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FEATURE ARTICLE

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Implications of the recent loss of Antarctic sea ice for phytoplankton and summer feeding habitats of salps and krill

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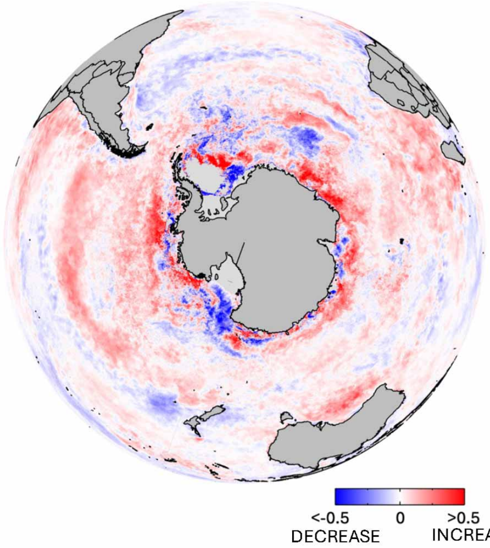
ABSTRACT: Antarctic sea ice showed a profound, step-wise reduction around 2016–2017, but the scarcity of modern time series means that we know very little about how Southern Ocean biota have responded. Given the paucity of direct field data, we combined satellite data with KRILLBASE, a large historical salp and krill database, to examine how the new, low-ice era has changed the feeding habitat of these key plankton species. Most (69%) of the Southern Ocean area has experienced an increase in mean summer chlorophyll *a* (chl *a*) values since the step-change in sea ice. We went beyond bulk chl *a* indices to classify the Southern Ocean into 14 optical water types based on their spectral reflectance. At this finer resolution, the 2 species showed more habitat differentiation than discernible from chl *a* alone, with salps being strongly correlated with those optical water types that increased in area after the 2017 reduction in sea ice. These water types have moderate phytoplankton concentrations (~0.4 mg chl *a* m^{-3}), and large expanses of the Indian-Pacific sector improved from being too oligotrophic into better feeding habitats for salps. We also show fundamental differences in habitat requirements of both species between the Atlantic and the Indian-Pacific sectors, but overall, our feeding habitat indices suggested that the modern low-ice era has become more favourable for salps. Antarctic sea ice is a crucial part of the climate system, and the recent era of extreme variability and record lows has major ramifications for food webs and biogeochemical cycles.



Nearly 70% of the Southern Ocean shows an increase in mean summer chlorophyll *a* concentrations since the 2016/2017 reduction in sea-ice, improving the feeding habitat for salps. Increase/decrease is measured as Log_{10}(Chl *a* 2017–2022) minus Log_{10}(Chl *a* 1998–2016).

Image: Robert Brewin

KEY WORDS: *Salpa thompsoni* · *Euphausia superba* · Sea ice · Regime shift · Chlorophyll *a* · Optical water types · Seascapes

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1. INTRODUCTION

The period 2016–2017 marked an abrupt decline in Southern Ocean sea ice extent (Purich & Doddridge 2023). Sea ice has remained around the new record low levels ever since, with the most recent austral summer of 2025 also witnessing near-record ice minima. This change is leading to a growing consensus that we have experienced a recent system shift or structural change in the sea ice environment (Hobbs et al. 2024, Raphael et al. 2025). Sea ice covers around half of the Southern Ocean area at its greatest winter extent, and, given that the sea ice reduction is occurring year-round, the area of ocean potentially impacted by this step change is substantial.

Sea ice has a myriad of impacts on the pelagic food web, both directly as a substrate and more indirectly, for example, through its melting and conditioning of the water column for subsequent productivity (Schmidt et al. 2018, Swadling et al. 2023, Schofield et al. 2024). Despite the known importance of sea ice, we know surprisingly little about how its recent and dramatic decline is impacting pelagic food webs (Siegert et al. 2023, Schofield et al. 2024, Wienecke et al. 2024). The reason perhaps reflects the fact that the change is still relatively recent, and, with the inevitable delay between sampling and publication, there are not yet enough years in the new low-ice era from which to discern a signal from the natural variability. This data deficit is also not helped by the reduction in large-scale field monitoring of the Southern Ocean (Hill et al. 2024), with notable examples being the reductions in the US AMLR and US LTER time series (Conroy et al. 2025).

Given that sea ice formation and melting impact nutrient supply, stratification and light climate, we may hypothesise that the large-scale, year-round reduction would have wide-ranging impacts on phytoplankton biomass and species composition, impacting higher trophic levels. Multi-decadal trends in bloom timing and phytoplankton concentration based on satellite-derived chlorophyll *a* (chl *a*) have been documented, both at circumpolar scales (Thomalla et al. 2023) and west of the Antarctic Peninsula, where it was related to declining sea ice (Ferreira et al. 2024). Importantly, however, a range of contrasting trends at both circumpolar and regional scales has been reported (Doddridge et al. 2025). These include, for example, an increase in iron stress explainable by changing primary production (Ryan-Keogh et al. 2023) or changing phytoplankton phenology but minimal trends in annual mean chl *a* west of the Antarctic Peninsula (Turner et al. 2024). Recently, a study of the circumpolar sea ice zone also found a strong inflection in phytoplankton composition around the time of the sea ice step change (Hayward et al. 2025), with a decline in diatoms and increases in cryptophytes and haptophytes. Clearly, many factors besides sea ice impact phytoplankton; however, the Hayward et al. (2025) study provides a logical basis to examine the satellite ocean colour record to compare the high- and low-ice eras in the context of habitat suitability for consumers of this phytoplankton.

Antarctic krill *Euphausia superba* (hereafter 'krill') and salps are key consumers of phytoplankton in the Southern Ocean. Both have enormous biomass, exhibit filter-feeding and swarming behaviours and play an important role in recycling and exporting nutrients (Pakhomov et al. 2002, Schmidt et al. 2016, Pauli et al. 2021, Yang et al. 2021, Décima et al. 2023). However, they have fundamentally differing roles in the food web: krill support an iconic food web including whales, penguins and seals (Fraser & Hofmann 2003) and are also the target of an expanding fishery (Meyer et al. 2020). Salps, by contrast, are gelatinous filter feeders, and while they do not support a fishery or the large iconic mammalian predators, our perception of their role in food webs has shifted substantially. They have higher carbon content than most gelatinous predators (Dubischar et al. 2012, McConville et al. 2017), and with the increasing use of genetic methods that enumerate soft-bodied prey (Ruiz et al. 2024), there is an increasing realisation of their importance in food webs as well as biogeochemical cycles (Henschke et al. 2016).

The high biomasses and contrasting food web roles of salps and krill have led to much debate over how the 2 species are faring under climate change (Loeb et al. 1997, Atkinson et al. 2004, Cox et al. 2018, Hill et al. 2024). Unfortunately, valuable time series and fieldwork to examine these issues are increasingly hard to resource (Hill et al. 2024, Conroy et al. 2025), and there are insufficient data to show whether or not the trends suggested in previous studies are continuing. Due to the lack of new, large-scale field sampling programmes that extend the existing salp and krill time series, we used recent developments in earth observation to determine whether the modern, low-ice era has coincided with more suitable summer feeding habitats for either salps or krill.

Bulk chl *a* is only a crude proxy of suitable feeding conditions for zooplankton, so here, we used a novel proxy by classifying the Southern Ocean into 14 optical water types (OWTs) based on their reflectance characteristics. We then linked the KRILLBASE records, a database of krill and salp abundance based on net sampling (Atkinson et al. 2017), to the relative dominance of the OWTs around each net sampling station. Based on the strength of positive or negative relationships with each OWT and its relative increase or decrease from the high-ice to the low-ice era, we quantified the extent to which the suitable feeding habitat for each species has shifted.

2. MATERIALS AND METHODS

2.1. Overview of approach

To address our hypothesis that the recent, post-2017 low-ice era coincides with an improvement in feeding conditions for krill relative to salps, we combined KRILLBASE, a circumpolar database compiling krill and salp net catch data (Atkinson et al. 2017), with satellite-derived coverage of 14 OWTs. Given that the sea ice step change is still relatively recent, after the decades when most of the circumpolar-scale net sampling for krill and salps took place, we were not able to analyse the krill and salp data in relation to the environment as a time series spanning this step change. Instead, we have matched each summer sampling station in KRILLBASE to climatologies of dominance of the 14 OWTs around the sampling site, to gauge which OWTs krill and salps tended to 'prefer', based on correlation analysis. We then quantified how much each of these OWTs had increased or decreased in area following the step change in sea ice, and from these values, we calculated an index of change in the suitability of feeding habitat for each species.

