Response to comments on the submitted manuscript: Greaves et al. - *The Southern Annular Mode (SAM) influences phytoplankton communities in the seasonal ice zone of the Southern Ocean*

13 February 2019

We thank the reviewer for their valuable feedback on this manuscript. These have identified several areas for improvement of the manuscript, which we have addressed below:

RC1 - Anonymous Referee #1, 16 November 2019

In this manuscript entitled "The Southern Annular Mode (SAM) influences phytoplankton communities in the seasonal ice zone of the Southern Ocean", the authors examine the role of SAM on phytoplankton communities in the SIZ of the Southern Ocean.

I think the document is not yet ready to be published, although the subject and results are really interesting.

- Certainly, the results are very interesting

The structure of the document is really difficult to follow at the moment.

- We have carefully reviewed and improved the structure of the manuscript in reference to the comments of both reviewers

I have listed some improvements that could be made to improve the clarity of the manuscript.

General comments: My main concern is related to the structure of the document, to many subsections, particularly in the sections on results and discussion (8 subsections for discussion, and 2 sentences for conclusion, 1 sentence in the section on results (3.1). The document, as it is now, is unbalanced and difficult to read and needs to be reorganized around major themes (seasonal, interannual variability and impact on phytoplankton communities for example for the discussion).

- We have refined the manuscript structure, which we consider will fix this issue

In this paper, the authors examined the role of SAM and seasonal variability on changes in phytoplankton communities, but some key environmental factors are really missing in this study, (1) mixing estimates (by estimating the depth of mixed layers, deriving wind stress)

- We don't have this information for each sample, or for the time periods prior – we are surmising that SAM influences wind-speed and subsequently mixed-layer-depth from the previously published observed and predicted positive relationship between the SAM and wind speed.
- While we are unable to estimate the correlations the referee asks for it is behest upon us to ensure that these factors are included in the manuscript, the variance from which probably contributes to the 62.5% of unexplained residual variance in this study

and (2) light measurements (in situ or satellite data)?

- We don't have this information for each sample

Because it can be suspected that changes in the intensity of the SAM will directly influence light-mixing regimes, and therefore changes in the composition of phytoplankton communities at the time of sampling?

This is particularly important given that the authors mention the interaction between mixing and phytoplankton dynamics in the discussion.

- It has been previously reported that SAM has been observed and predicted to relate to wind intensity (from line 83) – thus we used this to help explain how the identified maxima in SAM relationship with phytoplankton taxonomic composition could be plausible (from line 329)

In addition, the authors focused on understanding changes in the relative abundance of the main phytoplankton groups, but we have no idea how phytoplankton biomass could change annually with the SAM.

- Previous researchers have concluded that long term changes in the SAM will influence productivity: "*Lovenduski and Gruber (2005) predicted that increased SAM would support higher phytoplankton productivity, and subsequent analyses by Arrigo et 90 al. (2008); Boyce et al. (2010), and Soppa et al. (2016) have confirmed a positive relationship between the SAM and phytoplankton standing stocks and productivity south of 60°S in the SIZ*" (from line 88)
- We have now included satellite-derived estimates of Total Chlorophyll as an index of biomass which we had been able to obtain for 49 of the 52 samples, which also show a positive relationship with autumn SAM, i.e. higher SAM in autumn is associated with higher NASA satellite total chlorophyll in the following spring-summer (Table 2, reported in Results from line 294)
- The peak of SAM influence in the preceding autumn was also detected in response surfaces for NASA satellite total chlorophyll (correlation between SAM in autumn and NASA total chlorophyll is 0.5) and nutrient levels (correlation between SAM in autumn and $[PO_4]$ was -0.64 for all samples, and -0.84 for the later-in-season half of the samples) – these response surfaces will be included in the extra material (as drafted below). NASA satellite total chlorophyll and $[PO_4]$ are observationally independent of the taxonomic counts, so similar prior-autumn maxima for the correlation with SAM and these traits are supportive of our finding that "*time-averaged SAM signal in autumn influences phytoplankton community composition in spring to summer*"

The authors mentioned this briefly in the discussion (5.3), but can you access to any vertically integrated biomass proxies (vertically integrated chlorophyll, PP and satellite-derived estimates)?

- We inferred a productivity effect of SAM from nutrient drawdown, which showed reduced nutrients with more positive prior SAM indices, with the relationships with prior SAM indices (***SAM spring***, ***SAM prior***, and ***SAM autumn***) all being stronger when only the samples collected later in the season (the later half of samples) were included. In the SIZ of the Southern Ocean, surface-water nutrition is replenished through the winter by upwelling of deep ocean water at the Antarctic Divergence. The nutrient contents later in the spring-summer better reflect the total production over the spring-summer than do all samples, including those collected earlier in the spring-summer (as tabulated in the new Table 2). We have included the response surfaces for the correlation between the SAM and $[PO_4]$ in Supplementary Material (Fig. S1). This point is now discussed (from line 370)

- We have added NASA satellite total chlorophyll estimates which we had been able to obtain for 49 of the 52 samples, which also show a positive relationship with SAM, i.e. higher SAM is associated with higher NASA satellite total chlorophyll (now in Table 2)

This comment is related to the last one, but we have no idea where we stand with respect to phytoplankton phenology. In Figure 1, it would be nice to have satellite-derived time series of chlorophyll a, for example. The problem I see here is that the SAM could perhaps also change the phytoplankton phenology (bloom duration or timing for example).

- We have added time-series NASA satellite total chlorophyll to Figure 1

And perhaps what the authors have defined as interannual variability driven by the SAM can simply be related to a sampling of different phenological states. It would be important for me to check this point.

- No way to confirm this for certain, however:
- The CAP analysis fits multiple covariates, apportioning variance to each – the variance in community composition explained by the time through the spring-summer that a sample was collected (***DaysAfter1Oct***) was orthogonal to the variance explained by the SAM, and thus we conclude the apparent variance associated with the SAM to be independent of the variance associated with sampling "**different phenological states**" associated with the time through the spring-summer.
- More positive SAM in the prior spring (***SAM spring***) and ***SAM prior*** (SAM prior to each sample) may result in the productive season commencing earlier, and thus organisms that show a decline in relative abundance through the season might show a lower relative abundance at a given time with higher ***SAM spring*** and ***SAM prior*** : 10 of the 22 taxa showed a significant correlation the time through the spring-summer of collection, of these, with 4 taxa showed a relationship with both ***SAM spring*** and ***SAM prior*** supporting the possibility that ***SAM spring*** and ***SAM prior*** were leading to an effective sampling later in the phenotypic succession (i.e. three taxa having negative relationship with sampling date and both ***SAM spring*** and ***SAM prior***, one taxon having positive relationship with sampling date and both ***SAM spring*** and ***SAM prior***). However, the other six taxa showing significant relationship with sampling date did not confirm this relationship.

Specific comments: l.186-186: Can you add a table in the paper or in the supplementary materials listing these taxa (the 4 in all the samples, and the 11 in 90% of the samples)?

- New Table has been added as Table 3, listing taxa

Table: Table 1: Long.E is indicated two times as variable, is it an error?

- Yes, a typing error – the second occurrence of Longitude in Table 1 should have been Latitude – this is now corrected

RC2 - Damiano Righettim, 21 November 2019

(i) Key concepts (SAM or SAM index) are not clearly defined. The SAM definition leaves it open to the reader, how the sign of the SAM index is calculated, and whether atmospheric pressure or water pressure constitutes the SAM index.

- We have edited the text and added more simplistic description of the SAM: in the Introduction from line 66, and in the Methods line 160
- The SAM is an atmospheric index, we will clarify by adding the word "*atmospheric*" to the Introduction paragraph of section 1.2 (line 66)

There is a problem with clarity of statements and consistency of word use (e.g., different expressions are used for the same thing), and a lack of clear correspondence between hypothesis, methods, and key results. I provide detailed examples on clarity below.

- These have been edited to correct inconsistencies

(ii) My main conceptual critique point is that the impact of the time-averaged SAM signal in autumn on phytoplankton community composition in spring to summer has not been firmly tested by the data shown.

- The relationship between time-averaged SAM signal in autumn on phytoplankton community composition was apparent in the analysis, and reasonable (being the time ice was forming) but otherwise untestable. However:
- Correlations with the empirically defined SAM range in the autumn and the relative abundances of 12 of the 22 taxa supported the conclusion. Further:
- The peak of SAM influence in the preceding autumn was also detected in response surfaces for NASA satellite total chlorophyll (correlation between SAM in autumn and NASA total chlorophyll is 0.5) and nutrient levels (correlation between SAM in autumn and [PO_4] was -0.64 for all samples, and -0.84 for samples collected in the latter half of the season) – these response surfaces have been included in the Supplementary Material (Figs. Si and S2). NASA satellite total chlorophyll and [PO_4] are observationally independent of the taxonomic counts. Detecting similar prior-autumn maxima for the correlation with SAM and these traits are supportive of our finding that "*time-averaged SAM signal in autumn influences phytoplankton community composition in spring to summer*" and the discussion has been improved to reflect this (Results line 293, Discussion line 370)

The study demonstrates that it is possible to average the daily SAM index in a way that a significant part of the variation in community composition can be explained in next spring/summer, yet it is unclear why microbial species that live on timescales from days to weeks, would respond to the SAM signal with a time-lag of several months.

- We have included more detail in the discussion to address this issue (Discussion from line 290)

I suggest that relationships between a more positive state of SAM in autumn and temperature, wind speed, mixed-layer depths, and nutrient levels in spring to summer—factors that may directly shape phytoplankton composition—shall be evaluated, to support the paper's message.

- "**relationships between a more positive state of SAM in autumn and temperature, wind speed, mixed-layer depths, and nutrient levels in spring to summer**" are beyond the scope of this paper – The SAM is already a proxy for such variables as wind speed, mixed depth (and thus light availability), nutrient upwelling, all of which are regarded as primary determinants of phytoplankton community structure. Others have made observations/predictions of the influence of the SAM on wind-speed and mixed-layer-depths as cited (from line 82).

- We don't have wind-speed and mixed-layer-depth for each sample, and we would require this information daily for the location of each sample for the year preceding each sample, and arguably for a range of locations around each sample. Whilst this would be an interesting analysis, it is far beyond the scope of this paper, which was to determine if an effect of the SAM could be detected in the taxonomic composition of phytoplankton (as stated in our hypothesis).
- It is possible that SAM in the autumn influences SAM in the following spring – we did not identify a significant correlation between SAM in the autumn and SAM in the following spring (Table 2 of the submitted manuscript)

In section 4 ('Other relationships'), there are several relationships presented between predictors, yet the results are not presented in a structured way to support the hypothesis that SAM-induced changes in temperature, wind-speed, mixed-layer depth or nutrient concentrations affect community composition.

- We have removed the section 'Other relationships' and included relevant findings from this section elsewhere in the Results as appropriate.
- We did not hypothesise that "**SAM-induced changes in temperature, wind-speed, mixed-layer depth or nutrient concentrations affect community composition**", our hypothesis was: "*Based on the predicted and observed positive relationships between the SAM and phytoplankton productivity and biomass in the SIZ of the SO, we hypothesised that changes in the SAM could also elicit changes in the composition and abundance of the phytoplankton community.*" (line 93)

The current association between the SAM signal (or "SAM modes") described and community composition may not be causal. In the context of fast-lived organisms it seems crucial to test if the link between summer community composition and (preceding) SAM is plausible.

- Sure, may not be causal – but it is explicable, as discussed from line 328. Without conducting a series of overwintering experiments, there is no way to check for sure.
- Further, the empirically defined SAM autumn showed pairwise correlations with 12 of the 22 taxa identified.
- Further, SAM maxima were apparent in similar response surface analysis of the correlation between SAM and (a) NASA satellite total chlorophyll, and (b) [PO_4] in all samples, and (c) as a stronger correlation with [PO_4] when only the later-in-the-season half of samples were considered (analysis not included in original manuscript, but now to be included with response surface figures in Supplementary Material – as indicated above)

Recommendations

I suggest that the manuscript is thoroughly screened for clarity.

