCTURE IN CONTINENTAL SHELF WATERS OF THE WESTERN ANTARCTIC PENINSULA

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ABSTRACT

A previous study of the western Antarctic Peninsula (WAP) continental shelf that was based upon a multidisciplinary data set collected during austral summer of January 1993 identified a mechanism previously unrecognized that sets up a physical and chemical structure that supports enhanced biological production. This biological production occurs when the southern boundary of the Antarctic Circumpolar Current (ACC) flows along the shelf edge and produces onshelf intrusions of nutrient-rich Upper Circumpolar Deep Water (UCDW), thereby allowing site-specific diatom-dominated phytoplankton communities to develop. The enhanced biological production potentially affects all components of the marine food web in this region. In this analysis, we extend the area and seasons studied through similar analyses of multidisciplinary data sets collected on four additional cruises that cover all seasons. We find that this newly recognized forcing is active in other regions of the WAP shelf where similar conditions are found, is episodic, and is forced by non-seasonal physical processes. The meander frequency of the ACC has consequences for the timing and location of UCDW intrusions. When multiple intrusions are observed, each event may be in a different stage. Further, the occurrence of an event in one area does not necessarily imply that similar events are ongoing in other areas along the WAP shelf. While these UCDW upwelling events originate along the outer shelf, they have a signature that extends into the inner shelf region because of the deep topography which allows the inner shelf to be connected to the outer shelf. The frontal boundary between the intruded water and the shelf water is variable in location because of the episodic nature of the onshelf intrusions, being moved further inshore when one of these events is occurring. The frontal boundaries are characterized by distinct phytoplankton communities whose distribution along the circulation structure is identifiable by the unique presence of a chemotaxonomic marker (Chlorophyll b) in the near surface waters. These observations show clearly that the phytoplankton community structure on the WAP shelf is determined by physical forcing. Moreover, variability in this physical forcing, such as may occur via climate change, can potentially affect the overall biological production of the WAP continental shelf system.

INTRODUCTION

Recent analyses of coincident environmental and biological data sets collected in January 1993 along the continental shelf of the west Antarctic Peninsula (WAP) [Prézelin et al., 2000, *Journal of Marine Research*] identified a mechanism previously unrecognized that sets up a physical and chemical structure that supports enhanced biological production. This mechanism is provided by onshelf subsurface intrusions of Upper Circumpolar Deep Water (UCDW) which then upwell, producing elevated silicate/nitrate ratios and/or other constituents, such as trace metals. The result is diatom-dominated phytoplankton assemblages. Outside of these upwelling regions, which are associated with topographic variations, phytoplankton communities are dominated by taxa other than diatoms. Thus, the physical environment is a primary factor in structuring the phytoplankton community composition (Figure 1) and this physical-biological structure is reflected in the overall food web of the western Antarctic Peninsula.

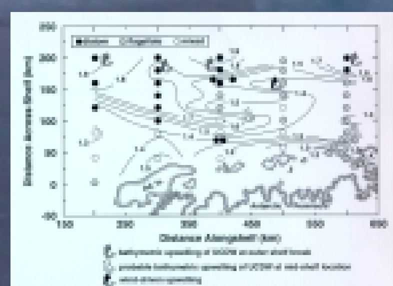

Figure 1. Summary of dominant phytoplankton community composition measured in January-February 1993 overlaid on the temperature maximum distribution below 250 m. The diatom-dominated communities are comprised of > 60% diatoms; flagellate-dominated communities are comprised of > 60% prymnesiophytes + pelagophytes; and mixed communities are those in which no algal group was > 60%. The grey arrows indicate the sites where upwelling of UCDW was due to bathymetric effects. The site of recent wind-induced upwelling is indicated by the black arrows; the clear arrow indicates a site of potential wind-induced upwelling. Figure from Prézelin et al. (2000, JMR).