Various approaches can be used for these habitat analyses. All face a trade-off between averaging out interesting patterns and the loss of explanatory power when data sets are divided extensively. Initial trials compared 2 indices of krill and salp abundance: namely, mean density (Fig. S1 in the Supplement at www.int-res.com/articles/suppl/m774p001_supp.pdf) and frequency of encountering swarms in various densities. Likewise, we explored different scales of analysis; for example, matching the sampling stations to OWTs that were both specific to the actual months of sampling or based on long-term climatologies for the month of sampling. Spatially, we compared various resolutions and found that a pragmatic distinction was to divide the Southern Ocean into 2 broad sectors: Atlantic and Indian-Pacific. This reflects first the large differences in habitat preferences between these areas, with krill having a much more oceanic distribution in the Indian-Pacific sector (Atkinson et al. 2008). In addition, the 10 and 90° W lines of longitude formed a natural discontinuity in krill and salp sampling density between sectors (Atkinson et al. 2017). Clearly, feeding habitat is not the only variable influencing species distribution, and to provide context for our OWT analyses, we also examined krill and salp abundance in relation to water temperature, bathymetric depth and bulk chl *a*.

2.2. Determination of OWTs and their areas

To provide a natural, global-scale classification of water types according to the biophysical properties, we used the Ocean Colour Climate Change Initiative (OC-CCIv6) source data set. While this data set also provides indices of chl *a*, this commonly used metric is a single, derived product, itself based on a suite of optical data. Our approach instead was to use, in addition to chl *a*, these source data to obtain a higher resolution of consistently classified water types. We used the approach and classification scheme described fully in Jackson et al. (2017). In brief, ocean colour remote sensing provides reflectance in the visible part of the electromagnetic spectrum, and the approach incorporates these into a fuzzy classification building on that by Moore et al. (2009) and using globally distributed data, including data from the Southern Ocean. This method provided a natural classification into 14 statistically separable OWTs, whose basic optical properties are illustrated in Figs. 1 & 2 (see Table 1 for quantification). The 14 successive OWTs tended to coincide with increasing mean and ranges in chl *a* concentration, although OWTs 5 and 9 departed slightly from this trend. Based on this product, the source data set we used was a 4 km pixel resolution, monthly temporal coverage spanning 1998–2022.

A monthly time series of the coverage of each OWT was calculated for 2 sectors south of 55° S: the Atlantic sector (10–90° W) and the remaining Indian-Pacific sector for the period spanning 1998–2022. Monthly OWT images were created by taking the monthly mode OWT for each pixel. The total area covered by pixels of each OWT was then calculated at each monthly interval to construct the time series of OWT areas. An increase in the number of ocean colour satellites after 2002 led to a substantial increase in pixel coverage (Sathyendranath et al. 2019). For this reason, the increase in total area of all 14 OWTs (i.e. total available feeding habitat) after 2017 was estimated as the December to March mean area of water south of

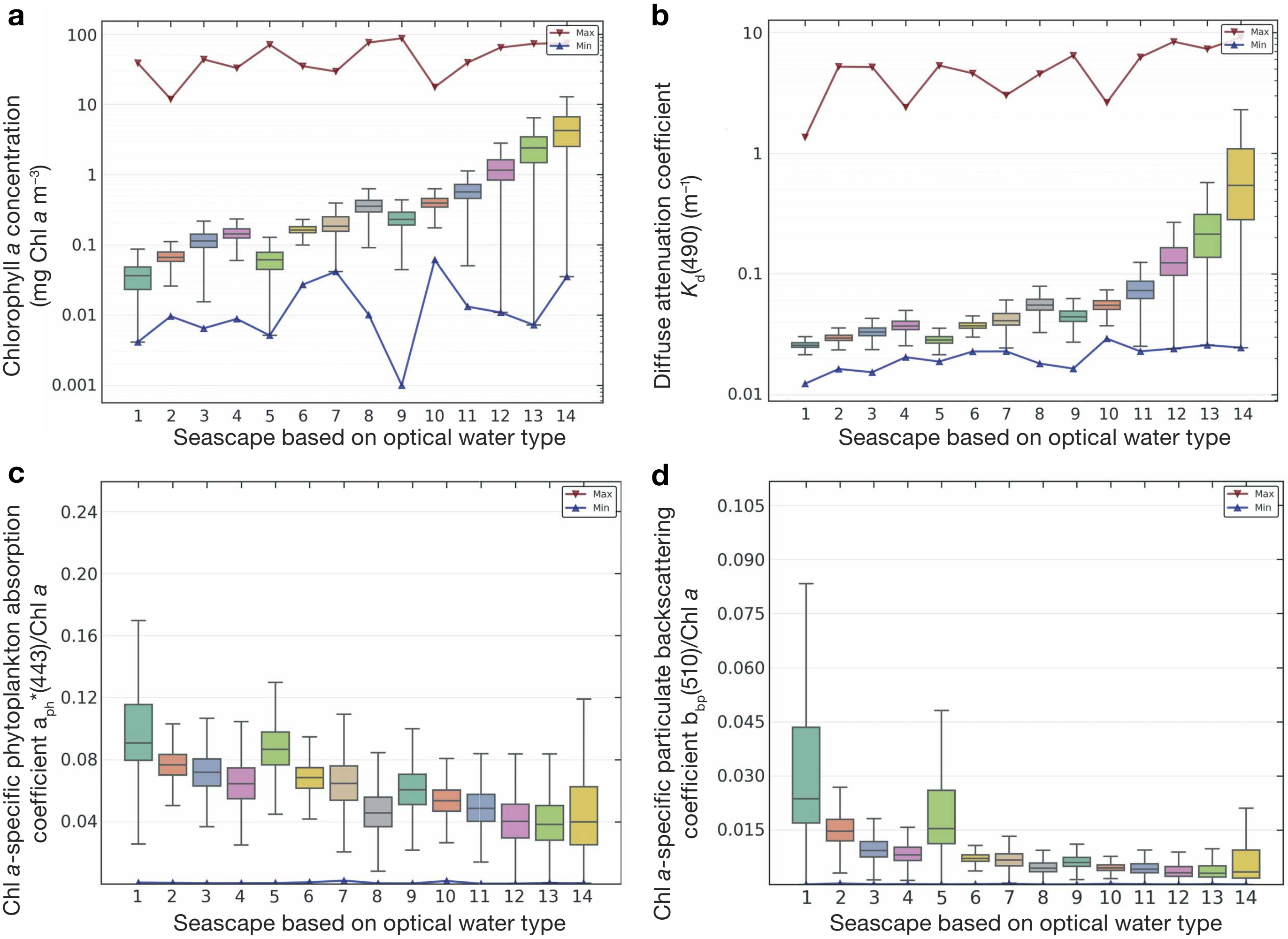

Fig. 1. (a) Chlorophyll (chl *a*) concentration; (b) diffuse attenuation coefficient, $K_d(490)$; (c) chlorophyll-specific phytoplankton absorption coefficient ($a_{ph}^{*}(443) = a_{ph}(443)$ / chl *a*); (d) chl *a*-specific particulate backscattering coefficient, $b_{bp}(510)$ / chl *a*. The boxes represent first and third quartiles; whiskers are 1.5 times each quartile

55° S without an OWT designation spanning 2003–2016, minus the equivalent value from 2017–2022. Absent data for a pixel for a month meant that there was no open water visible, either due to cloud cover or ice cover. Total pixel calculated area (including absent data) south of 55° S was 33.2 million km^2, slightly larger than the area often calculated for the Southern Ocean south of the Antarctic Polar Front, due to this front being far south of 55° S in the Pacific sector.

Maps of modal monthly OWTs were often a partial mosaic of multiple OWTs; so to ease viewing, these maps were smoothed into 'seascapes' (Laurenson et al. 2025) that presented clearer boundaries between broad regions that were dominated by a single OWT. The processing to compute the bio-optical seascapes from the OWTs included a binary opening, binary dilation and nearest neighbour interpolation, typical in image processing analysis techniques.

