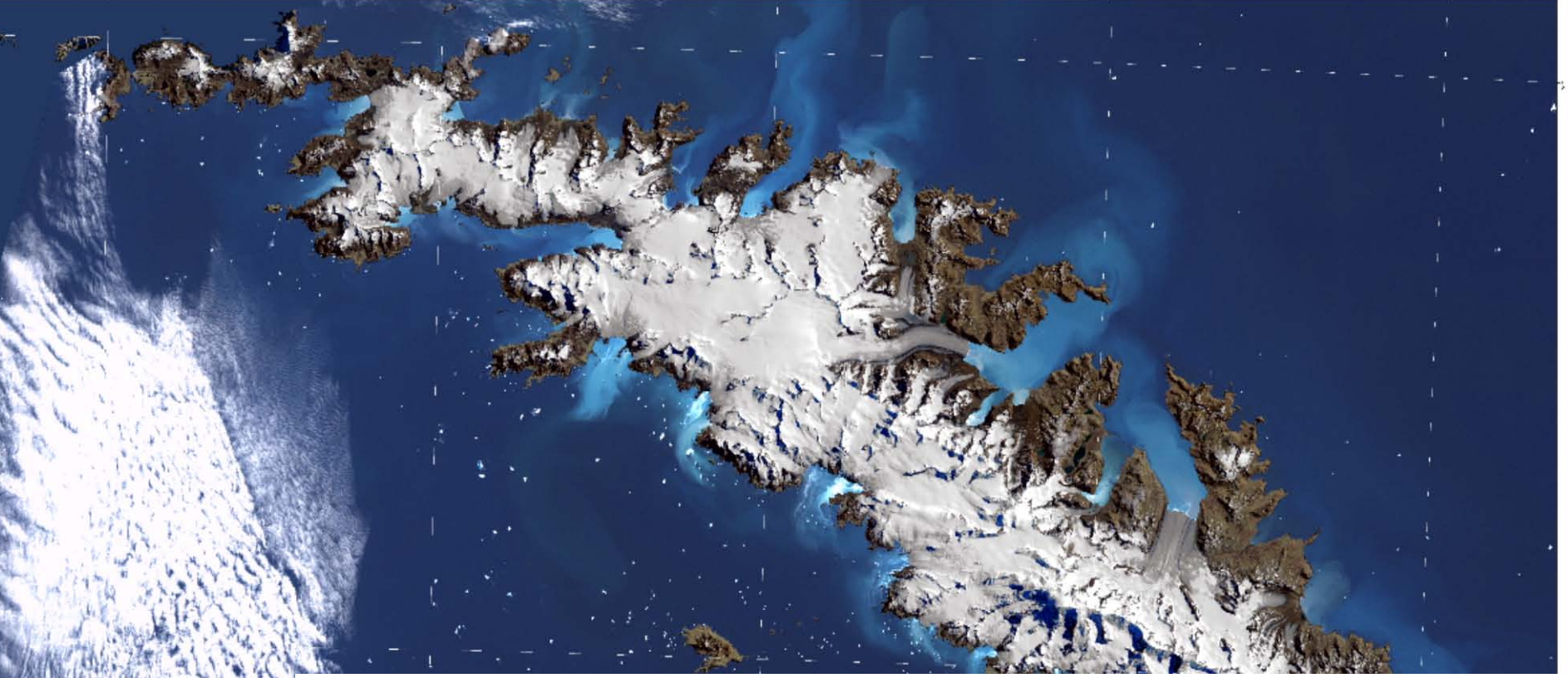

Depletion and fertilisation of the South Georgia phytoplankton bloom by Antarctic krill