The analyses presented in Prézelin et al. (2000) are confined to a time in the austral summer when the WAP continental shelf is ice free, light is available, grazing is potentially at a maximum, surface mixed layers and/or seasonal pycnocline exist, and surface water temperatures are maximum. Also, this study focused on a limited region (400 km alongshore) of the WAP shelf. Thus, for the mechanism described by Prézelin et al. (2000) to be considered general it is necessary to address the question: Is the newly recognized forcing seasonally dependent and/or representative of processes over a larger portion of the WAP continental shelf?

Table 1. Summary of cruises to the west Antarctic Peninsula.

Dates	Number of CTD Stations	Number of Biological Stations	Area Covered (km^2)
7 to 21 November 1991	27	19	20,000
January to February 1993*	47	40	80,000
25 March to 15 May 1993	155	79	180,000
23 August to 30 September 1993	42	34	60,000
11 January to 7 February 1994	48	28	54,000

*Data from January-February 1993 are presented in Prezelin et al. (2000) and reprints of this paper are available.

To address this question we examined data from four additional cruises (Table 1) to the WAP shelf that overlap and extend the spatial coverage of the January 1993 data set. These additional data sets used sampling, methodology, and analytical procedures that were identical to those used for the January 1993 data set. The data from these cruises allow coverage of all seasons as well as a repeat of the austral summer period. Four of the five cruises used in these analyses are from the same year which allows an assessment of changes of variable dynamics on time scales of a few weeks to months.

RESULTS: TEMPERATURE MAXIMUM BELOW 200 M

The distribution of the temperature maximum below 200 m (Fig. 2) shows the movement of UCDW onto the west Antarctic Peninsula continental shelf. The southern boundary of the Antarctic Circumpolar Current (ACC) is indicated by the 1.8°C isotherm, water warmer than 1.5°C indicates unmodified UCDW, and temperatures less than 1.5°C indicates UCDW that has mixed with shelf water (modified UCDW). Characteristics of the individual distributions are:

November 1991 (Fig. 2A) - UCDW is present along the outer portion of the study region; central and inner shelf is covered by modified UCDW.
NOTE: Sea ice was present over the study region during this period.

March-May 1993 (Fig. 2B) - The southern boundary of the ACC is located along the outer shelf region and has meandered onshelf at the southern, central and northern parts of the study region; modified UCDW is found over the majority of the central and inner shelf; isolated areas of 1.5°C water in the southern portion of the study region are associated with relatively new onshelf intrusions of UCDW.

August-September 1993 (Fig. 2C) - The southern boundary of the ACC has meandered onshelf and an intrusion of UCDW is occurring on the outer portion of the shelf in the southern part of the study region; the central and inner shelf are covered by modified UCDW.

January-February 1994 (Fig. 2D) - The southern boundary of the ACC is located along the outer portion of the southern study region; modified UCDW covers the central and inner shelf; the region of 1.5°C water in the central portion of the study region indicates newly intruded UCDW that may have been stranded on the shelf.

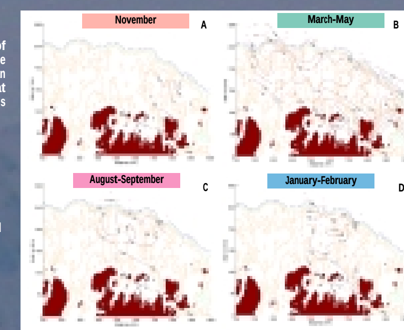

Figure 2. Distribution of the temperature maximum below 200 m observed A) November 1991, B) March-May 1993, C) August-September 1993, and D) January-February 1994.

RESULTS: PERCENT DIATOM COMMUNITY

The hypothesis being tested is that diatom-dominated phytoplankton assemblages are associated with regions where UCDW intrudes onto the WAP continental shelf. Thus, the relative percentage of diatoms versus other phytoplankton taxa (e.g. phytoflagellates) provides a means for testing this when used in conjunction with the environmental data sets.