2.3. Salp and krill data

The krill and salp database used is known as KRILLBASE (Atkinson et al. 2017). This database is a circumpolar composite of all available net samples for post-larval krill and salps (predominantly *Salpa thompsoni* with a smaller component of *Ihlea racovitzai*, with individual numbers counted whether as aggregate or solitary life forms). Krill are mobile and can evade nets, and because KRILLBASE is a composite database including many different types of gear, the krill catch densities were standardised to adjust them to a single, efficient net capture method: a large (RMT 8) net deployed at night on 1 January (see Atkinson et al. 2017 for details of standardisation). KRILLBASE data span from 1926 and comprise only pre-fixed station data, with hauls targeted on aggregations excluded. Data are pres-

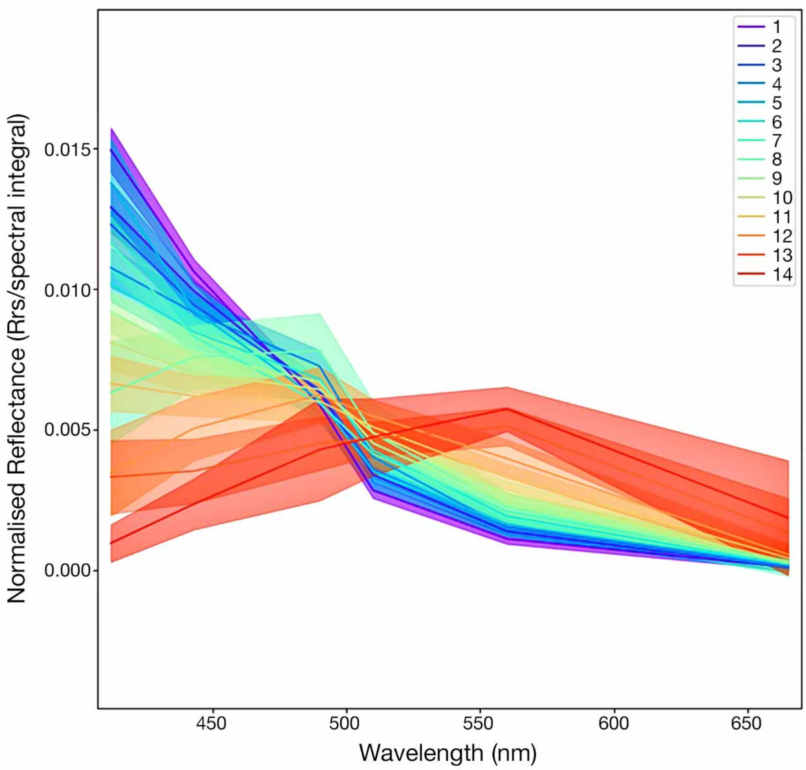

Fig. 2. Reflectance spectra of the 14 optical water types (OWTs). The lower-numbered OWTs are bluer with higher reflectances around 400–440 nm. As one moves up the seascape numbers, one moves into sequentially greener and eventually redder or browner waters (peak shifts to wavelengths >500) that are often highly scattering. This increased turbidity (higher scattering) can be seen from the flatter spectrum in the higher seascape spectra

ented as numbers of individuals under 1 m^2 within the sampled water column.

To screen KRILLBASE, we first removed a relatively small number of records taken outside the main ice-free, open water, phytoplankton growth season, spanning from December to March. Then we removed older data from the 1920s and 1930s, which is unlikely to be representative of the modern era observed by satellites. This screening left good coverage that spanned from 1976. Please note that 'years' are hereafter described not as calendar years but as austral summer years, such that 1976 spans from December 1975 to March 1976. Most KRILLBASE data, especially those data outside of the Atlantic sector, are from the last century and the first decade of this century. This attenuation of sampling effort in recent decades is particularly severe for salps, so we augmented the data with an additional 1987 net hauls for salps from this century, spanning up to 2020. These data were provided by one of the authors (E.A.P.) and obtained from recent sampling expeditions, mainly from the USA within the Atlantic sector. Therefore, sampling coverage spanned 1976–2016 for krill and 1976–2020 for salps.

Data were then further screened to ensure that a representative portion of the vertical distribution of each species was sampled. For krill, to maintain consistency with previous data analyses (Atkinson et al. 2022), we selected only those stations where the top sampling depth was 20 m or shallower and the bottom sampling depth was 50 m or deeper. As salps tend to perform more extensive vertical migrations, we selected a deeper bottom sampling depth criterion for salps of at least 100 m for consistency with Atkinson et al. (2004). In practice, the sampling depth ranges for both species were much larger, with the median value for both species being 170 m after this screening. After the screening steps, we were left with sizeable data sets in both sectors. In the Atlantic sector (10–90° W), we had 4190 and 6817 salp and krill records, respectively, while in the remaining (Indian-Pacific) sector, we had 1610 and 1915 records.

KRILLBASE records include basic environmental data such as bathymetric depth and water temperature. Mean water depth of sampling was calculated by overlaying the sampling stations on Gebco 2014 Grid bathymetry (www.gebco.net) and calculating a mean value within 10 km of the sampling station, excluding pixels on land. Long-term average February sea surface temperature was also derived for each net sampling location. These values are climatological sea surface means for February, averaged over the years 1979–2014, based on data downloaded in July 2016 from http://apps.ecmwf.int/datasets/data/interim-full-moda/levtype=sfc/. Data were provided on a 0.75° × 0.75° grid, and we extracted mean values with the same 10 km buffer method used for the bathymetry.

2.4. Krill and salp habitat analysis

We linked each salp and krill sampling station to the relative weighting of each of the 14 OWTs. The first step was to obtain a long-term (1998–2022) monthly climatology value (i.e. a separate climatology for each of December, January, February and March) for the relative weighting value of each of the 14 OWTs for each 4 × 4 km pixel. We then superimposed the KRILLBASE sampling stations (Atkinson et al. 2017) on this grid and extracted the nearest 3 × 3 pixel patch covering the station for the month in which it was sampled. The respective OWT weighting for each KRILLBASE station was thus obtained as the median value obtained from this pixel patch.

Following earlier work (Atkinson et al. 2008, Yang et al. 2021), we present our analysis not in terms of individual stations, but as aggregated blocks of stations equal in number. These blocks were determined by ranking all stations according to the value of the predictor variable under test, namely each of the 14 OWTs and chl *a*, temperature and water depth. We then divided the ranked data into 20 subsets with the same number of stations in each. For each of these 20 portions, we then calculated a mean value of the predictor variable and a mean value of the response variable.

We performed further trials over the indices of salp and krill density to use. We compared indices based on mean density within each of the 20 equal-sized portions of the data (Fig. S1) as well as the frequency of encountering high 'swarm' densities, of which we tested thresholds of 1, 10 or 100 ind. m^{-2}. The best results (i.e. the highest R^2 values) were obtained by plotting the fraction of hauls in each data block that contained >10 ind. m^{-2}, so we used this abundance index. The approach of dividing the data into equal-sized blocks and calculating the fraction of hauls with swarm densities in each block appeared to be a reasonable compromise between giving swarms the weighting they deserve in the analysis, but preventing the chance nature of sampling them from having an undue influence on the results.

2.5. Testing of appropriate scale for analyses

We experimented with initial trial analyses to determine an appropriate scale of analysis. Given that krill and salps both form dense aggregations that can reduce the density of the prey, we wanted to avoid circularity of cause and effect by constructing an analysis at a suitably large scale to show which habitats 'suit' each species rather than looking at possible local-scale depredations of food around their aggregations. We therefore chose to match the salp and krill abundances to the long-term (1998–2022) climatological mean OWT values specific to the month of sampling, and this choice also provided a greater volume of satellite data for the comparison. Using these long-term climatologies, we had the choice to compare either with the same period of salp and krill observations (spanning 1998–2000) or the larger, longer-term modern era data set spanning 1976–2000. We computed both (Fig. S2) and found that the main conclusions (i.e. a substantial improvement in feeding conditions for salps relative to krill in the Indian-Pacific sector) were supported by both approaches. However, because the whole post-1976 time period provided substantially more match-up data (Fig. S1), particularly for the Indian-Pacific sector, we present those results here.

2.6. Calculating change in feeding habitat suitability

We defined a simple metric of change in feeding habitat suitability based on 2 component values: the strength of positive or negative Spearman correlation coefficient between the fraction of swarms in the data blocks and their respective dominance of each OWT, multiplied by the extent to which that OWT had increased or decreased between the high- and low-ice eras. We thus defined the change in habitat suitability index (I) as $I = \Sigma$(change in area of OWT_i × correlation coefficient of krill/salps with OWT_i), summed across all 14 OWTs ($i = 1$ to 14). Thus, for example, in the Indian-Pacific sector, salps tended to be strongly positively correlated with several OWTs that had increased greatly in their extent since the step change in sea ice, while being negatively correlated with OWTs that decreased in extent. Both of these types of multiplicative relationships (double positive and double negative), when summed, tended to yield a strongly positive value of I. Conversely, negative relationships with OWTs that increased in area, or positive relationships with those OWTs that decreased in area, both tended to yield lower values of I.