- We have carefully reviewed and improved the manuscript to improve the clarity, readability and pertinence of the text, including the removal of extraneous words

Second, besides further testing the associations of the SAM signal of autumn with physicochemical factors known to affect phytoplankton composition (and whether these associations are in line with expectation), I suggest splitting the 22 taxa into ecological test groups, which are expected to

respond differently to changing mixing-, wind-, and nutrient patterns under a more positive SAM state. These expectations can be presented as specific hypotheses in the introduction.

- With respect, the niches of Antarctic phytoplankton are not sufficiently well known to identify ecological test groups of phytoplankton that are expected to respond differently to the environmental changes wrought by SAM. Instead and importantly, for the first time this paper identifies indicator species for the effects of SAM: winners and losers under increasingly positive values of SAM.
- We do not believe that we have enough information about enough of the identified taxa to be able to sensibly break the identified taxa into groups that will lead to a sensible group-based analysis of responses to SAM. Not a great deal is known about many identified Southern Ocean polar hard-shelled phytoplankton taxa, which have previously largely been only identified at the genera level, and we have identified significant differences in the behaviour of taxa within single genera.
- We have included discussion around this point from line 389.

Such a biological approach has been partly implemented by comparing small diatoms (presumably better adapted to stable waters) with large diatoms (presumably better adapted to strong mixing). Yet the results of this test lack a graphical presentation in the manuscript, across all taxa.

- We will interpret the observed results with reference to organism size and shape to infer any influence
- However, size is not necessarily a useful parameter upon which to aggregate taxa, as whilst some taxa are always small, others have been identified as both large and small taxa.

Species may be grouped further into warm, temperate, or polar species, depending on their global distributions (e.g. using observations from OBIS and GIBF; Righetti et al., 2019) and their responses may differ under SAM-induced warming/cooling.

- This is implausible. The species are almost exclusively Antarctic in geographic range. The Polar Front is a very effective barrier to the transmission of phytoplankton from warmer waters and, as above, their niches are poorly known. Only 10 of the 22 taxa/taxa-groups considered in our research had data-records in OBIS (table below) – not enough to meaningfully group the taxa for analysis – we have included Discussion around this point from line 389.

Similarly, R-strategist (fast growing, light stress tolerant species) and S-strategists (slow growing, nutrient stress tolerant species) may be grouped together (Brun et al., 2015), as they may respond oppositely to changing nutrient levels.

- Brun et al (2015) reproduces the *R-S-strategist* classification of organisms from Reynolds (2006): of the 22 taxa/taxa-groups in our study, only 4 were classified (as *R-strategists*), and 5 were classified as "*unclassified*", with 15 not included in Brun et al (2015)'s reproduction of Reynolds (2006). Given the paucity of *R-S-strategist* classifications (4 out 22 taxa with classifications) it would be inappropriate to specifically overlay the *R-S-strategist* framework on the taxonomic data we have collected.
- We have included discussion of the *R-S-strategist* classification in our re-worked discussion (from line 390).

Additionally, species with large vs. small cells may show opposite responses to changing turbulence and wind regimes (Margalef, 1997, 1978).

- We were not able to make any meaningful conclusions regarding cell size and shape and the degree of influence of the SAM (some species are always small, others are large and small)

Finally, predicting the response of siliceous vs. calcareous taxa to SAM constitutes an exciting hypothesis: these groups have shown opposite responses to deeper mixing or nutrient entrainment (Cermeño et al., 2008).

- The area studied was the Seasonal Ice Zone (SIZ) which is situated over the ocean upwelling zone of the Antarctic Divergence – nutrients in the surface waters of the SIZ are replenished over the six months when the sea surface is ice-covered and when there is almost no productivity (or consumption of nutrients). It is considered a high-nutrient, low-chlorophyll zone. In this region of annual winter nutrient replenishment, the influence of mixed-layer depth is less than most other areas of the world's ocean. The area falls outside the analysis of Cermeño et al., (2008), whose sampled area extended southward to only well north of the Antarctic Divergence, and would not be expected to conform to the trends observed by Cermeño et al., (2008) due to the replenishment of nutrients every winter in the area of our study.

With respect to the clustering techniques used to describe communities I cannot give detailed recommendations, as the metrics used are beyond my expertise.

Detailed comments

There are too many comments to be listed. I therefore give examples for selected paragraphs, with comments on clarity, for each:

Abstract:

- Line 3: How many variables were tested?

- We have amended the text to include

- Line 6: How many species (genera, higher taxa) were included among the 22 taxa?

- We have amended the text to include

- Line 7: I do not understand 'CAP'. This term has not been introduced.

- We have amended the text to include the full name of the CAP procedure

- Lines 8, 9, 11, 17: The following terms are used: taxonomic community composition, taxa composition, phytoplankton community structure, taxonomic composition of phytoplankton. While I understand that the authors strive to include stylistic variation, the reader is confused by the multiple expressions. Do they denote the same thing or not? I recommend using use the same expression for the same thing. Else, once an expression is clear, an abbreviation of the latter may be used therein, as long as it denotes the same thing.

- We have amended the text to make the terms consistent

- Line 10: Unclear to me, if the correlation is significant or not.

- We have amended the text to include "($p<0.05$)" as appropriate

- Line 13: Unclear to me, if "response" means a response of abundance or not.

- We have amended the text to clarify: "relative-abundance response"

- Line 15: Before, the expression "SAM index" was used, not "higher SAM". Does "higher SAM" refer to a more positive state of the SAM index?

- We have amended the text for consistency in referring to the SAM

- Line 17: Confusing, as taxonomic composition of phytoplankton is not the same thing as a standing stock (or a "pasture") of biomass of phytoplankton.

- We have amended the text to clarify

- Line 16: It is unclear to me, if the expression "pelagic ecosystem" is suitable in the context of a sea ice transition zone.

- We have removed the word "*pelagic*" to avoid confusion

- Line 16: It is unclear, how many of the total species that were studied, responded significantly to SAM. Thus, it is unclear, if this result is important or general.

- We have amended the text to clarify

- Line 10 ff: It is surprising that 'day of sampling' explains more variation in community composition than any other locally sampled environmental factor (SST, nutrients, etc). An interpretation on why this is the case would help the reader to assess the plausibility or importance of this result.

- The seasonal ice zone has been previously observed and reported to have a winter period (around 6 months) with little or no phytoplankton productivity when the sea-surface is frozen, and a well-characterised bloom and systematic taxonomic succession through the spring-summer months as sea-ice melts – we will include this point in the Abstract (it is already in the Introduction and in the Discussion)

Introduction:

- Line 21-23: The first two sentences are partially repetitive.

- We have improved the text (line 26)

- Line 21 ff: The paragraph wants to establish the importance of phytoplankton productivity in the study area for global phytoplankton productivity. While the reader understands that a larger fraction (~30%) of carbon fixed by phytoplankton is exported in the study region, relative to the global average (~ 20% exported) it remains unclear, if the study region is globally important. What is the area-weighted contribution of the study region to global phytoplankton C-export?

- We have included a statement to this effect (line 33)

1.2 The Southern Annular Mode

- Line 58 ff: Clarify the definition of SAM (see above). The reader cannot grasp how the sign of SAM is calculated or linked to changing pressure gradients, and thus how it is associated with physicochemical changes in the study system.

- The calculation of SAM is beyond the scope of this paper, except in the most general terms – the SAM index used was calculated by NOAA (USA) and the wording of its description is as NOAA wants it reported.
- We have edited the text and added more simplistic description of the SAM: in the Introduction from line 66, and in the Methods line 160

- Line 64 ff: SAM vs. SAM index vs. SAM state vs. SAM mode. Please use consistent expressions throughout the manuscript. …… and the use of "mode" in both the context of SAM and community composition may confuse the reader

- We have removed all references to SAM maxima as <u>MODES</u> to remove confusion with <u>MODE</u>=MAXIMA and SOUTHERN ANNULAR <u>MODE</u>, that is, we have just defined the terms *SAM spring* and *SAM autumn* and refer to them by name without using the term "*mode*".

In addition, "taxon" could always refer to both a species and a group of species.

- We have modified the text to use "*taxa-group*" to refer to a single taxa-group

2.1 Phytoplankton composition and abundance

- Line 116: One reads as if the abundance of phytoplankton communities was sampled. As much as I understand, the abundance of species or taxa was sampled. (Then, an abundance-weighted community composition was calculated?).

- We have amended the text to remove any suggestion that "**abundance of phytoplankton communities was sampled**"

2.3 Statistical analysis

- Line 151 ff: The methods section needs clarification, structurally and through editing. In this section, I have difficulties to understand whether three or more sets of analyses were performed based on the phytoplankton field data, and which of these analyses is most important to test the key hypothesis of the paper,

- We will edit methods to improve clarity

….. and at what temporal resolution the analyses were performed.

- We have included more description of the derivation of the response surfaces to improve ease of understanding (from line 204)

- Line 152: Has "community structure" really been correlated to "environmental covariates"? If I understand correctly, the abundance data was related to possible environmental drivers, per species. In this case, please specify: e.g. …and species abundance between samples

- The correlation between the community structure (as determined from the ordination) and each environmental covariate was calculated according the procedure outlined in ter Braak (1995) and attributed to Dargie (1984) – we have included more explanation of CAP analysis for greater ease of interpretation for readers not familiar with CAP analysis (from line 185)

- Line 151 ff: It is not clearly motivated, why clustering of community-level samples is suitable to identify the effect of SAM on community composition. To me, the number of 52 samples seems rather low already, and each degree of freedom may be valuable.

- We have included more descriptive text to clarify (from Methods line 175, and Results line 276)

3. Results

- The first results presented to the reader are abundance-distributions of taxa across samples. Yet, the reader might expect that the most important piece of evidence to elucidate the role of SAM for phytoplankton composition is first presented.

- The logic behind the analysis and presentation of the data in relation to the hypothesis has been explained in the first paragraph of the *Results* section (line 220)
- We have re-arranged the *Results* section to put abundance information later, i.e. Section 3.1 "*Observed abundance*" has become Section 3.3 (line 313), with Section 3.1 becoming "*The influence of SAM on phytoplankton taxonomic composition*"

- Line 206 ff. Can P, n, and R2-values be provided for the correlations?

- The text has been modified to include specification of p with all in-text correlations
- P-values are not tabulated - currently reported correlations in tables are formatted to indicate when $p<0.05$ and when $p<0.05/20$ for Bonferroni correction

- Table 1: I do not understand, why nutrients are excluded in this table.

- nutrient levels are an effect of phytoplankton, not a cause, in this high-nutrient-low-chlorophyll environment that is nutrient-replenished through the winter – i.e. more growth through the productive spring-summer leads to less nutrition at the end of the summer – text has been included to explain this (line 157, 295, 425 onwards)

- Figure 5. The caption remains vague. What are the "several underlying assumptions" of linear regression? Relevant to be discussed in the caption?

- The caption has been improved by removal of the words "*though clearly several underlying assumptions of linear regression would not be met*" from the caption

Overall, the manuscript requires a clear structure in order to show to what degree the SAM signals may matter to community composition, based on (ecological) hypotheses tested and data. The support in the data for this message, and the evaluation of the manuscript are complicated at current and warrant further attention.

- We have made many changes throughout the manuscript to improve clarity and reduce wordage

The Southern Annular Mode (SAM) influences phytoplankton communities in the seasonal ice zone of the Southern Ocean

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Abstract.