November 1991 (Fig. 4A) - Diatom-dominated phytoplankton communities are found in the inner portion of the study region; the two inner-most stations on the northern transect were characterized by diatom abundance that was in excess of 65% (not shown).

March-May 1993 (Fig. 4B) - Diatom-dominated phytoplankton communities occur over essentially the entire central shelf region; less than 50% dominance by diatoms occur along the outer shelf region; less than 50% diatom dominance occurs in the inner shelf.

August-September 1993 (Fig. 4C) - Diatom-dominated communities cover the outer, central and inner shelf over most of the study region; lowest diatom abundance occurs at the southern part of the study region at the outer shelf.

January-February 1994 (Fig. 4D) - Low diatom abundance is found over the entire study region; some increase in diatom abundance at the outer shelf.

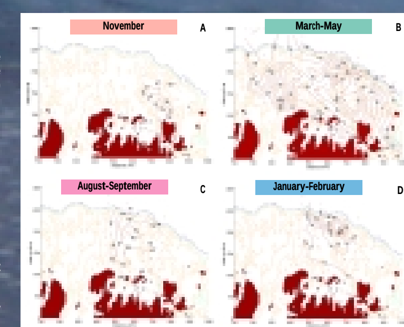

Figure 4. Distribution of the percentage of diatoms in the phytoplankton community observed A) November 1991, B) March-May 1993, C) August-September 1993, and D) January-February 1994. Values represent integrations of fucoxanthin pigment concentrations over the upper 100 m of the water column.

INTRUSION DEVELOPMENT

Comparison of the integrated nutrient ratios for all cruises (Figure 6) shows a progression that is consistent with a region that is undergoing episodic forcing that in turn produces variability in the phytoplankton community assemblages. Periods of no or minimal intrusion effect, such as January 1994, are characterized by average silicate:nitrate ratios, high nitrate:phosphate ratios, and dominance by phytoflagellates. The January 1993 period represents forcing by a new intrusion and a mature intrusion stranded on the shelf (see Prézelin et al. 2000 for details) and the corresponding nutrient ratios show this progression. The March-May 1993 period represents strong forcing by multiple intrusions and the August 1993 period is representative of an early stage intrusion. The November 1991 data set, however, does not fall within these patterns. November 1991 was a heavy sea ice year and about one-half of the nutrient and phytoplankton measurements for this period are from the marginal ice zone. Thus, the sea ice is playing a role in structuring the phytoplankton community assemblages.

The more extensive space and time coverage of the March-May 1993 cruise provides good resolution of multiple intrusion events that span a range physical and biological development. Each was characterized by a dominant phytoplankton community, different physiological states (as evidenced by the nutrient ratio distributions), and different environmental conditions.
The characteristics of the different intrusion stages are summarized as:

New UCDW intrusion - confined to outer shelf, water temperatures of 1.8 to 1.5°C at 200-250 m, silicate:nitrate ratio of 2.8 to 3.5 at 200 m, nitrate:phosphate ratios of 10 to 12, low phytoplankton biomass, diatom-dominated community developing

UCDW intrusion that is upwelling/exchanging with surface waters - water temperatures of 1.8 to 1.5°C, silicate:nitrate ratio decreasing, nitrate:phosphate ratio increasing, diatom dominance increasing relative to background value, potential biomass increase (possibly not observed due to advection and/or grazing), onshelf movement of temperature maximum

Well-developed UCDW intrusion - temperature maximum moved onto shelf and extending to mid to inner shelf region, water temperatures of 1.4 to 1.6°C, silicate:nitrate ratio of less than 2.0 at depth of 200 m, nitrate:phosphate ratio of 12 to 14, dominance by diatoms decreasing, increase in phytoflagellates and other phytoplankton species, potential biomass increase (possibly not observed due to advection and/or grazing)