2.7. Statistical analyses

All plotting of the KRILLBASE data and their comparison with environmental variables (e.g. water depth, temperature) was done in ArcMap (v.10.2.2). Subsequent matching of KRILLBASE station data with the OWTs and calculation of climatologies was done in Python (v.3.10.8). Calculation of Spearman correlation coefficients to determine the indices of changing habitat suitability was done using Minitab (v.17).

3. RESULTS

3.1. Sea ice loss coincides with increased areas with elevated phytoplankton concentrations

Both the minimum and maximum sea ice extent transitioned to a low era in 2017 (Fig. 3a), the year identified as the onset of the step-wise reduction in the changepoint analysis of Purich & Doddridge (2023). For subsequent analyses of change in habitat suitability, we have therefore divided the satellite data into 2 eras: the modern low-ice era (2017–2022) and the preceding era spanning 1998 (the first austral summer of ocean colour coverage) to 2016, here termed the 'high-ice era'. This decline in sea ice is year-round, reflected in both sea ice concentration (Fig. 3b) and sea ice area with at least 15% concentration (Fig. 3c,d).

During both the high and low sea ice eras, summer chl *a* concentrations followed the well-documented pattern of high values near and downstream of iron-fertilised shelves and islands, interspersed with land-remote, high-nutrient–low-chlorophyll (HNLC) belts (Fig. 4a,b). Looking at the trends in chl *a* between the

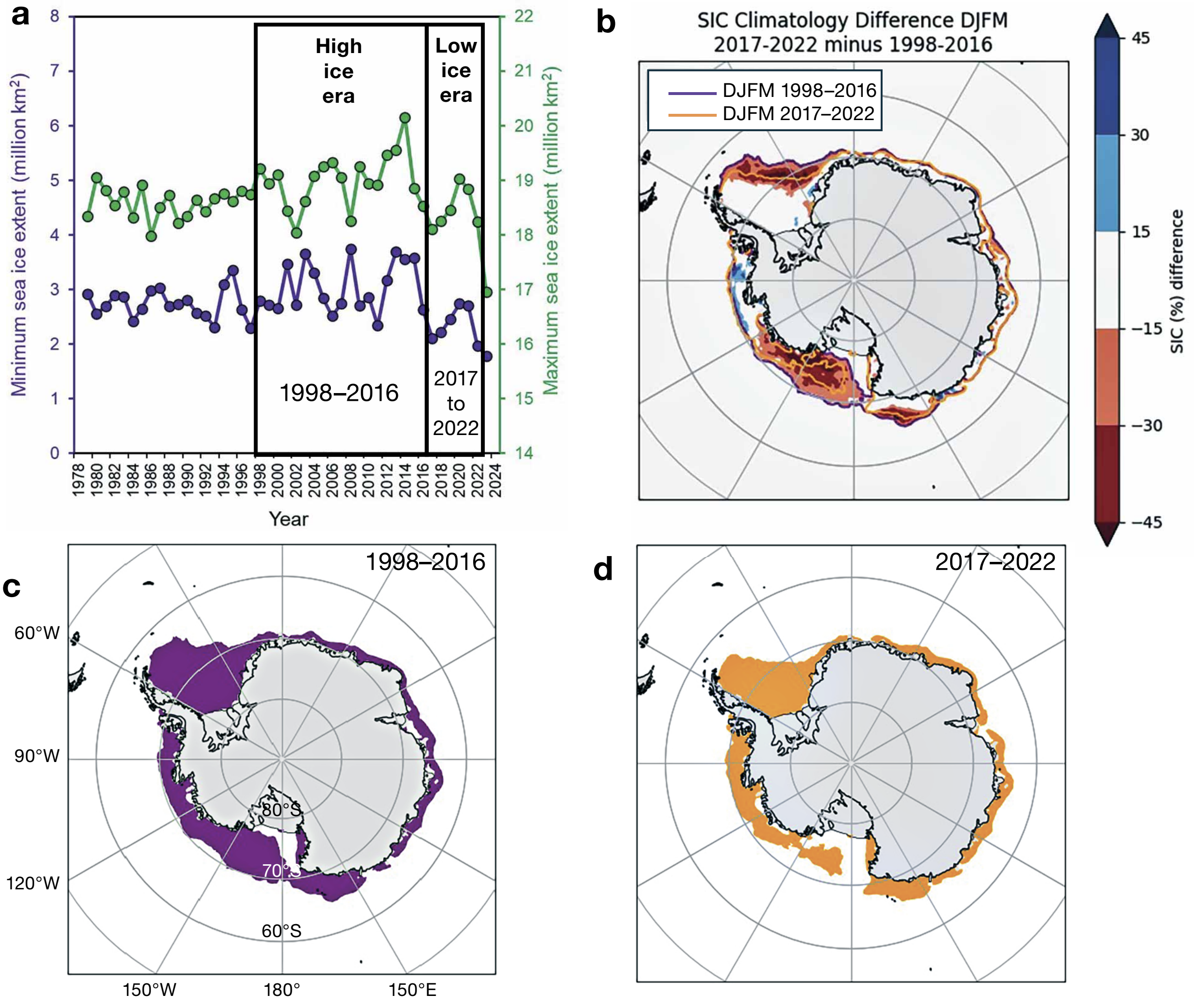

Fig. 3. (a) Annual minimum and maximum sea ice extents showing the abrupt transition to low-ice conditions in summer 2017. Note the change in scale. Data are from the 5 d sea ice product from the NSIDC Sea Ice Index (http://nsidc.org/data/seaice_index), using data from the Defence Meteorological Satellite Program (DMSP) series of passive microwave remote sensing instruments (Fetterer et al. 2017). Based on this step change in the austral summer of 2017 (Purich & Doddridge 2023), we defined 2 eras: from 1998 (the start of available chl *a* products) to 2016 as the 'high-ice era' and 2017–2022 (the last year with available OWT data) as the 'low-ice era'. (b) Change in median sea ice concentration (SIC) based on climatological summer (December–March; DJFM) median concentrations for the high- and low-ice eras. Also depicted are the median 15% concentration edges of sea ice for each era. (c,d) Median extent of summer climatological summer (December–March) 15% sea ice concentration for the respective high- and low-ice eras

successive eras (Fig. 4c), there were strong increases at higher latitudes interspersed with hotspots of strong decrease, particularly around the Ross, Weddell and Lazarev Seas. However, when considering the whole area south of 55° S with available pixel samples in summer in both eras (i.e. 31.2 million km^2), a substantial majority (69%) of this area experienced an increase in mean summer chl *a* following the sea ice step change (Fig. 4d). This change reflected large areas of lower latitude, lower chl *a* within the main easterly flow of the Antarctic Circumpolar Current, which showed consistent, albeit modest, increases.

Fig. 5 shows the OWTs for both Atlantic and Indian-Pacific sectors listed according to their change in area from the high-ice to the low-ice era. In the Indian-Pacific sector, the large increases in area of some OWTs, such as 8, 9 and 11, are partially offset by losses in others, such as OWTs 4 and 6 (Fig. 5a). The OWTs that increase tend to be higher-number ones, often signifying moderate-to-high chl *a* concentration (Fig. 1, Table 1), while the decreasing ones, such as OWT 4, tend to be low concentrations found in HNLC belts such as the southeast Pacific.

The maps in Fig. 5b show the OWTs that have been smoothed for viewing as 'seascapes' to depict the austral summer climatology for each era. These maps were computed by taking the pixel-by-pixel mode of all monthly seascape maps for December, January, February and March in each time period. By the nature of this averaging approach, this highlights the most frequently occurring OWTs per pixel. Less dominant but still important OWTs may not be captured in these maps of modal seascapes, even if, for some periods, they cover significant areas. This issue explains why some OWTs (such as OWT 6 in the Indian-Pacific sector) show big changes in overall area in Fig. 5a but are not depicted in the modal seascape maps of Fig. 5b.