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The micronutrient iron limits primary productivity over large parts of the world ocean, with the local inventory depending on new physical supply and chemical and biological recycling processes. While microbes are key agents in biogenic turnover and nutrient regeneration, large grazers have been associated with nutrient export via fecal pellets. Here we show that Antarctic krill can recycle similar amounts of dissolved iron to microbes (0.3-33 pM d^{-1}) and that this leads to enhanced phytoplankton biomass downstream of the island of South Georgia. Processes involved are, first, krill's ability to feed efficiently on large diatoms with subsequent release of dissolved iron (5 nmol DFe $krill^{-1}$ d^{-1}) and second, their ingestion of glacial flour, which lifts adsorbed non-bioavailable iron into the food web. While phytoplankton abundance in the main krill habitat on the South Georgia shelf is controlled by grazing, fertilising effects override in a large area downstream. Here, bloom duration increases from 11 to 14 weeks and average chl *a* concentration from 1.0 to 1.3 µg L^{-1} in years with high krill activity. The South Georgia phytoplankton bloom supplies the foundation for an enormous biomass of wildlife on the island and in surrounding waters (including penguins, fur seals, albatrosses and whales) and at the same time it provides the largest atmospheric carbon drawdown in ice-free waters of the Southern Ocean. Antarctic krill play a crucial role in this system not only as a food source for higher predators, but also in recycling nutrients and fertilising the bloom.

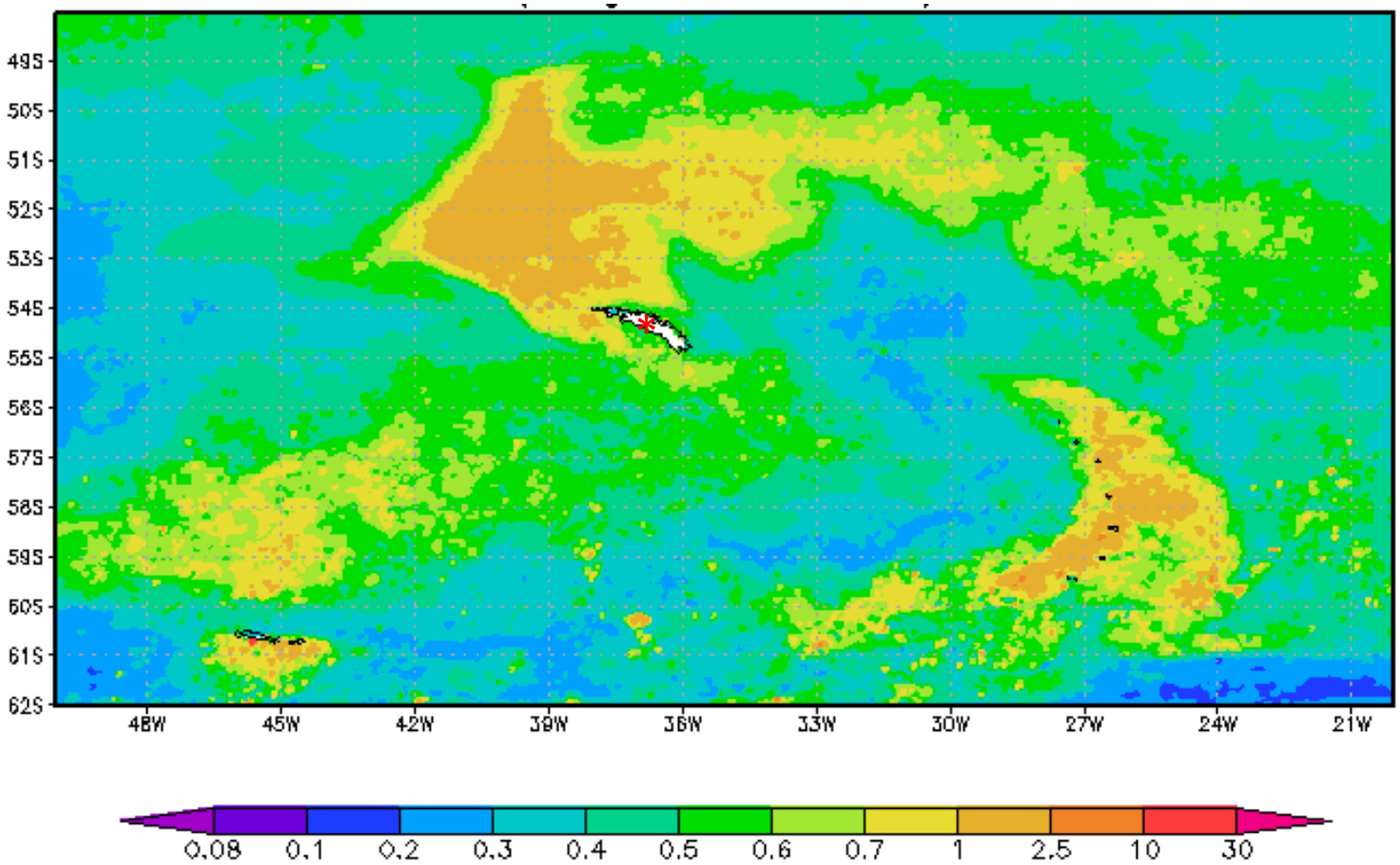
'Giovanni' was used to extract weekly chlorophyll *a* concentrations for 40 boxes of 1°latitude x 1°longitude across the South Georgia bloom area using MODIS data from 2002-2014. We regressed the bloom duration and median chl *a* concentration in these boxes against an annual index of krill activity, to produce a matrix of slope values. Negative values cluster on the South Georgia shelf indicating krill grazing impact, while positive slope values are found for a large area downstream of the island indicating fertilising effects due to high krill abundances.