Old/waning UCDW intrusion - Stranded on shelf/detached from southern ACC boundary, water temperatures of 1.5 to 1.35°C, silicate:nitrate ratio increases above 2.0, nitrate:phosphate ratio decreases, diatom dominance decreases, dominance by other phytoplankton taxa increases

Non-UCDW intrusion - water temperatures less than 1.3°C at 200 m, variable nutrient ratios, variable nutrient concentrations, and mixed phytoplankton community. These conditions occur in the areas affected by outflow from Gerlache Strait and the coastal current frontal boundary. Other regions, such as semi-enclosed bays, are similar, but may have dominance by diatoms or other taxa at certain times.

RESULTS: SILICATE TO NITRATE RATIO AT 200 M

The silicate:nitrate ratio provides a history of the water masses on the WAP continental shelf. New intruded UCDW has a ratio of 3.0-3.5. Deviations from this ratio are suggestive of biological modification of this water as it moves onto the continental shelf, as described below.

November 1991 (Fig. 3A) - Reduced values are found throughout the area sampled; increased ratio values are found around the outer part of the study area.

March-May 1993 (Fig. 3B) - Reduced values are found along the outer part of essentially the entire region; the higher values in the central-inner shelf in the southern portion of the study region are indicative of newly intruded UCDW; the ridge of higher ratio values across the central shelf suggests recent intrusions of UCDW that may have become stranded; ratio values in excess of 2.6 over most of the shelf suggest that UCDW has recently covered the region.

August-September 1993 (Fig. 3C) - Ratio values less than 2.0 occur in the outer and central shelf in the southern part of the study region: ratio values over the remainder of the study region are between 2.0 and 2.5,

January-February 1994 (Fig. 3D) - Low ratio values are found along the outer shelf region and over the shelf in the northern and southern portions of the study region; ratios in excess of 2.0 are only found at at the outer shelf in the southern part of the study region.

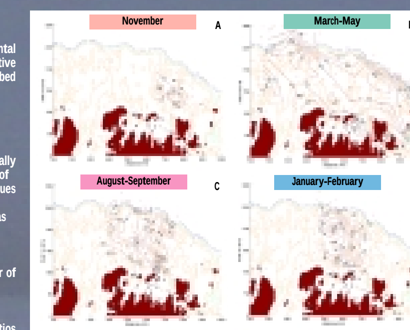

Figure 3. Distribution of the silicate to nitrate ratio at 150 to 200 m observed A) November 1991, B) March-May 1993, C) August-September 1993, and D) January-February 1994. Nutrient ratio values represent integrations over the upper 150 m of the water column.

RESULTS: PHYTOPLANKTON PIGMENT DISTRIBUTION

The spatial distribution of pigments provides an approach for characterizing the phytoplankton community composition and the progression of species assemblages in response to physical forcing. The dominant pigment communities (Fig. 5), defined as presence greater than 50%, provides a means of relating phytoplankton distribution to the distribution of the temperature maximum and the silicate:nitrate ratio. For the following plots the large circles represent a dominance of greater that 50%. The hatched circles represent the phytoplankton population that would have been dominant had either of the less dominant pigments not been present. The different pigment groups are shown as: lavender color represents Prymnesiophytes; brown represents Diatoms; green represents Chlorophyll b; gold represents Dinoflagellates.

November 1991 (Fig. 5A) - Prymnesiophytes dominate the outer study region; diatoms dominate the inner region; enhanced chlorophyll b concentrations are associated with the mixed pigment community between the two dominant groups.

January-February 1993 (Fig. 5B) - Diatom-dominated communities are found on the outer shelf; prymnesiophytes are found on the inner shelf; increased chlorophyll b concentrations are associated with mixed communities; low concentrations of dinoflagellates occur in the mid-shelf area.

March-May 1993 (Fig. 5C) - Diatom-dominated communities cover most of the shelf area; chlorophyll b concentrations are higher than in other seasons and cover much of the shelf; highest chlorophyll b concentrations are associated with regions characterized by mixed communities.