Ozone depletion and climate change are causing the Southern Annular Mode (SAM) to become increasingly positive, driving stronger winds southward in the Southern Ocean (SO), with likely effects on phytoplankton habitat due to possible changes in ocean mixing, nutrient upwelling, and sea ice characteristics. This study examined the effect of the SAM and 12 other environmental variables on the abundance of siliceous and calcareous phytoplankton in the seasonal ice zone (SIZ) of the SO. ~~Samples~~ Fifty-two surface-water samples were collected during repeat ~~transects~~ resupply voyages between Hobart, Australia, and Dumont d'Urville, Antarctica, centred around longitude 142° E, over 11 consecutive austral spring-summers (2002 – 2012), and spanning 131 days in the spring-summer from 20th October to 28th February. Twenty-two ~~taxa~~taxa-groups, comprised of individual species, groups of species, genera or higher taxonomic groups, were analysed using CAP analysis (constrained analysis of principal coordinates), cluster analysis and correlation. ~~The SAM significantly affected phytoplankton community composition, with the greatest influence exerted by a SAM index averaged~~ Overall, satellite-derived estimates of total chlorophyll and measured depletion of macronutrients both indicated more positive SAM was associated with greater productivity in the SIZ. The greatest effect of SAM on phytoplankton communities was the average value of SAM across 57 days ~~centred on~~ in the previous austral autumn centred around 11th ~~March in the preceding autumn , explaining~~ of March, which explained 13.3 % of the variance ~~of taxa composition during the following spring-summer, and showing correlation in community composition in the following spring/summer. This autumn SAM index was significantly pair-wise correlated (p<0.05)~~ with the relative abundance of 12 of the 22 ~~taxa resolved. The day through the spring-summer that a sample was collected exerted the greatest influence on phytoplankton community structure (15.4 % of variance explained), reflecting the extreme seasonal variation in the physical environment in the SIZ that drives phytoplankton community succession. The response of different species of *Fragilariopsis* spp. and *Chaetoceros* spp. differed over the spring-summer and with the SAM, indicating the importance of species-level observation in detecting subtle changes in pelagic ecosystems. This study indicated that higher~~ taxa-groups resolved. More positive SAM favoured increases in the relative-abundance of large *Chaetoceros* spp. that predominated later in the spring-summer and reductions in small diatom taxa and siliceous and calcareous flagellates that

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predominated earlier in the spring-summer. ~~Such changes in the taxonomic composition of phytoplankton,~~ Individual species

25 belonging to the abundant *Fragilariopsis* genera responded differently to the SAM, indicating the importance of species-level observation in detecting SAM-induced changes in phytoplankton communities. The day through the spring-summer on which a sample was collected explained a significant and larger proportion (15.4 %) of the variance in the phytoplankton community composition than the SAM, yet this covariate was a proxy for such environmental factors as ice-cover and sea surface temperature; factors that are regarded as primary drivers of the extreme seasonal variability in phytoplankton communities

30 in Antarctic waters. The impacts of SAM on phytoplankton, which are the pasture of the SO and principal energy source for Antarctic life, ~~may alter both carbon sequestration and composition of higher tropic levels of the SIZ region~~ would have ramifications for both carbon export and food availability for higher trophic levels in the SIZ of the SO.

1 Introduction

35 Phytoplankton are the primary ~~produces~~ producers that feed almost all life in the oceans. ~~Seasonal~~ In the Southern Ocean (SO), defined as the southern portions of the Atlantic Ocean, Indian Ocean, and Pacific Ocean south of 60°S (Arndt et al., 2013), spring-summer phytoplankton blooms in the seasonal ice zone (SIZ) ~~of the Southern Ocean (SO)~~ feed swarms of krill which, in turn, are key food for sea-birds, fish, whales and almost all Antarctic life (Smetacek, 2008; Cavicchioli et al., 2019). Phytoplankton also play a critical role in ameliorating global climate change by capturing carbon through photosynthesis. Around

40 one third of the carbon fixed by phytoplankton in SIZ of the SO sinks out of the surface ocean (Henson et al., 2015), ~~appreciably~~ more than the global ocean average of around 20 % (Boyd and Trull, 2007; Ciais et al., 2013; Henson et al., 2015). This sequestration of carbon to the deeper ocean is thought to last for climatically significant periods of time, likely hundreds to thousands of years (Lampitt and Antia, 1997). ~~Consequently,~~ Total productivity within the SIZ of the SO has been estimated at 68 - 107 Tg C yr^{-1} from 1997 to 2005 (Arrigo et al., 2008), and consequently SO phytoplankton play a role in mitigating the accumu-

45 lation of anthropogenic greenhouse gasses in the world's atmosphere (Boyd and Trull, 2007; Deppeler and Davidson, 2017). Even so, the SIZ shows a net release of CO_2 from the ocean to the atmosphere due to off-gassing of carbon-rich deep-ocean water upwelling at the Antarctic Divergence (Takahashi et al., 2009). Any changes in the composition and abundance of phytoplankton in the SIZ are likely to influence both the trophodynamics of the SO and the ~~sequestration of atmospheric carbon~~ contribution of the region to ocean-atmospheric carbon flux.

50 Global standing stocks of phytoplankton are estimated to be declining at around 1 % per year, a decline largely attributed to rising surface ocean temperature (Boyce et al., 2010). Furthermore, global phytoplankton productivity is predicted to drop by as much as 9 % from years 1990 to 2090 (RCP8.5 *Business As Usual*), with a decline across most of the Earth's ocean area (Bopp et al., 2013). In contrast, higher latitudes, including the SIZ of the SO, are predicted to experience an increase in productivity due to ~~(1) reduced~~ changes to seasonal ice extent and duration ~~leading to the water column receiving more light for~~

55 ~~longer~~ (Parkinson, 2019; Turner et al., 2013) and/or ~~(2)~~ increased upwelling of nutrient-rich deep ocean water at the Antarctic Divergence (Steinacher et al., 2010; Bopp et al., 2013; Carranza and Gille, 2015).

1.1 Importance of the SIZ phytoplankton bloom

The Antarctic SIZ is one of the most productive parts of the SO ~~south of 60°S~~ (Carranza and Gille, 2015). It is also a significant component of the global carbon cycle by virtue of both carbon sequestration ~~and export~~ by phytoplankton (Henson et al., 2015)
60 as well as upwelling and off-gassing of carbon-rich deep ocean water (Takahashi et al., 2009). It is one of the largest and most variable biomes on Earth, with sea ice extent varying from around 20 million km^2 during winter to only 4 million km^2 in summer ~~(Turner et al., 2015; Massom and Stammerjohn, 2010)~~ (Turner et al., 2015; Massom and Stammerjohn, 2010; Parkinson, 2019). The most macronutrient-rich surface waters of the SIZ occur over the Antarctic Divergence, a circumpolar region of the SO located at around 63°S where carbon- and nutrient-rich water upwells to the surface, supplying the nutrients that drive much of
65 the phytoplankton production in the SO (Lovenduski and Gruber, 2005; Carranza and Gille, 2015) ~~and releasing CO$_2$ into the atmosphere (Takahashi et al., 2009).~~ .

In winter, phytoplankton growth is limited by light availability and temperature. In spring and summer, phytoplankton can proliferate in the high light, high nutrient waters that trail the southward retreat of sea ice (Fig 1a,b) (Wilson et al., 1986; Smetacek and Nicol, 2005; Lannuzel et al., 2007; Saenz and Arrigo, 2014; Rigual-Hernández et al., 2015). The SIZ supports
70 high phytoplankton standing stocks and productivity ~~in waters where~~ , and phytoplankton abundance in blooms can double every few days (Wilson et al., 1986; Sarthou et al., 2005). ~~Phytoplankton productivity in the SIZ is generally highest around the time of maximum solar irradiation (?) but is characterised by large-scale spatial and temporal variability (Martin et al., 2012) with only 17-24 % of ice edge waters experiencing phytoplankton blooms in any spring-summer period.~~ Wind speed is the primary determinant of phytoplankton bloom development in the SIZ, with calmer conditions fostering shallow mixed depths that
75 maintain phytoplankton cells in a high light environment and maximise productivity (Savidge et al., 1996; Fitch and Moore, 2007). Phytoplankton populations are characterised by large-scale spatial and temporal variability (Martin et al., 2012) with only 17-24 % of ice edge waters experiencing phytoplankton blooms in any spring-summer period (Fitch and Moore, 2007).

1.2 The Southern Annular Mode

The Southern Annular Mode (SAM), which is also ~~variously also~~ called the High-Latitude Mode and the Antarctic Os-
80 cillation, is the principal mode of atmospheric variability over the SO (Gong and Wang, 1999; Marshall, 2003). The SAM reflects the position and intensity of a zonally symmetric structure of atmospheric circulation in the southern hemisphere, circling the earth (annular) at around 50° south, and it has been defined as the alternating pattern of strengthening and weakening westerly winds in conjunction with high to low pressure bands (Ho et al., 2012). The SAM is estimated either from station measurements as the difference in normalised zonal mean atmospheric sea-level pressure between ~~40°S and~~
85 ~~65°S (Gong and Wang, 1999; Marshall, 2003). The SAM is the principal mode of atmospheric circulation at high latitudes of~~

~~the Southern Hemisphere, and variation in the SAM typically describes around 35 % of total Southern Hemisphere climate variability (Marshall, 2007). The SAM is currently the dominant large-scale mode through which climate change is expressed on the SO (Thompson and Solomon, 2002; ?; ?; ?)~~40° S and 65° S (Gong and Wang, 1999; Marshall, 2003), or from Principal Component analysis of gridded data of atmospheric pressure or temperature, at sea-level or at a geopotential height (Ho et al., 2012).

90 Between 1979 and 2017 the value of daily SAM averaged 0.04 index points, ranged from -5.13 to 4.64 and had a standard deviation of 1.38 (NOAA, 2017). Average monthly SAM varied from -2.7 to 2.5 index points over the 11 years studied (Fig. 1c).

There is a trend toward ~~increasing~~ more positive SAM from 1979 to 2017 of 0.011 index points per year (NOAA, 2017), attributed to both ozone-depletion (Thompson and Solomon, 2002; Arblaster and Meehl, 2006; Gillett and Fyfe, 2013; Jones et al.,

95 2016) and to increasing atmospheric greenhouse gas concentrations (Thompson et al., 2011). The long-term average SAM ~~index~~ is now at its ~~highest~~ most positive level for at least the past 1,000 years (Abram et al., 2014). Continuing increases in atmospheric greenhouse gasses are expected to drive further positive increase in the SAM ~~index~~ in all seasons (Arblaster and Meehl, 2006; Swart and Fyfe, 2012; Gillett and Fyfe, 2013), despite the expected recovery in stratospheric ozone concentrations to pre-ozone hole values by around 2065 (Son et al., 2009; Schiermeier, 2009; Thompson et al., 2011; Solomon et al., 2016).

100 ~~More positive SAM has been associated with lower atmospheric pressure at sea level~~ A more positive SAM indicates the occurrence of a strengthening circumpolar vortex (Marshall, 2003; Ho et al., 2012) leading to stronger westerly winds and increased storminess ~~(Kwok and Comiso, 2002; Hall and Visbeck, 2002; Marshall, 2007)~~at high latitudes (Hall and Visbeck, 2002; Kwok an These changes are particularly marked south of 60°S in the atmospheric Southern Circumpolar Trough (Hines et al., 2000; Mackintosh et al., 2017), a region characterised by strong winds with variable direction (Taljaard, 1967). Stronger winds

105 associated with more positive SAM may result in increased transport of surface water northward from the Antarctic Divergence by Ekman drift (Lovenduski and Gruber, 2005; DiFiore et al., 2006), potentially driving increased upwelling of nutrient- and carbon-rich deep ocean water at the Antarctic Divergence (Hall and Visbeck, 2002). More positive SAM is also associated with reduced near-surface air temperature over the SIZ due to an increased frequency of strong southerly winds and increased cloud cover ~~(Lefebvre et al., 2004; Sen Gupta and England, 2006)~~(Lefebvre et al., 2004; Sen Gupta and England, 2006; Marshall, 2007).