3.2. Relationships of salps and krill to their environment differ between sectors

Based on their climatological average summer distributions, both species have high concentrations in the Atlantic sector (Fig. 6), although salps are more evenly distributed around Antarctica than are krill, with further hotspots in other sectors. To provide an index of abundance, the frequency of encountering swarm densities (i.e. >10 ind. m^{-2}; see Fig. 7) had better predictive ability than measures of mean density (Fig. S1). Using the preferred swarm frequency metric, the relationships of krill and salps with chl *a* (Fig. 7a), water temperature (Fig. 7b) and water depth (Fig. 7c) varied both between species and between sectors. With the exception of salps in the Atlantic sector, the highest densities of both taxa tended to be at intermediate chl *a* concentrations (roughly around 0.4 mg chl *a* m^{-3}). The salp distribution in the Atlantic sector was very different to this prevailing pattern, with some of the highest swarm concentrations in low chl *a* waters.

For the relationships with temperature, the sectoral differences were not obvious; instead, the species differed markedly in their thermal preferences. Salp frequencies were highest in waters with summer tem-

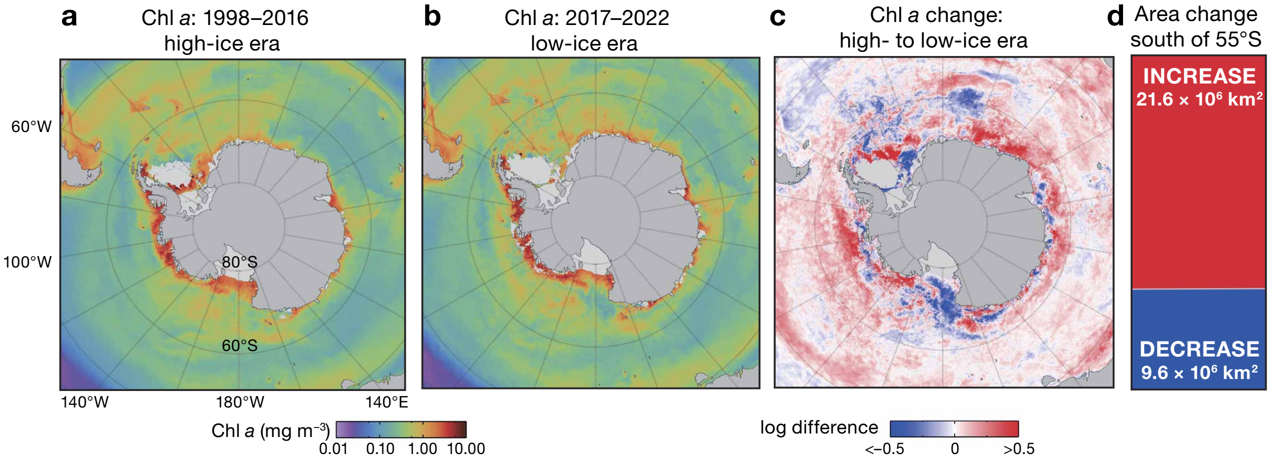

Fig. 4. (a,b) Austral summer (December–March) chl *a* climatologies of the high- and low-ice eras. (c) Change in austral summer mean chl *a* concentrations between the 2 eras, defined as the difference between the logged values, with red signifying an increase. (d) Relative division of areas experiencing an increase and decrease in mean austral summer chl *a* concentration from the high- to the low-ice era. Based on pixels with data in both eras, 69% of the 31.2 million km^2 of the Southern Ocean south of 55° S experienced an increase in mean chl *a* concentrations

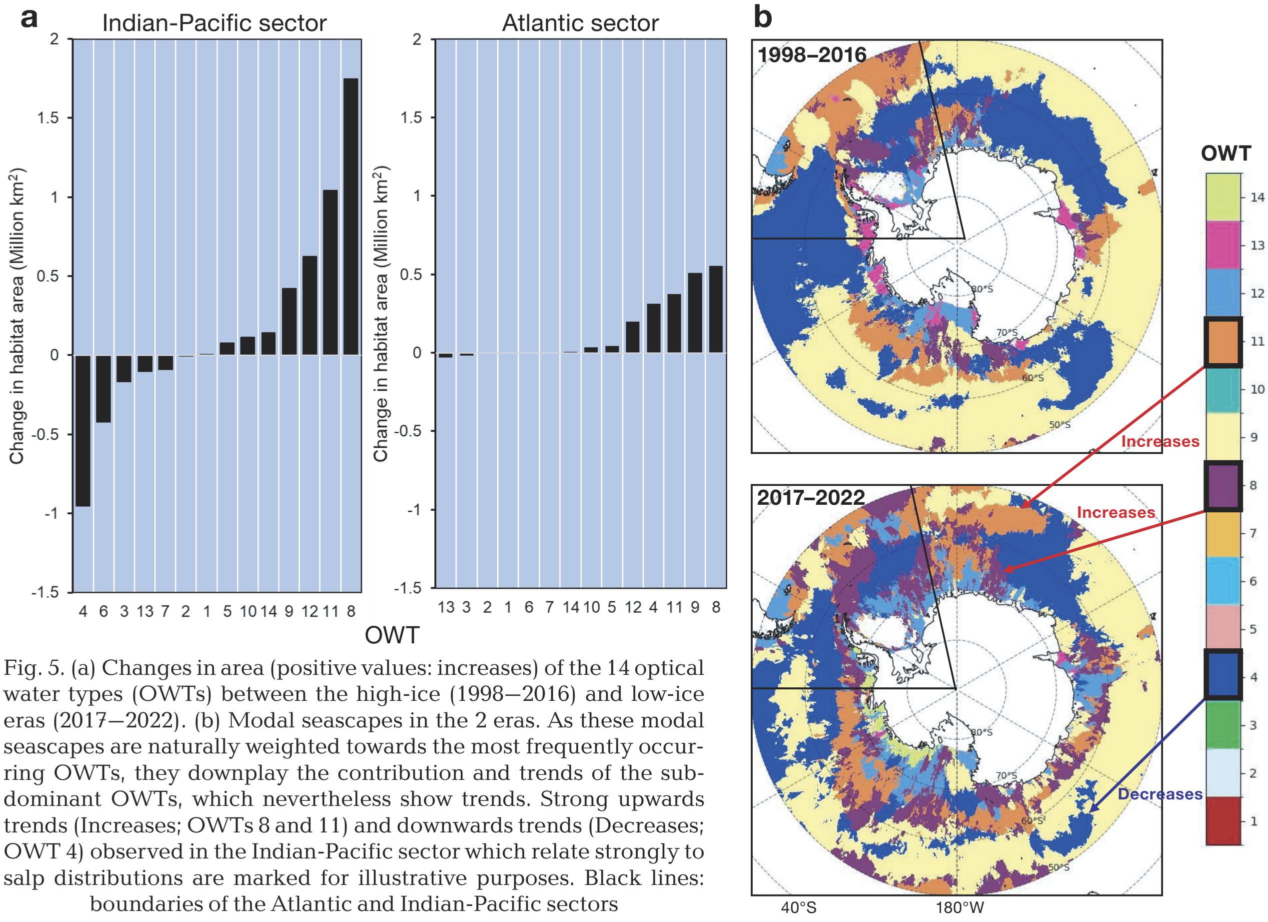

Fig. 5. (a) Changes in area (positive values: increases) of the 14 optical water types (OWTs) between the high-ice (1998–2016) and low-ice eras (2017–2022). (b) Modal seascapes in the 2 eras. As these modal seascapes are naturally weighted towards the most frequently occurring OWTs, they downplay the contribution and trends of the subdominant OWTs, which nevertheless show trends. Strong upwards trends (Increases; OWTs 8 and 11) and downwards trends (Decreases; OWT 4) observed in the Indian-Pacific sector which relate strongly to salp distributions are marked for illustrative purposes. Black lines: boundaries of the Atlantic and Indian-Pacific sectors

peratures around 2°C, whereas krill peaked in waters of <0°C. Both species and sectoral differences were clear for the relationship with bathymetric depth. Salp numbers were lowest in shallow shelf waters, especially in the Indian-Pacific sector, whereas for krill, frequencies were maximal in shallow waters of the Atlantic sector, but minimal in equivalent depths of the Indian-Pacific sector.