(1) Phytoplankton bloom intensity and duration are governed by

- Light (Photosynthetically active radiation, Mixed Layer Depth)
- Nutrients (N, P, Si, Fe)
- Grazing

(2) The **South Georgia*** phytoplankton bloom is one of the largest in the Southern Ocean

Chlorophyll *a* climatology derived from MODIS (July 2002-October 2014)



Chl *a* (µg L^{-1})

(3) The **South Georgia** bloom lasts longer than other blooms in the Southern Ocean

Region (Lat; Lon)	**Bloom area (km^2)**	**Summer maximum Chl *a* ($\mu g\ L^{-1}$)**	**Summer median Chl *a* ($\mu g\ L^{-1}$)**	**No of weeks with elevated Chl *a* ($\geq 0.5\ \mu g\ L^{-1}$)**
Ross Sea (73.5°S-79°S; 160°E-152°W)	480 000	2.9 ± 1.3	1.3 ± 0.5	13.4 ± 4.2
Amundsen Sea (71°S-75°S; 100°W-125°W)	222 000	4.4 ± 1.7	1.5 ± 0.5	12.8 ± 1.3
Bellingshausen Sea (70°S-73.4°S; 75°W-95°W)	178 000	3.3 ± 2.4	1.3 ± 0.9	10.8 ± 3.9
South Georgia (49.4°S-54.5°S; 36°W-41.7°W)	160 000	2.4 ± 1.0	1.0 ± 0.2	23.9 ± 4.1
Weddell Sea (71°S-75.5°S; 20°W-30°W)	149 000	1.7 ± 1.6	0.7 ± 0.6	7.0 ± 4.6
Prydz Bay (66.5°S-70°S; 70°E-81°E)	99 000	3.3 ± 1.6	1.3 ± 0.5	12.7 ± 2.3
East Antarctic Peninsula (63.5°S-65.5°S; 54.5°W-59.5°W)	33 000	2.5 ± 2.1	0.7 ± 0.5	6.8 ± 5.5
Kerguelen Islands (46.8°S-49.5°S; 69.9°E-72.6°E)	25 000	2.7 ± 2.0	0.7 ± 0.1	16.7 ± 2.9