110 Sea ice extent around the Antarctic continent shows zonal relationships with the SAM~~:~~, with positive relationships between the SAM and ~~sea-ice~~ sea ice extent in the Western Pacific and Indian sectors of the SO ~~(the Indian sector was sampled in this work)~~ and negative or non-existent relationships in other sectors (Kohyama and Hartmann, 2016). Wind also affects the nature of the sea ice, breaking up floes via wave interactions, increasing flooding, ~~and if blowing from the south, both opening the pack ice and leading to new frazzle ice formation (Massom and Stammerjohn, 2010)~~changing pack ice density (compressing or opening

115 up the pack) and contributing to ice formation by generating frazzil ice (Massom and Stammerjohn, 2010; Squire, 2020). Lower sea-surface temperatures have been observed to lag positive SAM events by one to four months (Lefebvre et al., 2004; Meredith et al., 2008)~~. Such~~, and changes in the SAM may take weeks to months to be manifested in phytoplankton communities (Sen Gupta and England, 2006; Meredith et al., 2008)~~, while extreme~~. Extreme SAM events might ~~impact phytoplankton community composition~~also impact phytoplankton communities for multiple years (Ottersen et al., 2001).

By ~~mediating~~ modulating upwelling, ocean mixed depth, air temperature, and ~~sea-ice~~ sea ice characteristics and duration, it is likely that ~~increases in the~~ a more positive SAM will affect the composition and abundance of phytoplankton in the SIZ of the SO. Lovenduski and Gruber (2005) predicted that ~~increased~~ more positive SAM would support higher phytoplankton productivity, and subsequent analyses by ~~Arrigo et al. (2008); Boyce et al. (2010)~~ Arrigo et al. (2008), Boyce et al. (2010), and Soppa et al. (2016) have confirmed a positive relationship between the SAM and phytoplankton standing stocks and productivity south of 60°S in the SIZ.

1.3 The Hypothesis

Based on the predicted and observed positive relationships between the SAM and phytoplankton productivity and biomass in the SIZ of the SO, we hypothesised that changes in the SAM could also elicit changes in the composition ~~and abundance~~ of the phytoplankton community. To test this hypothesis, we conducted a scanning electron microscopic survey of hard-shelled phytoplankton in surface waters of the Antarctic SIZ using samples collected between October and February each spring-summer over 11 consecutive years (2002/03 – 2012/13). We then related the composition of these communities to environmental variables including the SAM.

2 METHODS

Fifty-two surface-water samples were collected from the seasonal ice zone (SIZ) of the Southern Ocean (SO) across 11 consecutive austral spring-summers from 2002/03 to 2012/13. The samples were collected aboard the French re-supply vessel MV L'Astrolabe during resupply voyages between Hobart, Australia, and Dumont d'Urville, Antarctica, between the ~~20th~~ 20th October and the ~~1st March~~ 28th February. Most samples were collected from ice-free water, although some were collected south of the receding ice-edge (Fig. 1a).

The sampled area was in the ~~high latitude SO (Fig. 1b) in the south-east corner of the Australian Antarctic Basin~~ Indian sector of the SO, spanning 270 km of latitude between 62° S and 64.5° S, and ~~625km~~ 625 km of longitude between 136° E and 148° E (Fig. 2 inset). The area lies >100 km north of the Antarctic continental shelf break, in waters >3,000 m depth.

Samples were obtained from the clean seawater line of the re-supply ~~ship~~ vessel from around 3 m depth. Each sample represented 250 ml of seawater filtered through a 25 mm diameter polycarbonate-membrane filter with 0.8 μm pores (Poretics). The filter was then rinsed with two additions of approximately 2 ml of MilliQ water to remove salt, then air dried and stored in a sealed container containing silica gel desiccant. Samples were prepared for scanning electron microscope (SEM) survey by mounting each filter onto ~~metal stubs~~ a metal stub and sputter coating with 15 nm gold or platinum. Only organisms possessing hard siliceous or calcareous shells were sufficiently well preserved through the sample preparation technique that they could be identified by SEM, and included diatoms, coccolithophores, silicoflagellates, Pterosperma, parmales, radiolarians, and armoured dinoflagellates.

2.1 Phytoplankton ~~composition and~~ relative abundance

~~Example of phytoplankton identification on a single SEM image. Overlying letters are taxa-codes for individual phytoplankton taxa used in analysis; codes in parenthesis are rare taxa.~~

The composition ~~and abundance~~ of the phytoplankton community of each sample was determined ~~with the aid of~~ from x400 magnification images captured using a JEOL JSM 840 Field Emission SEM. Cell numbers for each phytoplankton taxon were counted in ~~randomly selected digital images of SEM fields taken at x400 magnification~~ a random selection of captured images taken of each sample. Each captured image (Fig. 2) ~~. Each image~~ represented an area of 301 x 227 μm (area 0.068 mm^2) of each sample filter, which was captured at a resolution 8.5 pixels per μm. A minimum of three SEM fields were assessed for each sample, with more fields assessed when cell densities were lower. On average, 387 cells were counted for each sample. Taxa were classified with the aid of Scott and Marchant (2005), Tomas (1997), and expert opinion. Cell counts per image were converted to volume-specific abundances (cells per ml) by dividing by 0.0348 ml of sea-water represented by each captured image.

A total of ~~19,943 phytoplankton organisms were identified and counted: 18,872 diatoms, 322 Parmales, 173 coccolithophores, 81 silicoflagellates, and 45 Petasaria. A total of~~ 48 phytoplankton taxa were identified, many to species level. Because the diatoms *Fragilariopsis curta* and *F. cylindrus* could not be reliably discriminated at the microscope resolution employed, they were pooled into a single taxa-group. Other taxa were also grouped, namely *Nitzschia acicularis* with *N. decipiens* to a single group, and discoid centric diatoms of the genera *Thalassiosira*, *Actinocyclus* and *Porosira* to another. Rare species, with maximum relative abundance <2 %, were removed from the data prior to analysis as they were not considered to be sufficiently abundant to warrant further analysis (Webb and Bryson, 1972; Taylor and Sjunneskog, 2002; Świło et al., 2016). After pooling taxa and deleting rare taxa, twenty-two taxa and taxonomic-groups (species, groups of species and families) remained to describe the composition of the phytoplankton community. A total of 19,608 phytoplankton organisms were identified and counted: 18,989 diatoms, 322 Parmales, 177 coccolithophores, 81 silicoflagellates, and 45 Petasaria.

Phytoplankton abundance data were converted to relative abundance by dividing each value by the total abundance of the 22 taxa-groups in the sample. This alleviated variation among samples as a result of dilution, a phenomenon whereby the abundance of cells in surface waters can be reduced in a matter of hours by an abrupt increase in wind speed and associated increase in the mixed layer depth (Carranza and Gille, 2015), diluting near-surface cells into a greater water volume. However, relative abundance has the disadvantage that blooming of one species will cause a reduction in relative abundance of other present species, when their absolute abundances may not have changed.

2.2 Environmental covariates

Phytoplankton abundances were related to a range of environmental covariates available at the time of sampling. These included the SAM, sea surface temperature (*SST*), *Salinity*, time since sea ice cover (*DaysSinceSeaIce*, defined below), minimum latitude of sea ice in the preceding winter, latitude and longitude of sample collection, the days since 1st October that a sample

was collected (***DaysAfter1Oct***), the year of sampling (~~year~~*year*, being the year that each spring-summer sampling season began), the time of day that a sample was collected, and ~~macro-nutrient concentrations:~~ satellite-derived total chlorophyll content. Macronutrient concentrations, phosphate (PO_4), silicate (SiO_4) and nitrate + nitrite (hereafter nitrate, NO_x), were included as indicators of nutrient drawdown as a proxy for phytoplankton productivity (Arrigo et al., 1999).

~~Water samples for dissolved macro-nutrients were collected, frozen on ship, and later analysed at CSIRO in Hobart using standard spectrophotometric methods (Hydes et al., 2010).~~ Daily estimates of the SAM were obtained from the ~~US NWS~~ United States National Weather Service Climate Prediction Center's website and ~~are~~ were the NOAA Antarctic Oscillation Index values based on 700-hPa geopotential height anomalies ~~(NOAA, 2017)~~(Ho et al., 2012; NOAA, 2017) – we used these estimates principally because daily values were readily available, other available estimates were largely seasonal averages only (Ho et al., 2012). Geopotential height anomalies are the difference in altitude of a specified atmospheric pressure from the average height of that pressure, in this case 700-hPa, or about 3 km altitude. Water samples for dissolved macronutrients were collected, frozen on ship, and later analysed at the Commonwealth Scientific and Industrial Research Organisation in Hobart, Australia, using standard spectrophotometric methods (Hydes et al., 2010). The variable ***DaysSinceSeaIce*** was defined as the time since sea ice had melted to 20 % cover, after Wright et al. (2010), as determined from daily Special Sensor Microwave/Imager (SSM/I) sea ice concentration data distributed by the University of Hamburg (Spreen et al., 2008). Total chlorophyll content was estimated for each sample location by estimating the total chlorophyll content over a 20 x 20 km area centred at each sample location, for all available times from 31 August to 1 May in the year of sampling (monthly observations) (Acker and Leptoukh, 2007; GMAO, 2017), and interploating between observations to estimate total chlorophyll content on the date sampled (some examples are reproduced in Supplementary Material - Figure S3). By this method total chlorophyl was estimated for 49 of the 52 samples, the remainder of samples having a paucity of data which precluded estimation.

~~To examine the lag in the expression of the SAM on phytoplankton community composition, two response surfaces were constructed relating the variance in phytoplankton community composition explained by the SAM to the temporal positioning of the period over which daily SAM was averaged. These were derived by evaluating separate CAP analyses (described below) based on daily SAM averaged across a range of days {1, 3, 5, ... 365} centred on~~

2.3 Statistical analysis

Three statistical analysis were undertaken to explore the hypothesis: (i) ~~each calendar day individually (1 Jan – 31 Dec) through the year associated with each sample; and~~ constrained analysis of principal coordinates (CAP, (Anderson and Willis, 2003)) was used to estimate the influence of multiple environmental covariates in simutaneously explaining community composition; (ii) ~~lagged from 1 to 365 days prior to each sample collection date.~~

2.4 ~~Statistical analysis~~

~~Clustering~~ clustering techniques were used to explore similarities in phytoplankton community composition ~~and abundance among samples , and distance-based redundancy analysis (Legendre and Anderson, 1999) and correlation analysis were used~~

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215 ~~to relate community structure to~~ among samples and define significantly different sample grouping based on similarities in their phytoplankton community structure; and (iii) correlation analysis was used to support observed relationships between phytoplankton community structure and environmental covariates. ~~The~~

For CAP and cluster analysis, relative abundance data were ~~converted to relative abundance by dividing each abundance estimate by the total abundance of the 22 taxa in the sample, then~~ square-root-transformed to reduce possible dominance of
the analysis by a few abundant taxa. ~~Relative abundance was used to alleviate variation among samples as a result of dilution,~~
220 ~~a phenomenon whereby the abundance of cells can be reduced in a matter of hours by an abrupt increase in wind speed and associated increase in the mixed layer depth (Carranza and Gille, 2015), diluting near-surface cells into a greater water volume. However, relative abundance has the disadvantage that blooming of one species will cause a reduction in relative abundance of other present species, when their absolute abundances may not have changed.~~ The Bray-Curtis dissimilarity
index (Bray and Curtis, 1957) was used to calculate the resemblance of samples based on their community structure. The
225 advantage of this index for the cell count data was that similarity among samples was not strongly affected by the absence of taxa. ~~Hierarchical agglomerative clustering based on average linkage was performed on the Bray-Curtis resemblance matrix. Significant differences among sample clusters were determined according to the similarity profile (SIMPROF) permutation method of Clarke et al. (2008), based on alpha = 0.05 and 1,000 permutations.~~

~~Constrained analysis of principal coordinates (CAP , (Anderson and Willis, 2003)) was used to estimate the influence of~~
230 ~~environmental covariates in explaining community composition. This procedure~~ CAP distance-based redundancy analysis
(Legendre and Anderson, 1999) used the Bray-Curtis resemblance matrix to partition total variance in community composition into unconstrained and constrained components, with the latter representing the variation due to the environmental covariates. A forward selection strategy was used to choose the optimum model containing the minimum subset of constraints required to explain the most variation in phytoplankton community structure (Legendre et al., 2011). Linear projections of
235 significant covariates were plotted as arrows in the ordination diagram, indicating the direction and magnitude of effects that were correlated with changes in the phytoplankton community (Davidson et al., 2016). The variance in phytoplankton community structure (as determined from the ordination) explained by each environmental covariate was calculated according the procedure outlined in Ter Braak and Verdonschot (1995) and attributed to Dargie (1984). Taxa were added to the CAP plots as weighted site-averages for each species, thereby indicating the relative influence of the fitted environmental constraints on
240 each phytoplankton ~~taxon/group~~ taxa-group.