August-September 1993 (Fig. 5D) - Diatoms dominate the study region; prymnesiophyte-dominated communities are found only along the southern part of the study region and at the ends of the across-shelf transects; chlorophyll b concentrations are low over the entire region.

January-February 1994 (Fig. 5E) - Prymnesiophytes and dinoflagellates dominante the study region; chlorophyll b concentrations are low.

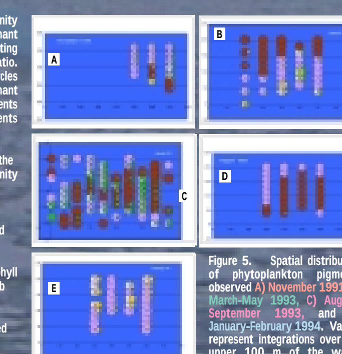

Figure 5. Spatial distribution of phytoplankton pigments observed A) November 1991, B) March-May 1993, C) August-September 1993, and D) January-February 1994. Values represent integrations over the upper 100 m of the water column. The large circles represent a dominance of greater that 50%. The hatched circles represent the phytoplankton population that would have been dominant had either of the less dominant pigments not been present. The different pigment groups are shown as: lavender represents Prymnesiophytes; brown represents Diatoms; green represents Chlorophyll b; gold represents Dinoflagellates.

CIRCULATION PATTERNS AND PHYTOPLANKTON COMMUNITIES

A dominant pattern seen in the distribution of the temperature maximum below 200 m is the onshelf intrusion of UCDW, which originates off the shelf in response to variability in the southern boundary of the ACC. The southern boundary of the ACC is seen along the outer shelf in all cruises (Fig. 2) and onshelf movement of UCDW occurs at the outer shelf in the southern (Figs. 2B-D) and northern (Figs. 2A-D) study region. Thus, these locations are preferred sites for onshelf movement of this water. Subsequent upwelling of the UCDW provides an environmental structure that is conducive to the development of diatom-dominated phytoplankton communities (Fig. 4), which is seen in reduced silicate:nitrate ratios (Fig. 3) and phytoplankton pigment distribution (Fig. 5).

The intrusions move onshelf and in some areas extend into the inner shelf region via deep across-shelf troughs that connect the inner and outer shelf regions. This produces the regions of enhanced diatom abundance along the inner shelf in the southern part of the study region observed in the March-May 1993 cruise (Fig. 4B), for example. This area is transected by the Marguerite Trough, which allows UCDW to move from the outer shelf into Marguerite Bay. Similarly, the high diatom abundances along the middle portion of the study area (Fig. 4B,C) may be sustained by across-shelf movement of UCDW via the trough that extends from the shelf break towards Anvers Island.

The frontal boundary between the newly intruded UCDW and the modified CDW that covers the shelf below the permanent pycnocline provides a second type of circulation structure on the WAP continental shelf. The location of this frontal boundary is variable because of the episodic nature of the onshelf intrusions. It is found further inshore when one of these events is occurring. This boundary forms another distinct phytoplankton community structure that is characterized by the presence of chlorophyll b, no to low diatoms biomass, and phytoflagellate-dominated communities (Fig. 5). Thus, this phytoplankton assemblage represents a transitional community between oceanic and shelf populations.

The inner portion of the WAP is characterized by a southerly-flowing coastal current which is characterized by low salinity and temperature, which produces a frontal boundary with shelf waters. This inner shelf current is best resolved by the March-May 1993 cruise (Fig. 2B) and the phytoplankton assemblages associated with it at this time were not dominated by diatoms (Fig. 4b).

Temperature and phytoplankton observations from the near vicinity of Anvers Island tend to appear anomalous relative to adjacent observations (not shown). This area is affected by outflow from the Gerlache Strait and as such it represents an environment with different environmental conditions. This this represents a fourth type of habitat.