Table 1. Seascape class-specific mean ± SD values for chl *a* concentration (mg m^{-3}); diffuse attenuation coefficient, $K_d(490)$ (m^{-1}); chlorophyll-specific phytoplankton absorption coefficient, $a_{ph}{}^{\star}(443)$ (m^2 mg^{-1}); and chl *a*-specific particulate backscattering coefficient, $b_{bp}{}^{\star}(510)$ (m^2 mg^{-1}) in oceanic and shelf waters. Results are based on 14 respective component optical water types

Seascape	Chl *a*	K_d(490)	$a_{ph}{}^{\star}$(443)	$b_{bp}{}^{\star}$(510)
1	0.039 ± 0.076	0.026 ± 0.012	0.105 ± 0.060	0.034 ± 0.030
2	0.095 ± 0.175	0.032 ± 0.026	0.078 ± 0.043	0.016 ± 0.062
3	0.141 ± 0.226	0.035 ± 0.026	0.073 ± 0.036	0.011 ± 0.017
4	0.170 ± 0.172	0.040 ± 0.02	0.065 ± 0.029	0.009 ± 0.009
5	0.077 ± 0.219	0.030 ± 0.034	0.093 ± 0.069	0.023 ± 0.043
6	0.185 ± 0.207	0.039 ± 0.028	0.068 ± 0.018	0.008 ± 0.008
7	0.251 ± 0.390	0.046 ± 0.041	0.066 ± 0.036	0.007 ± 0.004
8	0.408 ± 0.352	0.060 ± 0.036	0.048 ± 0.074	0.005 ± 0.006
9	0.269 ± 0.245	0.047 ± 0.029	0.062 ± 0.163	0.007 ± 0.007
10	0.435 ± 0.273	0.059 ± 0.030	0.054 ± 0.014	0.005 ± 0.004
11	0.654 ± 0.438	0.081 ± 0.049	0.050 ± 0.021	0.005 ± 0.008
12	1.338 ± 0.892	0.147 ± 0.110	0.043 ± 0.032	0.005 ± 0.007
13	2.650 ± 1.753	0.257 ± 0.220	0.043 ± 0.240	0.005 ± 0.013
14	5.016 ± 3.877	0.887 ± 1.014	0.043 ± 0.113	0.008 ± 0.015

3.3. The modern low-ice era may provide enhanced salp feeding habitat in the Indian-Pacific sector

The standout result from our index of changing habitat suitability was that the recent, low-ice era strongly favoured salps in the Indian-Pacific sector (Fig. 8). This result reflected the highly significant positive relationships with several water types that increased greatly in area. By contrast, there was little convincing evidence for any change in summer feeding conditions for krill or for either species in the Atlantic sector. Salps in the

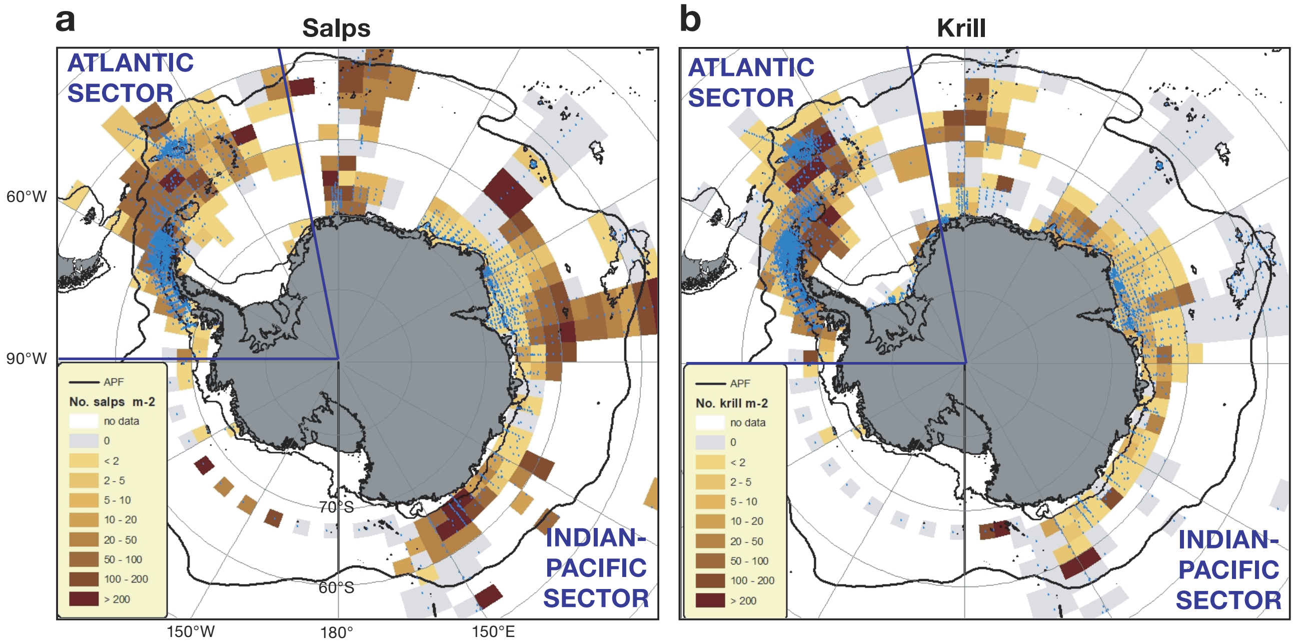

Fig. 6. Gridded mean density of (a) salps (from 5800 stations) and (b) krill (8734 stations) based on post-1976 climatologies for December–March. Stations (blue dots) were matched to optical water types and are plotted on a 2° latitude by 5° longitude grid. Blue lines: 10–90° W Atlantic sector, which was analysed separately from the remaining Indian-Pacific sector. APF: Antarctic Polar Front

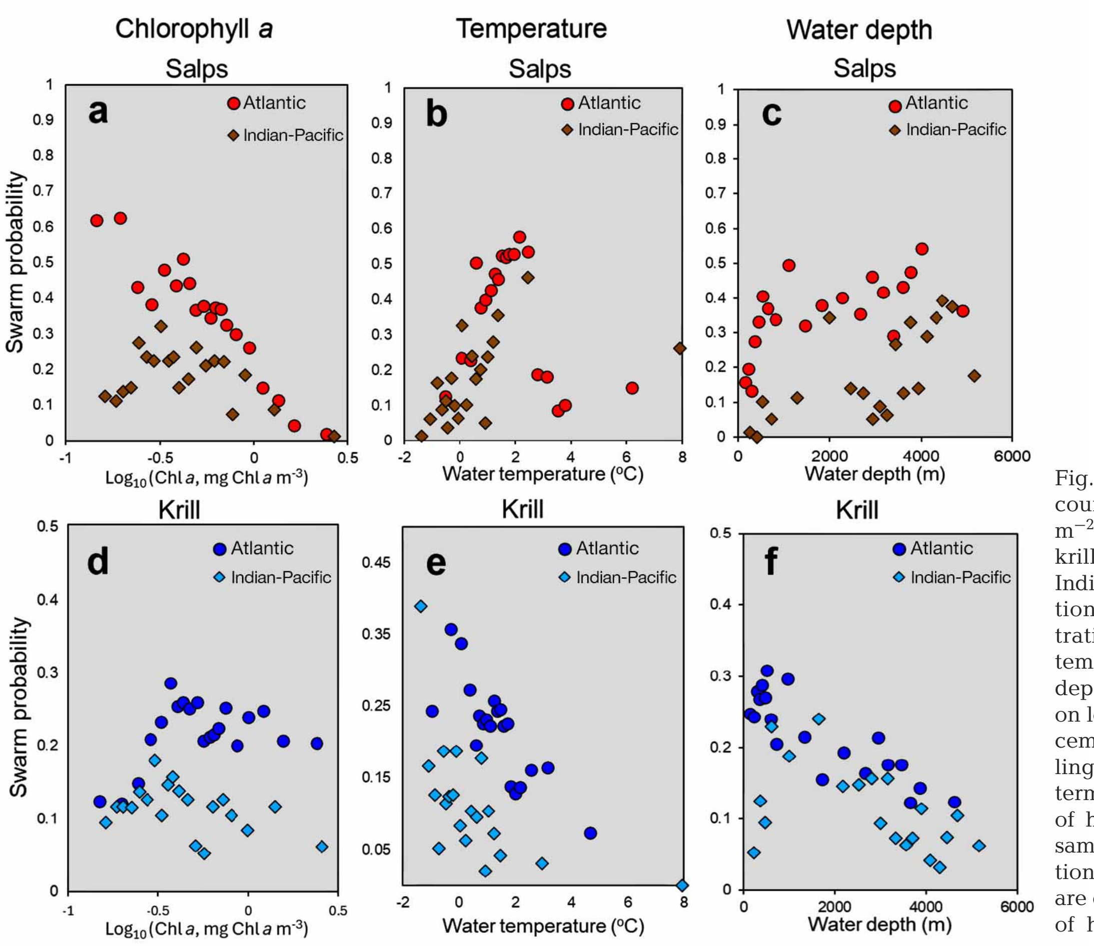

Fig. 7. Probability of encountering swarms (>10 ind. m^{-2}) of (a–c) salps and (d–f) krill in the Atlantic and Indian-Pacific sectors in relation to (a,d) chl *a* concentration; (b,e) surface water temperature; and (c,f) water depth of sampling, based on long-term (post-1976, December–March) net sampling data matched to long-term summer climatologies of habitat conditions at the sampling stations (see Section 2.4). Swarm probabilities are calculated as the fraction of hauls with >10 ind. m^{-2}