Hierarchical agglomerative clustering based on average linkage was performed on the Bray-Curtis resemblance matrix. Significant differences among sample clusters were determined according to the similarity profile (SIMPROF) permutation method of Clarke et al. (2008), based on $\alpha=0.05$ and 1,000 permutations.

Pair-wise correlation analyses were performed using Pearson's correlation coefficient r to explore the relationships ~~amongst~~
245 among environmental variables, and between these environmental variables and the relative abundances of phytoplankton taxa (Rodgers and Nicewander, 1988). Given the large number of pair-wise correlations considered, we applied a Bonferroni

correction to give consideration to family-wise error rate by setting alpha, which is usually α=0.05 (Gibbons and Pratt, 1975; Cohen, 1990), to α/~~m where m~~ m where m is the total number of correlations considered. Recognising that α/~~m~~ m may be conservative (Nakagawa, 2004), we indicated when calculated correlations were significant at both ~~p~~α<0.05 and at Bonferroni corrected ~~p~~α<0.05/~~m~~m.

Response surfaces were used to display the variance explained from individual CAP analyses according to the number of days averaged, and the mid-point (or lagged mid-point) of the range of days averaged, for each aggregated SAM index. These allowed identification of maxima in correlation between the SAM and phytoplankton community structure. Response surfaces were derived by evaluating separate CAP analyses for each combination of (i) the temporal positioning of the daily-SAM averaging range and (ii) the length of the daily-SAM averaging range. In constructing the response surfaces, the range of averaged daily-SAM was centred on (i) each calendar day individually (1 Jan – 31 Dec) through the year associated with each sample, and alternatively (ii) relative to the time of sampling and lagged from 1 to 365 days prior to each sample collection date, in one day increments. The length of the SAM averaging range was varied in one day increments from zero to plus and minus 182 days from the centre of the range. Similar response surfaces were constructed relating the correlation between averaged daily-SAM and (i) total chlorophyll, and (ii) [PO$_4$].

Data management and manipulation, summary statistics, correlation analysis, and scatter plots were undertaken in Microsoft Excel (2016) and R (R Core Team, 2016). Cluster analysis and SIMPROF were undertaken using the R package ~~clustsig~~ *clustsig* (Whitaker and Christman, 2014). CAP analyses were conducted using the capscale function in the R package ~~vegan (?)~~*vegan* (Dixon, 2003).

3   RESULTS

3.1   ~~Observed abundance~~

~~Abundance of individual taxa averaged 133 cells per ml and ranged to a maximum of 8,796 cells per ml. Of the 22 taxa/groups identified in this study (hereafter taxa), four taxa were identified in all 52 samples and 11 taxa were identified in more than 90 % of samples.~~

3.1   ~~CAP analysis and pair-wise relationships~~

3.1   The influence of SAM on phytoplankton community composition

CAP analysis and pairwise correlation analysis both indicated that variation in the Southern Annular Mode (SAM) significantly influenced phytoplankton community composition. Corroborating these other analysis, clustering analysis grouped samples based upon community composition, indicating that there was significant variation between groups of samples that might be explained by known environmental variables such as the SAM.

Table 1. Variance in the ~~relative abundance~~ community composition of 22 phytoplankton ~~taxa~~ taxa-groups attributable to constraining environmental covariables in the CAP analysis.

CAP analysis	variance category	covariate	variance	fraction of total variance
(a) Variables fit individually as the only constraining covariate		*DaysAfter1Oct*	0.61	15.4 %
		SST	0.57	14.6 %
		SAM autumn	0.52	13.3 %
		Long.E	0.47	11.9 %
		SAM spring	0.41	10.3 %
		SAM prior	0.39	9.9 %
		DaysSinceSeaIce	0.23	5.9 %
		Salinity	0.18	4.7 %
		Year	0.13	3.4 %
		~~*Long.E*~~*Lat.S*	0.10	2.5 %
		Minimum latitude of ~~sea-ice~~ sea ice the previous winter	0.06	1.6 %
(b) Optimum multi-covariate model	variance explained by all constraining covariables		1.48	37.5 %
	individual constraining covariables	*DaysAfter1Oct*	0.61	15.4 %
		SAM autumn	0.50	12.6 %
		Long.E	0.21	5.2 %
		SAM prior	0.17	4.3 %
	Unexplained residual		2.46	62.5 %
	Total variance in taxa-composition between samples		3.94	100 %

Empirical identification of the time between variation in the SAM and the manifestation of this variation in the phytoplankton community structure revealed three ~~modes (maxima)~~ maxima in phytoplankton community composition explained by the SAM. The first of the maxima was an autumn seasonal SAM ~~mode~~ index (*SAM autumn*), which was determined to be the average of 57 daily SAM estimates centred on the preceding 11th March (11th Feb – 8th Apr). ~~This mode~~ *SAM autumn* explained up to 13.3 % of the variance in ~~taxonomic composition (*SAM autumn*,~~ community composition estimated through CAP analysis (Fig. 3a, Table 1a). The second of the maxima was a spring seasonal ~~mode~~ index (*SAM spring*), which was determined to be the average of 75 daily SAM estimates centred on 25th October (20th Sep – 3rd Dec). ~~This mode~~ *SAM spring* explained up to 10.3 % of variance in taxonomic composition (*SAM spring,* Fig. 3a, Table 1a). Unlike the other ~~modes~~ maxima that were related to the time of year, the third ~~mode~~ of the maxima was timed relative to the date of sample collection

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285 for each sample and comprised the average of the 97 daily SAM estimates centred 102 days prior to each sample collection date. It explained 9.9 % of the variance in phytoplankton composition (***SAM prior***, Fig. 3b, Table 1a). ~~The mean standard error on estimates of the SAM indices were 0.14 SAM index units for **SAM autumn** and **SAM spring**, and 0.13 for **SAM prior** (Table 2a).~~ Note that ***SAM prior*** and ***SAM spring*** temporally overlapped to varying extents across the 52 samples (Fig. 4) and so were not entirely independent covariates: for example, a sample collected in the summer had previous days contributing to

290 both ***SAM prior*** and ***SAM spring***.

~~Scatter-plots: (a,b) examples of phytoplankton taxon relative abundance versus **SAM autumn**; (c) taxa correlations with **SAM autumn** (*r.SAM autumn*) versus taxa correlations with **DaysSinceSeaIce** (*r.DaysSinceSeaIce*); and (d): **Long.E** of sample collection versus **DaysAfter1Oct**. Each figure shows Pearson's correlation coefficient (*r*) and p associated with the relationship. A line of least-squares best fit is provided to give an indication of trend, though clearly several underlying assumptions of linear~~

295 ~~regression would not be met.~~

~~(a) CAP analysis of phytoplankton taxonomic composition. Dots represent individual samples, with colours corresponding to significant clusters (Fig. 6b). The 22 phytoplankton taxa/groups are overlain as weighted averages of their sample scores (red abbreviations, after Fig. 2) with positions plotted with a three-times exaggeration of distance from the origin to more easily visualise their relationships with constraining environmental variables. Linear projections of the significant constraining~~

300 ~~environmental covariates appear as blue arrows, the length and angle of which represents the magnitude and direction of influence of each variable on community composition. The inset shows the taxa located close to the origin, diatoms fri and eye collocating. (b) Cluster analysis dendrogram of the 52 samples based on similarities in phytoplankton community structure, using colour to show 7 significantly different groups (numbered 1-7, solid lines, $\alpha < 0.05$). Sample labels contain: season and voyage (e.g. 0809v2b = Austral Spring-Summer over 2008-09, voyage designation 2, sample b is the second sample obtained~~

305 ~~from the SIZ during that voyage); **SAM autumn** value, **SAM prior** value, and the **DaysAfter1Oct** value.~~

~~The optimum multi-covariate CAP analysis showed that the autumn mode (**SAM autumn**)explained the most variance in community composition of the three identified SAM modes~~ The optimum CAP model contained four covariates that explained the variation in phytoplankton community composition among samples (Table 1b). While four CAP axes were statistically significant (p<0.05), the first two axes together explained a total of 31.1 % of the variation in community taxonomic

310 composition, and the third and fourth axes together only explained a further 6.4 % (not tabulated). Thus Fig. 6 illustrates most of the variance explained by the CAP analysis. ***SAM autumn*** explained the most variance in community composition (12.6 %) ~~, while the prior-to-sampling mode (~~and ***SAM prior*** ~~)~~explained a further 4.3 % of variation ~~when fitted as the second constraining SAM covariate~~ (Table 1b). These two SAM indices were moderately and significantly positively correlated (~~r.~~ *r* 0.51, Table 2c, p<0.001). Both showed similar negative correlations (Table 2b) with the relative abundances of the small di-

315 atoms *Fragilariopsis rhombica* (~~relationship with **SAM autumn**~~ depicted in Fig. 5a) and *Nitzschia acicularis/decipiens*, and the coccolithophorid *Emiliana huxleyi*, and similar positive correlations with the abundances of larger diatoms *Chaetoceros atlanticus*, *Chaetoceros dichaeta* and *Dactyliosolen antarcticus*. A further six taxa showed a correlation with ***SAM autumn*** but not ***SAM prior***, namely positive correlations with *Chaetoceros concavicornis/curvatus*, *Fragilariopsis kerguelensis* (~~relationsip~~

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~~with *SAM autumn* depicted in~~ Fig. 5b), *Pseudo-nitzschia lineola*, and *Thalassiothrix antarctica*, and negative correlations

320 with *Dactyliosolen tenuijunctus* and the *Parmales*. Three taxa showed correlations with *SAM prior* but not *SAM autumn*, namely positive correlations with *Chaetoceros neglectus* and the silicoflagellate *Dictyocha speculum*, and a negative correlation with *Petasaria heterolepis*. ~~In the optimum multi-covariate CAP analysis (Table 1b, Fig. 6a) the first four CAP axes were statistically significant (p<0.05), the first two axes together explained a total of 31.1 % of the variation in community taxonomic composition, and the third and fourth CAP axis together explained a further 6.4 % (not tabulated).~~

325 ~~Following cluster analysis, SIMPROF identified seven significantly different groups (p<0.05), with samples loosely grouped on the basis of their within-season successional maturity (*DaysAfter1Oct*) and the SAM index (Fig. 6b). The coloured groups of samples in the 2D representation of the optimum multi-covariate CAP analysis (Fig. 6a) are coloured according to the clusters identified in Fig. 6b, with their positioning further indicating the influences of *DaysAfter1Oct* and the SAM index on cluster groupings. This showed samples in clusters 3 and 4 (Fig. 6b) were commonly associated with more positive SAM, while those~~

330 ~~in clusters 5, 6 and 7 were associated with negative SAM values. Samples in clusters 2 and 5 were commonly collected earlier in the spring-summer period (lower *DaysAfter1Oct*) while those in clusters 1, 4, 6 and 7 were commonly collected later (Fig. 6).~~

Fifteen of the 22 ~~taxa~~ taxa-groups showed significant (p<0.05) pairwise correlations with one or more of the SAM ~~modes~~ indices, with *SAM autumn* being the most influential (Table 2b) ~~. Of the 12 taxa showing a correlation between their relative abundance~~

335 ~~and *SAM autumn* (Table 2b), six also showed a~~ showing significant correlation with ~~the sample collection date (*DaysAfter1Oct*). Of these, three taxa were negatively correlated with both *SAM autumn* and *DaysAfter1Oct* (i.e. had maximum abundance early in the season). Conversely, two taxa were positively correlated with both *SAM autumn* and *DaysAfter1Oct*. A similar but stronger relationship was seen between individual taxon correlations with *SAM autumn* and *DaysSinceSeaIce*. That is, taxa showing a negative correlation between relative abundance and *SAM autumn* were more likely to show a negative~~

340 ~~abundance-correlation~~ 12 of the 22 taxa-groups. When applying the conservative Bonferroni-adjusted $\alpha=0.0025$, seven taxa-groups showed significant correlation with *DaysSinceSeaIce*, ~~i.e those whose maximum relative abundance occurred earlier after the opening of the winter's sea ice, and vice versa (r: 0.49, p<0.05, Fig. 5c). Individual taxon abundance relationships with *SAM spring* and *SAM prior* did not exhibit trends with individual taxon relationships with either~~ any SAM index and four with ~~*DaysAfter1Oct**SAM autumn*~~ or *DaysSinceSeaIce*.