The phytoplankton community assemblages from the November 1991 cruise show a large diatom-dominated phytoplankton bloom in the inner portion of the northern-most across-shelf transect (not shown). This bloom occurred early in the austral spring in a semi-enclosed bay and was associated with the marginal ice zone.

TEMPORAL VARIATIONS

Seasonal independence. An important conclusion arising from the comparisons between the series of cruises is that phytoplankton production on the WAP is SEASONALLY INDEPENDENT. What is observed on this shelf supports episodic production that is driven by variability in the southern boundary of the ACC relative to the WAP shelf break which in turn is is driven by larger scale climate-related processes rather than by local seasonal forcing.

The temperature and phytoplankton distributions from January 1994 show no UCDW intrusions on the WAP shelf, mixed phytoplankton assemblages, and average nutrient ratios. These distributions likely represent a baseline state for the WAP continental shelf. It should be noted that these conditions were observed in the austral summer when conditions are optimal for biological production. Thus, intrusions of UCDW are needed to stimulate phytoplankton community development/succession and biological production (evidenced by changes in nutrient ratios) on the WAP continental shelf.

Temporal variability of individual intrusion events. The occurrence and progression of an intrusion event in one area of the shelf is independent of intrusions that are occurring in other regions of the WAP shelf. Thus, at any given time one or more intrusions, in different stages of development, may be present on the WAP continental shelf. This can provide considerable spatial variability in production which must be taken into account when attempting system-wide production estimates.

FINAL COMMENTS:

Why are UCDW intrusions an unrecognized process on Antarctic continental shelves?

1- Previous studies have not routinely measured phytoplankton community composition, so part of the reason for not recognizing the importance of this process can be attributed to sampling approaches. Future studies of biological production on Antarctic continental shelves should incorporate community composition measurements.

2- Biological studies typically focus on the upper 100 m of the water column, which does not capture the subpycnocline inputs of UCDW. Thus, the role of deeper processes in controlling upper water column phytoplankton community structure is not recognized. Antarctic continental shelf waters are weakly stratified which allows tight coupling between deep and surface processes. This characteristic of the environment needs to be incorporated into biological studies.

3- The phytoplankton communities that develop in response to intrusion and subsequent upwelling of UCDW are at depths that are not detectable via remote sensing of chlorophyll distributions with sensors such as SeaWiFS. An implication of this is that primary production estimates made for Antarctic continental shelf waters from ocean color data will be underestimates.

4- Generally low chlorophyll biomass is observed in Antarctic shelf waters, which can be assumed to indicate low production. However, the low biomass may reflect 1) heavy grazing of a highly productive system and 2) a high probability of advective loss via the ACC and shelf currents. Thus, chlorophyll biomass estimates should be constrained with coincident measures of primary production rates, grazer biomass, grazer rates, and circulation.

5- The traditional method of estimating primary production is based on radio isotope methods that provide instantaneous rates. These approaches generally underestimate production rates. Nutrient drawdown methods give higher production rates, especially for environments that are characterized by high grazing and advection. Thus, future studies of primary production on Antarctic continental shelves should incorporate more than one approach for estimating rates.

6. Subsurface intrusions of oceanic waters have been observed in other regions, such as the southeastern U.S. continental shelf, the east coast of Japan, the west coast of South Africa, and east coast of Australia. Estimates of the nutrient and carbon fluxes associated with intrusion events on these continental shelves show that these events account for the majority of the organic matter production. Thus, the existing historical data sets for Antarctic continental shelf would benefit from reanalysis.

7. The subsurface intrusions UCDW on the WAP continental shelf provides a mechanism to 'push and pull' material off the shelf at some frequency that is related to the location of the southern boundary of the ACC. Thus, studies of this region need to take into account the ACC and be flexible enough to adapt to sampling a variable environment. Failure to do this, will result in missing a major portion of the signal that is controlling the biological production of this system.

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