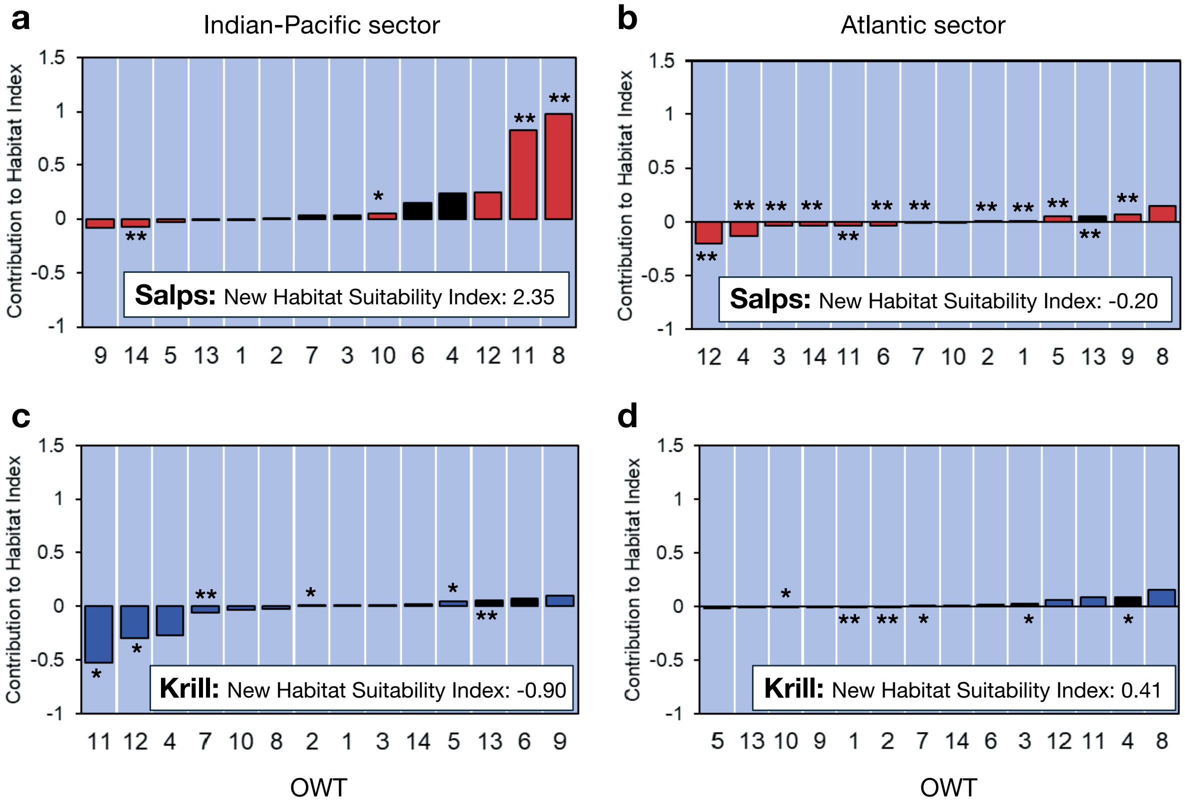

Fig. 8. The new era of low sea ice is associated with substantially better summer feeding habitat for salps in the Indian-Pacific sector. Bars for each optical water type (OWT) represent the product of change in its habitat area from the high to low sea ice era and the correlation of krill or salps with that habitat area. Double negatives (decline in area and negative correlation) multiply to a positive (black bars). The net sum of all bars represents the overall new habitat suitability index, *I*, with values given in each panel. Asterisks indicate Spearman correlation significance: $^*p < 0.05$; $^{**}p < 0.01$; symbols above the axis: positive correlations between swarm probability and OWT weighting; symbols below the axis: negative relationships. Changing habitat suitability indices are compared between the (a,c) Indian-Pacific sector and (b,d) Atlantic sector (see Section 2.6)

Atlantic sector had a series of highly significant positive correlations with low-number OWTs (typically low chl *a*) and equally strong negative relationships with high-number water types, with this tight coupling also seen in Fig. 7a. However, there was little overall change in our habitat suitability index, largely because there were either small or inconsistent changes in areas of these strongly correlated water types.

Our major finding was that the recent low-ice era favoured salps in the Indian-Pacific sector, so we have focussed on this finding in Fig. 9. The OWT analysis here shows some abrupt cut-offs in habitat correlation that are not apparent from simply looking at chl *a*. Relationships between salps and low-number OWTs (OWTs 1–7) were consistently negative, with a sharp transition to strongly positive (OWTs 8–11) before reverting to consistently negative for the most turbid waters (OWTs 12–14). Some of the relationships looked relatively tight and highly significant (e.g. with OWTs 10 and 11), suggesting that future work is needed to better characterise the taxonomic composition of these satellite-based OWT classifications. Nevertheless, the improved summer feeding for salps in the Indian-Pacific sector reflected strong positive correlations between salps and some of the medium-number OWTs, such as 8 and 11 (higher chl *a* concentrations), that were increasing, coupled to negative correlations with those OWTs, such as 4 and 6, that were declining.

4. DISCUSSION

The recent, sudden and year-round reduction in Antarctic sea ice represents a massive perturbation of the pelagic environment. It marks an increase in summer open water of over 1 million km^2 and concomitant changes in thickness and concentration of the remaining ice (Fig. 3b). As the reduction has been year-round, the sudden transition of regions from sea ice to open water impacts a far larger area than is sug-

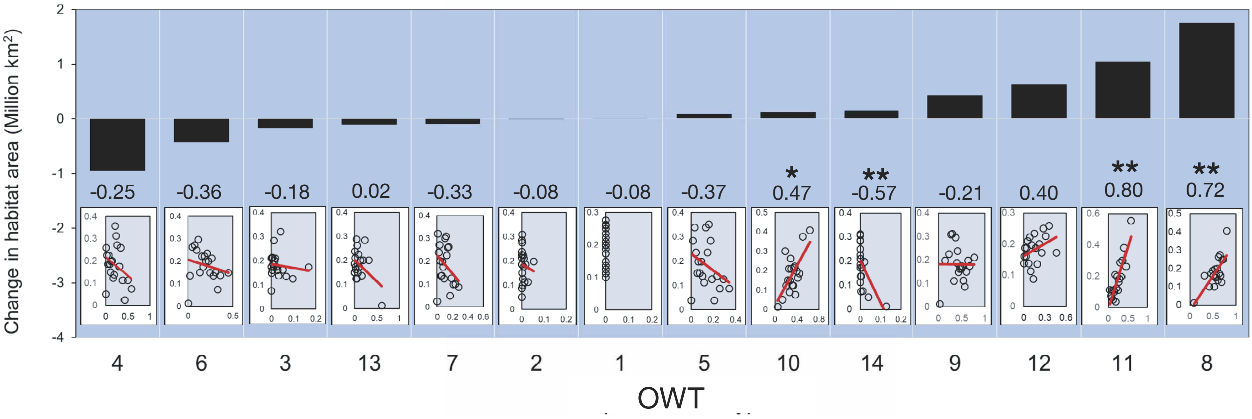

Fig. 9. Salps in the Indian-Pacific sector show strong affinity for the increasing optical water types (OWT) and negative associations with those that are declining. Bars represent changes in habitat area of the 14 OWTs in the Indian-Pacific sector (also depicted in Fig. 5a). Fitted linear regressions (red) are for illustrative rather than statistical purposes and show the trend in direction of relationships between salp swarm frequency (*y*-axis) and fractional weighting of the OWT in the vicinity of the sampling station (*x*-axis; see Section 2.4). Note the varying axis scales. Numbers above the plots are Spearman correlation coefficients: $^{*}p < 0.05$; $^{**}p < 0.01$

gested by maps of minimum extent before and after the step change. The last few years have seen what looks like a stabilisation at the new, lower-ice extents (Fig. 3a), and while climate models suggest that this sea ice should be declining, they rarely capture such an abrupt step from a high-ice to a lower-ice extent (Diamond et al. 2024). Clearly, we still have limited understanding of the causes of these crucial, environmentally sensitive dynamics.