345 *SAM prior* and *SAM spring* represented a similar time span in the spring immediately prior to sampling (Fig. 4) and were strongly and significantly correlated (~~r: ~~*r* 0.83, Table 2c, p<0.001). Samples were collected over a calendar range of 140 days (20 Oct. - ~~1 Mar~~28 Feb., Table 2a) and thus the ~~163-day ~~97-day period represented by *SAM prior* varied in its position in the calendar across the 140-day spread of the 52 samples (Fig. 4). ~~The modes ~~*SAM prior* and *SAM spring* also showed similar ~~correlation sign with taxonomic ~~correlation-sign with taxa-group relative abundances (Table 2b). It was not possible, however,

350 to determine whether the pre-season SAM influence was a spring effect or a prior-to-sampling effect, and whilst both appear to be important explanatory terms, only *SAM prior* was retained in the optimum CAP model (Table 1b).

In the optimum multi-covariate CAP model, *DaysAfter1Oct* explained the greatest proportion of the observed variance in phytoplankton community composition (Table 1b). *DaysAfter1Oct* was significantly correlated ($p < 0.0025$) with sea surface temperature (*SST*), *salinity*, and *DaysSinceSeaIce*, and the variable singly captured the most variation due to seasonal succession of the phytoplankton community. Alone it explained 15.4 % of the total variation (Table 1b) with its effect on the phytoplankton community being approximately orthogonal to that of the SAM (Fig. 6a). A weak positive relationship detected between *SAM autumn* and *DaysAfter1Oct* indicated a weak trend of sampling later in the spring-summer period in years with higher autumn SAM (r 0.32, Table 2c, $p = 0.02$), but otherwise the SAM indices and *DaysAfter1Oct* were un-related.

Ten taxa-groups showed significant ($p < 0.05$) correlation between their relative abundance and *DaysAfter1Oct* (Table 2b): *Chaetoceros castracanei*, *C. neglectus*, *D. speculum*, *E. huxleyi*, *N. acicularis/decipiens*, *Parmales*, *P. lineola*, and the discoid centric diatoms showed negative relative-abundance correlations with *DaysAfter1Oct* indicating greatest relative abundance early in the spring-summer, while *C. concavicornis/curvatus* and *C. dichaeta* showed greater relative abundance later in the spring-summer. A negative correlation (-0.63, $p < 0.001$) was detected between the longitude of individual sample collection (*Long.E*) and *DaysAfter1Oct*, indicating that samples collected later in the spring-summer were more likely to have been collected towards the west in the sampled region (Table 2c, Fig. 5c).

Following cluster analysis, SIMPROF identified seven significantly different groups ($p < 0.05$, with samples loosely grouped on the basis of their within-season successional maturity (*DaysAfter1Oct*) and the SAM (Fig. 6b). Clustering showed that there were significant differences between the community composition of the samples, but clustering did not identify an effect of the SAM, at least not directly, since environmental covariates were not included in the cluster analysis. The group structure determined by cluster analysis was displayed in the CAP ordination (using colour) to demonstrate that samples that clustered together were indeed close to one another in the two-dimension (2D) ordination (Fig. 6a), with their positioning further indicating the influences of *DaysAfter1Oct* and the SAM on cluster groupings. This lended confidence that the 2D ordination was a reasonable approximation to the full, high-dimensional structure. As we knew the values for the environmental covariates for each sample, it was possible to determine the correlation between the 2D CAP solution and each environmental covariate. We displayed these correlations as a projected vector (arrow) where direction indicates the sign and length indicates strength. This showed samples in clusters 3 and 4 (Fig. 6b) were commonly associated with more positive SAM, while those in clusters 5, 6 and 7 were commonly associated with more negative SAM values. Samples in clusters 2 and 5 were commonly collected earlier in the spring-summer period (lower *DaysAfter1Oct*) while those in clusters 1, 4, 6 and 7 were commonly collected later (Fig. 6).

Other considered environmental covariates that did not significantly influence community composition were the time though the day that a sample was collected, and the minimum latitude reached by sea ice cover in the previous winter (Supplementary material Table S1).

3.2 ~~Correlations among taxa~~Influence of the SAM on phytoplankton productivity

385 ~~The relative abundances of the 22 phytoplankton taxa were largely unrelated among samples. Of the 231 pairwise correlations between these taxa, only 35 were significantly positive and 18 were significantly negative~~ Two indicators of the influence of the SAM on phytoplankton productivity were derived: (i) the influence of the SAM on satellite-derived total chlorophyll; and (ii) the influence of the SAM on macronutrient concentrations, indicating nutrient drawdown associated with productivity. Satellite-derived total chlorophyll showed positive correlation with all SAM indices: r=0.50 (p<~~0.05, Extra material S2).

390 ~~Applying a Bonferroni correction reduced these significant correlations to 15 positive and 8 negative relationships.~~ 0.001) with ***SAM autumn***, r=0.72 (p<0.001) with ***SAM prior***, and r=0.69 (p<0.001) with ***SAM spring*** (Table 2c). Peaks in correlation of total chlorophyll with the SAM were evident in the preceding autumn, spring, and prior-to-sampling in response surfaces for NASA satellite total chlorophyll, along with a peak in early winter (Supplementary Material Fig. S1). However, it is noteworthy that our comparisons between satellite-derived total chlorophyll and the SAM have been limited here to estimates associated

395 with only the 52 samples in this study. Results supported the presence of a positive relationship between productivity and the SAM, but the limited number of comparisons mean the results are only indicative.

4 ~~Other relationships~~

The observed concentrations of the ~~macro nutrients nitrate~~ macronutrients NO_x, ~~phosphate~~ PO_4, and ~~silicate~~ SiO_4 showed significant negative correlations with ***SAM autumn*** (r= -0.39, -0.56, -0.42 respectively, Table 2d, p: 0.005, <0.001, 0.002

400 respectively). The concentrations of these nutrients showed stronger negative correlations with ***~~DaysAfter1Oct~~***~~(r: -0.77, -0.73, -0.56~~***SAM autumn*** when the 50 % of samples collected latest in the spring-summer season were considered. (r -0.58, -0.74, -0.51, Table 2~~d~~e, p: 0.002, <0.001, 0.008 respectively). Macronutrient concentrations were unrelated to either ***SAM prior*** or ***SAM spring*** (Table 2d).

~~Sea surface temperature (***SST***) and ***DaysSinceSeaIce*** also showed positive correlations with ***DaysAfter1Oct*** (r: 0.92 and

405 0.56 respectively, Table 2c), and ***Salinity***~~ Peaks in negative correlation of the SAM on [PO_4] were evident in the preceding autumn and spring prior to sampling in response surfaces, with the peaks being more negative when only the 50 % of samples collected later in the spring-summer were considered (Supplementary Material Fig. S2). The concentrations of macronutrients also showed expected decline through the spring-summer: correlations between [NO_x], [PO_4], and ***~~Long.E~~*** ~~showed negative correlations with~~ [SiO_4], with ***DaysAfter1Oct*** ~~(r: -0.43 and -0.63, Table 2c). When individually fitted as the first constraining

410 covariate in a CAP model, ***SST***~~were -0.77, ***~~Long.E~~***-0.73, ***~~DaysSinceSeaIce~~*** ~~and ***Salinity*** explained 14.6 %, 11.9 %, 5.9 % and 4.7 % of variation in phytoplankton community composition respectively (Table 1a). ***SST*** and ***DaysSinceSeaIce*** also showed pairwise relationships with taxa abundances like those detected with ***DaysAfter1Oct***, ***Long.E*** and ***Salinity*** but with opposite correlation sign~~ -0.56 respectively (Table 2~~e). Whilst ***SST***~~d, p: <0.001, ***~~DaysSinceSeaIce~~*** ~~and ***Salinity*** varied systematically through the season,they didn't explain more variance than ***DaysAfter1Oct*** and thus didn't appear in the optimum

415 multi-covariate CAP model (Table 1b). The significant negative correlation between the ***DaysAfter1Oct*** that a sample was~~

collected and the longitude that it was collected (r -0.63, Fig. 5d) indicated that samples collected earlier in the spring-summer were more likely to have been collected further to the east. <0.001, <0.001 respectively).

Neither relative taxonomic total cell volume, estimated using the method of Hillebrand et al. (1999), or inferred relative taxonomic total cell biomass, estimated using the method of Menden-Deuer and Lessard (2001), showed influence of any of
420 the SAM indices (results not shown

3.1 Observed taxonomic abundance and occurrence

Abundance of individual taxa-groups averaged 133 cells per ml and ranged to a maximum of 8,796 cells per ml (Table 3). Individual cell volume ranged from 8 μm^3 for the Parmales to >60,000 μm^3 for the diatoms *Dactyliosolen antarcticus* and *Thalassiothrix antarctica*. Average relative abundance ranged from 0.2 % for the diatom *Fragilariopsis ritscheri*, to 17 % for
425 the combined taxa-group *Fragilariopsis cylindrus/curta*. Of the 22 taxa-groups resolved in this study, four taxa-groups were identified in all 52 samples and 11 taxa-groups were identified in more than 90 % of samples (Table 3).

4 DISCUSSION

4.1 SAM and phytoplankton community composition

Our results show that the Southern Annular Mode (SAM) does indeed affect the ~~composition and abundance~~ community
430 composition of phytoplankton in the seasonal ice zone (SIZ) of the Southern Ocean (SO)~~, supporting our hypothesis~~. This conclusion was supported by a combination of three analyses. (i) Permutation-based analyses of cluster structure demonstrated that the 52 samples were separable into seven statistically different groups on the basis of community abundance composition of the 22 ~~taxa (Figure 6b)~~taxa-groups (Fig. 6b), and thus there was variation between samples that might be explainable with known environmental variables. (ii) CAP analysis identified the SAM as a significant explanatory variable on the structure of
435 the phytoplankton community (Table 1b) and showed that ~~identified clusters~~ groups identified in cluster analysis were generally distinguished by the SAM and *DaysAfter1Oct* ~~(Table 1b,~~ that a sample was collected (Fig. 6). (iii) 15 of the 22 ~~taxa~~ taxa-groups resolved showed significant (p<0.05) pairwise correlations between relative abundance and at least one of the three derived SAM indices (Table 2b). ~~The greatest single influence in phytoplankton community composition was seasonal succession, as represented by *DaysAfter1Oct*, which explained 15.4 % of variance in the multiparameter CAP model (Table 1b), however two~~
440 ~~modes of SAM explained a further 16.9 % in total and will be discussed first.~~

The ~~SAM mode~~ derived SAM index with greatest influence on phytoplankton community composition, *SAM autumn* (~~Fig~~Figs. 3, 4) explained 12.6 % of ~~variance in the multiparameter CAP model . It~~ the variance of phytoplankton community composition in the multi-variable CAP model (Table 1b). *SAM autumn* represented the average SAM around the time that sea ice was extending northward through the SIZ (Fig. 1a). At this time, phytoplankton productivity in the SIZ would have
445 declined to around 30 % of its mid-summer maximum (Moore and Abbott, 2000; Arrigo et al., 2008; Constable et al., 2014),

15

and phytoplankton would be preparing for winter by variously producing energy storage products, producing resting spores or cysts, reducing metabolic rate, and engaging in heterotrophic consumption for energy (Fryxell, 1989; McMinn and Martin, 2013). The formation of sea ice reduces available light by as much as 99.9 % (McMinn et al., 1999), severely limiting light for phytoplankton for ~~more than half a~~ around half of each year: at the range of longitude sampled, latitude 64° S was ~~sea-ice~~ sea

450 ice covered for half the time across the sampled years (Fig. 1a). Windier conditions associated with ~~higher *SAM autumn*~~ more positive SAM in autumn may delay the consolidation of sea ice into larger floes (Roach et al., 2018), extending the phytoplankton growing season, and possibly increasing the relative abundance of taxa that occur later in the ~~season. This~~ spring-summer season. The quantity of phytoplankton that survive the Antarctic winter is extremely low (McMinn and Martin, 2013), and the abundance of taxa present and their metabolic condition when the autumn sea ice forms may strongly influence their viability,

455 relative vigour and availability to seed the subsequent post-winter bloom. This possibility was supported by the observation that the only two ~~taxa~~ taxa-groups observed to have significantly (p<0.05) higher relative abundance later in the spring-summer, the *Chaetoceros* species *C. dichaeta* and *C. concavicornis/curvatus*, were both observed to also show significantly higher relative abundances when the ~~SAM in the preceding autumn was higher~~ preceding *SAM autumn* was more positive (Table 2b). ~~Higher SAM~~ Thus SAM induced effects on phytoplankton in the autumn ~~is expected to result in deeper autumn mixed layers,~~

460 ~~reducing the photosynthetic rate of individual phytoplankton cells as they cycle below the critical depth (??), whilst conversely enhancing potential phytoplankton productivity by maintaining the input of nutrient rich deep water to the euphotic zone. The quantity of phytoplankton that survive the Antarctic winter is extremely low (McMinn and Martin, 2013), and the abundance of taxa present when the sea ice forms may strongly influence the availability of phytoplankton to seed the subsequent~~ could well influence the phytoplankton community structure in the following year.

465 Extending the spring-summer ~~bloom. Extending the~~ productive season by delaying the autumn consolidation of sea ice may result in ~~greater~~ mpre prolonged declines in relative abundance ~~for~~ of taxa that are more prolific earlier in the ~~season~~ spring-summer, and may thus reduce the population from which the following post-winter bloom is initiated. Of the eight ~~taxa showing statistically~~ taxa-groups showing statistically higher (p<0.05) ~~higher~~ relative abundance earlier in the spring-summer, three showed corresponding statistically lower relative abundances with higher preceding *SAM autumn* (*Emiliana huxleyi*, *Nitzschia*

470 *acicularis/decipiens*, and *Parmales* spp., Table 2b), ~~although four of~~ supporting this conjecture. Of the remaining five ~~taxa showing~~ taxa-groups of the eight, four showed no detectable relationship with *SAM autumn*, and one (*Pseudonitzschia lineola*) showed a positive relationship.

Two other ~~SAM modes~~ derived SAM indices were found to influence phytoplankton: *SAM spring* and *SAM prior*. These ~~modes~~ indices were difficult to distinguish due to their largely overlapping time periods (Fig. 4), and they were strongly corre-

475 lated (~~r:~~ r 0.83, Table 2c), with similar influence on taxonomic abundances (Table 2b). *SAM prior* was the preferred parameter for the multiparameter CAP model, in which it explained 4.3 % of total variance. Windier and stormier conditions associated with higher SAM in the months prior to sampling would increase nutrient input to the euphotic zone from deeper waters (Lovenduski and Gruber, 2005), promoting productivity, whilst at the same time episodically diluting surface phytoplankton through deeper mixing. More stormy conditions may also have brought about a faster break-up of sea ice, promoting earlier

480 spring phytoplankton growth. Conversely, ~~it~~ windier conditions would also restrict stratification of the surface ocean, precluding phytoplankton bloom formation, lessening productivity (Fitch and Moore, 2007) and reducing the abundance of early blooming taxa. This may explain the responses of *Emiliania huxleyi* and the combined *Nitzschia acicularis/decipiens* group which both showed early maximum abundances and also negative correlations with **SAM spring** and **SAM prior** (Table 2b). ~~Six other taxa~~ Five other taxa-groups with early maximum abundance (negative correlation with **DaysAfter1Oct**) showed no

485 detectable correlation with **SAM spring** and one (*Pseudonitzschia lineola*) showed a positive relationship, indicating that their ~~abundance was~~ abundances were determined by environmental factors that prevail early in season but not those factors altered by variations in the SAM.

Historically, the variance in the SAM is lower in the spring quarter ~~is lower~~ than in other quarters ~~(NOAA 2005)~~(NOAA, 2005), perhaps explaining why **SAM spring** and **SAM prior** explained less variation in community composition than **SAM autumn**.

490 ~~The small *Chaetoceros neglecta* and the lightly silicified *Dictyocha speculum* both showed positive relationships with~~

We expected the SAM prior to sampling (**SAM prior** ~~but not with **SAM autumn** or **SAM spring**. Yet both these taxa also showed a strong influence~~ and **SAM spring**) would influence phytoplankton composition, while we expected SAM in the winter to have a lesser influence because the surface-ocean is insulated from atmospheric conditions by sea ice. These expected influences of SAM were observed (Fig. 3). The influence of SAM the previous autumn was not expected but is

495 considered a real influence as it coincides with the time when sea ice is forming and thus a critical time for phytoplankton preparing to hibernate the half-year of **DaysAfter1Oct** ~~on their relative abundance and the strength of this relationship may have obscured any pairwise correlation with the SAM and other variables~~ice-cover. We also observed similar correlation between **SAM autumn** and (i) NASA satellite total chlorophyll and (ii) macronutrient concentrations across all samples, and (iii) as a stronger correlation with macronutrient concentrations when only the samples collected in the latter half of the season were

500 considered (Table 2c, d, and e respectively). We also observed maxima in autumn SAM influence in response surface analysis of the correlation between SAM and (i) NASA satellite total chlorophyll, and (ii) [PO_4] in all samples, and (iii) as a stronger maxima with [PO_4] when only the samples collected later in the season were considered (Supplementary Material Figs. S1 and S2). Both total chlorophyll and [PO_4] were observationally independent of the taxonomic cell counts, and whilst [PO_4] was estimated from parallel samples as the taxonomic analysis, NASA satellite total chlorophyll had no material connection with

505 collected samples, being linked only geographically and temporally, and thus offers independent support for the unexpected conclusion that phytoplankton community composition in the spring-summer is influenced by SAM in the previous autumn. The empirically defined **SAM autumn** also showed significant ($p<0.05$) pairwise correlations with 12 of the 22 taxa-groups resolved (Table 2b).

The SAM typically describes around 35 % of total observed Southern Hemisphere climate variability (Marshall, 2007).

510 Hence only a third of any covariance between ~~climate~~ the atmosphere and phytoplankton community composition might be expressed as covariance between the SAM and community composition, and thus the variance in community composition due to variation in climate could well be greater than we detected with the SAM.

17

4.2 ~~Taxa influenced by~~ Effect of SAM on phytoplankton taxa

Nothing has been previously reported with respect to the climatic preferences of the majority of taxa identified in this study. Only 10 of the 22 taxa-groups considered in our research had data-records in the Ocean Biogeographic Information System (OBIS, 2020), and only four of the identified taxa were classified as R- or S-strategists in Brun et al. (2015)'s reproduction of Reynolds (2006) classification: not sufficient to meaningfully group the 22 taxa-groups for analysis. Some of the observed taxa have been reported showing various relationships with environmental factors, including ~~SST~~sea-surface temperature, time through the season, and latitude, but often at ~~a~~ the taxonomic level of genera rather than ~~at~~ a species level (Burckle et al., 1987; Chiba et al., 2000; Waters et al., 2000; Green and Sambrotto, 2006; Gomi et al., 2007). We, however, observed ~~different~~ differing responses to environmental variables among closely related taxa. This was exemplified by the opposite correlations of *Chaetoceros* species *C. dicheata* and *C. neglectus* with **DaysAfter1Oct** (0.48 and -0.70 respectively, Table 2b) and the opposite correlations of *Fragilariopsis* species *F. rhombica* and *F. kerguelensis* with **SAM autumn** (-0.39 and 0.52 respectively, Fig. 5a,b). The strong and opposite response to these variables by species belonging to the same genus indicates the importance of species-level observation in detecting subtle changes in pelagic phytoplankton communities.

The abundance of *Emiliania huxleyi*, the dominant coccolithophorid in the world's oceans (Cubillos et al., 2007), showed a moderate negative relationship with all three identified SAM indices, and a weak negative relationship with **DaysAfter1Oct** (Table 2b). It also showed a moderate negative relationship with the year of sample collection, suggesting abundance declined in the SIZ over the study period. Cardinal et al. (2007) reported a near absence of coccolithophorids south of the Polar Front (latitude ~~55°~~55° S), and ~~(Cubillos et al., 2007)~~ Cubillos et al. (2007) reported surface-water *E. huxleyi* abundances declining southward through the SIZ to near absence by ~~65°~~65° S. No variation in the relative abundance of this species with latitude was seen across the ~~62°~~62° S to 64.5~~°~~° S latitudinal range sampled.

4.3 ~~The effects of SAM on biomass~~

~~Our study clearly showed that variation in the SAM coincided with variation in the structure of the phytoplankton community, but we did not detect any influence on total estimated phytoplankton cell volume or volume-inferred phytoplankton biomass.~~ A third of analysed taxa, comprising 7 taxa and 23 % of all counted cells, showed no detectable relationship with the SAM. This could be due to large errors associated with low counts of rarer taxa, because unaccounted variation was masking any relationship, or because the taxa were insensitive to the SAM. There is less chance of detecting relationships between taxa and environment variables when fewer individuals are counted, however some less represented taxa (e.g. *Emiliania huxleyi*) did show relationships with SAM indices. Five of the 22 taxa resolved showed no significant relationships with either the SAM or **DaysAfter1Oct**. All were comparatively scarce and together represented only 2 % of all cells counted. Assessing species compositions across a greater fraction of each sample, and thus counting more of the scarcer taxa, may have revealed relationships between these rarer taxa and environmental variables (Nakagawa and Cuthill, 2007). Yet it remains possible that these taxa are actually unaffected by seasonal succession and the SAM, instead responding to other environmental variables

that were not measured as part of this study, or that they remain as a persistent but relatively rare background taxa with respect to the overall phytoplankton assemblage.

4.3   The effects of SAM on productivity and biomass

Positive SAM has previously been shown to be associated with increased standing stocks and productivity of phytoplankton in the SIZ of the SO (Arrigo et al., 2008; Boyce et al., 2010; Soppa et al., 2016). In the SIZ above the Antarctic Divergence, 550 nutrients ~~consumed by phytoplankton from surface waters through the spring and summer are replenished by deep-water upwelling through the following winter . Thus,~~ are replenished from the deeper ocean through the unproductive winter and the levels of nutrition remaining at the end of summer integrate the total draw-down of nutrients by phytoplankton production over the entire spring-summer growing season (Arrigo et al., 1999). We observed this ~~drawdown~~ nutrient drawdown through the spring-summer as the negative correlation between all ~~nutrient~~ macronutrient concentrations and *DaysAfter1Oct* (Table 555 2d). We also observed a negative relationship between *SAM autumn* ~~and all macro-nutrient concentrations the following~~ all macronutrient concentrations in the spring-summer and the previous *SAM autumn* (Table 2d, Fig. 5d) suggesting that elevated SAM in autumn leads to greater productivity and thus greater nutrient drawdown during the following spring-summer.