While the causes of the sudden ice loss are unclear, equally poorly known are the consequences for Southern Ocean biota. Sea ice processes are a known problem area for large-scale models (Fisher et al. 2025), and the speed of recent change is analogous to the ongoing rapid reduction in Arctic sea ice, which changes the dynamics of primary production and promotes winners and losers within the food web (Lannuzel et al. 2020, Flores et al. 2023, Schmidt et al. 2024). In the Southern Ocean, salps and krill have often been cast as respective winners and losers (see Constable et al. 2014), but the picture is spatially more complex (Yang et al. 2021), and some of the evidence of past changes has been contested (Cox et al. 2018, Hill et al. 2024). With the decline in direct time series data on the 2 species, our satellite-based approach provides an alternative way to gauge how their summer feeding habitat is changing.

Previous studies have reached a range of conclusions over multi-decadal phytoplankton change in the Southern Ocean. At circumpolar scales, increasing indices of iron stress were suggested to be linked to a general decline in primary production over the last few decades (Ryan Keogh et al. 2023), while Thomalla et al. (2023), using the same 1998–2022 timespan as us, found changing bloom phenology and overall increases in both bloom magnitude (their Fig. 3) and the area of ocean increasing above a threshold of 0.25 mg chl *a* m^{-3} (their Fig. 5). Likewise, a circumpolar increase in phytoplankton is projected from model ensembles (Fisher et al. 2025). Studies west of the Antarctic Peninsula have also found a varied picture, with both increases that were related to sea ice (Ferreira et al. 2024) and a more stable long-term trend, albeit with altered phenology (Turner et al. 2024). Since the feeding and growth responses of zooplankton saturate in bloom concentrations, and because these blooms contribute strongly to mean chl *a* values, we have examined change not in terms of mean chl *a* but instead as areas experiencing increases or decreases (Figs. 4 & 5). We found that large belts of formerly low chl *a* increased after the sea ice transition, with an overall increase in chl *a* concentration in the large majority (69%) of the Southern Ocean (Fig. 4).

When the maps of chl *a* change (Fig. 4c) are interpreted in the context of salp and krill distribution (Fig. 6), the implication is that the increasing chl *a* would likely favour salps, since they were concentrated in the oceanic parts of the Indian-Pacific sector where this change was most widespread. Fig. 8 quantifies this observation, showing that in this sector, low-number OWTs such as 4 and 6 (low chl *a* values), which were negatively correlated with salps, were decreasing and being replaced by higher-number OWTs such as 8 and 11 (moderate chl *a* concentration), which correlated positively with salps. This explanation suggests that the large increase in feeding habitat suitability specifically for salps is due to large oceanic areas, formerly too low to support salps, now increasing to the moderate levels much more supportive of their blooms. This change does not favour krill, since they do not inhabit such low chl *a* habitats in the Indian-Pacific sector.

Salps are widely considered to be less dependent than krill on blooms of large diatoms (Moline et al. 2004, Schmidt & Atkinson 2016). These gelatinous filter feeders are thought to flourish in the low-productivity oceanic areas dominated by smaller phytoplankton (Perissinotto & Pakhomov 1998, Nishikawa & Tsuda 2001, Moline et al. 2004), since they perform extensive diel vertical migrations and use a filtration sieve capable of capturing micron-size picoplankton (Sutherland et al. 2010, Sutherland & Thompson 2022). However, it has been suggested that their diets do overlap (Drits & Semenova 1989, Pauli et al. 2021), albeit with a greater preference of krill for diatoms (von Harbou et al. 2011). Both species use fine mesh filters that are able to capture much smaller particles than are accessible to copepods (Schmidt & Atkinson 2016). Their habitats also partially coincide: krill may need deep-water habitats to complete their life cycle, thus overlapping with deep-migrating salps, whose blooms were found in recent years in high latitudes that are traditionally frequented by krill (Słomska et al. 2021). We found that the species do indeed differ according to their habitat preferences (Figs. 7 & 8), but these differences are relatively subtle; for example, with neither species being positively associated with either of the highest OWTs (13 and 14), which signify very high phytoplankton concentrations (>1 mg chl *a* m^{-3}).

While we show a separation in habitat types preferred by krill and salps, an important result was that the degree of separation varied greatly between sectors. The cause is uncertain, but there are environmental differences between sectors (for example, shallower bathymetry at low latitudes of the Atlantic sector), and we should not rule out genetic differences between sectors or adjacent regions (Shao et al. 2023) and high genetic diversity across adjacent regions (Batta-Lona et al. 2017, Goodall-Copestake 2017). These sectoral differences suggest an ability to adapt to differing conditions between sectors. In any case, the sectoral differences are important, and more work is needed to examine the causes and consequences of differences between sectors (Swadling et al. 2023). These sectoral differences also call for caution, both in upscaling to circumpolar habitat requirements from local surveys and in applying single formulations of habitat models to infer differences between sectors (e.g. Veytia et al. 2020, Merkel et al. 2023).

There are several important caveats to our study. A key point is that a myriad of factors, in addition to summer feeding conditions, impinge on the life cycle success of salps and krill. Changes in summer phytoplankton in parts of the Southern Ocean inhabited by salps may be a positive factor enabling them to bloom, but other factors related to the changing environment, food or predators throughout the whole year will dictate the population dynamics of both species. Another issue is that the OWTs were derived from a global-scale classification of marine waters based on their optical properties. While this classification included waters in the Southern Ocean, there are differences in optical properties between waters of the Southern Ocean and lower latitudes (Mitchell & Holm-Hansen 1991, Dierssen & Smith 2000, Robinson et al. 2021). Furthermore, our approach mapped long-term (1976—2020) krill and salp records to OWT climatologies derived from 1998 through 2020, despite the fact that distributions of both OWTs and zooplankton may change over time. However, matching only the krill and salp records from the satellite era gave the same major finding (i.e. that the salps in the Indian-Pacific sector were likely to be advantaged), albeit with much fewer data points (Fig. S2). Another caveat of using satellite data is that it does not penetrate far into the water column, and important features such as deep chlorophyll maxima are missed. However, because salps are able to vertically migrate down to avoid the highest chl *a* layers, our overall conclusion of changes favouring salps is likely to be supported.

Independent support for an increase in habitat suitability for salps relative to krill comes from a recent study using machine learning of satellite data trained on a large pigments database to characterise the relative dominance of diatoms, cryptophytes and haptophytes (Hayward et al. 2025). These authors found sharp inflections in the relative dominance of these 3 groups coincident with the sea ice step change, with a decline in diatoms and haptophytes but a dramatic increase in cryptophytes. The recent increases in the latter are also supported at the Antarctic Peninsula (Mendes et al. 2023). Diatoms (whether from sea ice or the pelagic realm) are considered favourable for krill (Schmidt et al. 2018), and cryptophytes are likely relatively more favourable to salps (Moline et al. 2004, von Harbou et al. 2011, Sutherland & Thompson 2022). Therefore, a shift from diatoms towards cryptophytes (Hayward et al. 2025) and our habitat change indices based on optical reflectance are independent but align with the concept of improving feeding habitat for salps. Clearly, however, we still need to understand how both the quantity and quality of food interact with other environmental factors to drive changes in salp and krill abundance across the Southern Ocean.

Changes in the relative dominance of krill and salps impact their dependent predator populations (Fraser & Hofmann 2003) and have implications for both krill fisheries management (Meyer et al. 2020) and the ability of the Southern Ocean to sequester carbon (Décima et al. 2023). With abrupt recent environmental changes affecting this region, yet declining field sampling, satellite imagery could become increasingly valuable. Impressively large *in situ* data sets are being compiled (Hayward et al. 2024) and can be combined with satellite-based water classifications such as the OWTs presented here. An improved taxonomic resolution of OWTs that are derived specifically for the Southern Ocean is an obvious next step, since chl *a* is a relatively crude index of food, and Fig. 9 suggests some quite distinct and strong positive relationships between salps and some OWTs. More large-scale field sampling is needed to compare with these results, alongside satellite and modelling developments. By combining these approaches, we can obtain a better understanding of how large shifts in sea ice cover impact polar food webs.

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