4.4   ~~Sensitivity of phytoplankton taxonomic composition to climate change~~

~~We detected the effect of variation in the SAM on the composition of phytoplankton communities in the SIZ (Table 1,~~
560 ~~2b), and on their productivity as inferred from nutrient draw-down (Table 2d). ? estimated climate change driven trends in chlorophyll and primary production would not become apparent in the SO until around 2055, as natural fluctuations in these variables are large relative to the effect of global warming. The climate of the SO is more variable than climates of lower latitudes due to interactions between atmosphere, ocean, and ice, making the detection of any signal of climate change difficult (Turner et al., 2015). Although change in surface air temperature is already apparent at equatorial latitudes,~~
565 ~~changed surface air temperature in the SIZ of the SO is not expected to be detectable until 2050 or later (?). Whilst our study did not show significant (α=0.05)increase in~~ *SAM autumn* ~~or~~ *SAM spring* ~~over the 11 years sampled, a statistically significant upwards trend of 0.01 SAM points per year has been seen over the period from 1979 through to at least 2014 (Arblaster and Meehl, 2006; Gillett and Fyfe, 2013; Jones et al., 2016). Nevertheless, the differing responses of phytoplankton taxa to their environment, and the integrating effect of successional change, enabled change in phytoplankton composition~~
570 ~~to be detected, suggesting that~~ The nutrient concentrations at the end of the ~~phytoplankton composition is a more sensitive indicator of environmental change than the direct temperature record.~~

4.4   ~~Seasonal succession in taxonomic composition~~

~~Phytoplankton taxonomic composition was expected to follow a successional progression through the~~ spring-summer ~~(?Arrigo et al., 1999; Ten of the 22 taxa showed a significant relationship between relative abundance and~~ *DaysAfter1Oct* ~~(Table 2b), the foremost~~
575 ~~explanatory environmental variable, explaining 15.4~~ productive season would be expected to best represent the productivity

over the season: we observed the correlation between nutrient concentrations and *SAM autumn* were higher when only the 50 % of total observed variance in phytoplankton taxonomic composition (Table 1a). This variable likely represented a proxy for many important unmeasured processes such as solar radiation, increasing mixed-layer depth, and variations in grazing mortality. *DaysAfter1Oct* also covaries with measured variables that also exhibit seasonal changes, including *Salinity*, *DaysSinceSeaIce*, sea surface temperature (*SST*) and the concentrations of macronutrients. Thus, it is unsurprising *DaysAfter1Oct* was the largest explanator of phytoplankton change. This variable, along with *DaysSinceSeaIce* and *SST*, and the range of environmental variables that covary with these environmental factors, drive the seasonal succession of the phytoplankton, from near-surface blooms of large diatoms at the marginal ice edge as it recedes southward across the SIZ, to small diatoms and flagellates forming deep chlorophyllmaxima once the nutrients have been depleted (Wright et al., 2010). *DaysAfter1Oct* has the limitation of being used as a linear variable in this analysis, potentially not detecting influences on taxa that peak mid-season when both solar radiation and productivity are at a maximum (?).

The significant correlation observed between *Long.E* that a sample was collected and *DaysAfter1Oct* that it was collected indicates that the resupply voyages earlier in the season were further east when they traversed the SIZ. This could have been due to avoidance of pack ice or some other navigational consideration of the resupply voyages, however it confounds the two variables and some of the variance attributable to *DaysAfter1Oct* may be due to geographic variation on the longitude of sampling. Longitude cannot be considered an absolute variable in temporal studies of surface water in the SIZ of the SO, as surface water is moving. Surface water north of the Antarctic Divergence (AD)has been recorded moving west to east at velocities in the order of 15 cm s^{-1}, and south of the AD, east to west at similar velocities (?). At this velocity, surface water would completely cross the 625 km of longitude sampled in the current study in 48 days (sampleswere collected over 131 calender days), and surface water sampled late in the samples collected later in the spring-summer may have been 1000 km to the east or west early in the were considered (Table 2e), further supporting the conjecture that higher SAM in the autumn is linked with greater productivity through the following spring-summerperiod. Further, surface water north of the AD has a northward component to its movement and surface water south of the AD has a southward component to its movement (??), and thus latitude is also confounded with *DaysAfter1Oct*, although velocities are much lower and the correlations observed here were not statistically significant (Extra Material S1).

The time since sea ice retreat has previously been identified as an important covariate for explaining phytoplankton population dynamics in the SIZ (???Wright et al., 2010). In this study, the*DaysSinceSeaIce* showed pair-wise relationships with abundances of taxa that were similar to those we observed for*DaysAfter1Oct*, although singly explaining less of the variance in taxonomic composition (5.9 % versus 15.4 % respectively - Table 1a). This difference was also observed in the relative abundances of individual taxa. For example, The observed positive relationship between total chlorophyll and all the SAM indices (*r* 0.5 to 0.72, p<0.0025, Table 2c), and the presence of spring and autumn maxima in the variance in total chlorophyll explained by the SAM (Supplementary material Fig. S1), further support the conjecture that more positive SAM is linked with greater total chlorophyll, and thus greater total productivity in the SIZ. The total chlorophyll data considered was limited to the 52 samples collected, that is, estimated for the times and locations of each sample collection. Estimates were coarsely determined

as interpolations of available monthly predictions (Supplementary material Fig. S3), and estimates could be obtained for only 49 of the 52 samples. Yet there are indicators of reliability in the sparse information: the diatom *Fragilariopsis rhombica* is always relatively small (Table 3), and when the relative abundance of ~~*Chaetoceros dichaeta* showed a positive relationship with *DaysAfter1Oct* (r: 0.48~~this taxon was high, total chlorophyll was lower (*r* -0.59, p<0.0025, Table 2b)~~and a lesser relationship with *DaysSinceSeaIce* (r: 0.37), while~~, and when the relative abundance ~~*Chaetoceros neglectus* showed a negative relationship with *DaysAfter1Oct* (r: -0.70) and lesser relationship with *DaysSinceSeaIce* (r: -0.40).~~

4.4 ~~Taxa not influenced by the SAM~~

~~A third of analysed taxa, comprising 7 taxa and 23 % of all counted cells, showed no detectable relationship with the SAM. This could be due to large errors associated with low counts of rarer taxa, because unaccounted variation was masking any relationship, or because the taxa were insensitive to the SAM. There is less chance of detecting relationships between taxa and environment variables when fewer individuals are counted, however some less represented taxa~~ of larger diatoms were high, total chlorophyll was also often high (e.g. ~~*Emiliania huxleyi) did show relationships with SAM indices.*~~ *Dactyliosolen antarcticus*, *r* 0.37, p<0.05, Table 2b).

~~Five of the 22 taxa resolved showed no significant relationships with either the SAM or *DaysAfter1Oct*. All were comparatively scarce and together represented only 2 % of all cells counted. Assessing species compositions across a greater fraction of each sample, and thus counting more of the scarcer taxa, may have revealed relationships between these rarer taxa and environmental variables (Nakagawa and Cuthill, 2007). Yet it remains possible that these taxa are actually unaffected by seasonal succession and the SAM, instead responding to other environmental variables that were not measured as part of this study, or that they remain as a persistent but relatively rare background taxa with respect to the overall phytoplankton assemblage.~~

4.4 ~~The first study relating the SAM to phytoplankton taxonomic composition~~Implications

This is the first study to show ~~an effect of changes~~ a link between variation in the SAM ~~index on~~ and the composition of phytoplankton communities in the SO, although ~~such findings have already~~ similar findings have been reported for other major climatic phenomena in other parts of the globe. The climatically similar Northern Hemisphere Annular Mode (NAM) causes increased westerly winds and deeper mixed layers at mid- to high northern latitudes in its positive phase (Nehring, 1998; Thompson et al., 2003; Kahru et al., 2011). The NAM has been related to the timing, abundance and biomass of phytoplankton taxa at high northern latitudes (Nehring, 1998; Belgrano et al., 1999; Ottersen et al., 2001; Blenckner and Hillebrand, 2002), and to delayed time of maximum chlorophyll in the North Atlantic Summer (Kahru et al., 2011). Similarly, the El Niño Southern Oscillation (ENSO) equatorial mode has been shown to influence the distribution and abundance of phytoplankton in the tropical oceans (Blanchot et al., 1992).

4.5 ~~Implications~~

The SIZ is a productive region of the SO (Moore and Abbott, 2000), and changes to the SIZ phytoplankton community have potentially far-reaching implications for the ecosystem services these organisms provide, including carbon ~~sequestration~~ export to the deep ocean and supporting the productivity of almost all Antarctic life. Increases in the relative abundance of the larger *Chaetoceros* spp. diatoms would favour grazing by large metazooplankton, especially krill (Boyd et al., 1984; Kawaguchi et al., 1999; Moline et al., 2004), which link phytoplankton to whales, seabirds, seals, and most higher Antarctic life forms (Smetacek, 2008). Such changes would also increase the efficiency of the biological pump as the larger phytoplankton sink more rapidly than small (Alldredge and Gotschalk, 1989), and increased grazing by krill would reparcel ~~the phytoplankton cells~~ some phytoplankton biomass into faeces that would also sink ~~fast~~ more rapidly (Cadée et al., 1992). Such changes in carbon flux and trophodynamics would act as a negative feedback on climate change by speeding the sequestration of carbon in the deep ocean.

Phytoplankton are the pastures of the oceans and it is not surprising that the climate in both autumn and spring influence the taxonomic composition of phytoplankton and their ecological progression through the productive spring-summer period in the SIZ. Climate change impacts have now been documented across every type of ecosystem on Earth (Scheffers et al., 2016; Harris et al., 2018) and the distribution, abundance, phenology and productivity of phytoplankton communities throughout the world are changing in response to warming, acidifying, and stratifying oceans (Hoegh-Guldberg and Bruno, 2010). The surprise is that changes in the taxonomic composition associated with the SAM were detectable over a relatively brief eleven-year monitoring period and despite all the other environmental factors that elicit variability in phytoplankton communities in the SIZ of the SO.

The SAM is predicted to become increasingly positive in the future (Arblaster and Meehl, 2006; Swart and Fyfe, 2012; Gillett and Fyfe, 2013; Abram et al., 2014; Solomon et al., 2016). Our results cannot necessarily be extrapolated to infer changes that will likely occur as the SAM continues to increase, as evolutionary responses can partly mitigate adverse effects on phytoplankton of longer-term climate change, and future climate changes are likely to impose other co-stressors on phytoplankton inhabiting these waters (Lohbeck et al., 2014; Schlüter et al., 2014; Deppeler and Davidson, 2017). The present study demonstrates, for the first time, that variation in the SAM influences the ~~taxonomic~~ community composition of phytoplankton in the SIZ of the SO. The relationships between the SAM and community composition were complex but significant, and the degree of observed ~~covariance~~ covariation warrants further investigation.

5 Conclusions

We found that the Southern Annular Mode ~~was influential on~~ influenced phytoplankton community composition in the seasonal ice zone of the Southern Ocean, second only to the influence of the seasonal succession variable (***DaysAfter1Oct***). ~~This influence suggests~~ SAM indices representing average daily SAM in the prior autumn and spring explained variation in the

community composition of 22 phytoplankton taxa-groups (comprised of individual species, groups of species, genera or higher taxonomic groups). There were indications that more positive SAM was also related to increased phytoplankton productivity in the SIZ, being associated with greater macronutrient drawdown and higher total chlorophyll in the spring-summer productive season. These observations suggest that the phytoplankton of the SIZ are indeed susceptible to changes in the SAM and thus possibly to climate change.

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