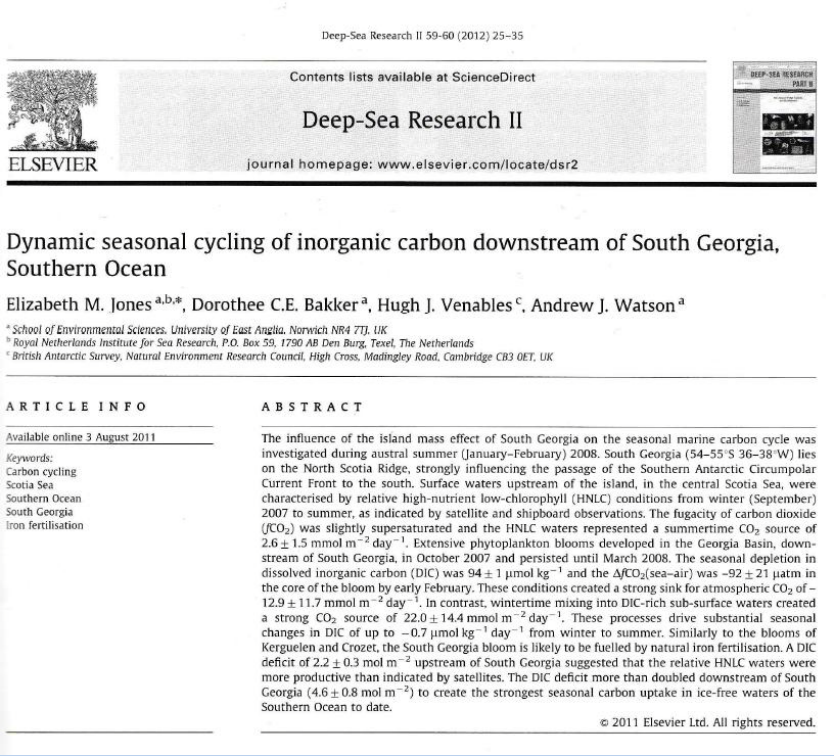
(MODIS, 2002-2014, mean ± 1SD)

(4) The **South Georgia** phytoplankton bloom

- supplies the foundation for magnificent wildlife on the island and in surrounding waters

4 million Antarctic Fur Seals
3 million Macaroni Penguins
1 million King Penguins
60000 tonnes of Patagonia Tooth fish
200000 tonnes of Ice fish
1000 pairs of Wandering Albatross
15000 pairs of Black-browed Albatross
12000 pairs of Grey-headed Albatross
5000 pairs of Southern Giant Petrel
Southern Right Whales

- and at the same time it provides the largest atmospheric carbon drawdown in ice-free waters of the Southern Ocean



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Dynamic seasonal cycling of inorganic carbon downstream of South Georgia, Southern Ocean

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ABSTRACT

The influence of the island mass effect of South Georgia on the seasonal marine carbon cycle was investigated during austral summer (January–February) 2008. South Georgia (54–55°S 36–38°W) lies on the North Scotia Ridge, strongly influencing the passage of the Southern Antarctic Circumpolar Current Front to the south. Surface waters upstream of the island, in the central Scotia Sea, were characterised by relative high-nutrient low-chlorophyll (HNLC) conditions from winter (September) 2007 to summer, as indicated by satellite and shipboard observations. The fugacity of carbon dioxide (fCO_2) was slightly supersaturated and the HNLC waters represented a summertime CO_2 source of 2.6 ± 1.5 mmol m^{-2} day^{-1}. Extensive phytoplankton blooms developed in the Georgia Basin, downstream of South Georgia, in October 2007 and persisted until March 2008. The seasonal depletion in dissolved inorganic carbon (DIC) was 94 ± 1 μmol kg^{-1} and the ΔfCO_2(sea–air) was -92 ± 21 μatm in the core of the bloom by early February. These conditions created a strong sink for atmospheric CO_2 of -12.9 ± 11.7 mmol m^{-2} day^{-1}. In contrast, wintertime mixing into DIC-rich sub-surface waters created a strong CO_2 source of 22.0 ± 14.4 mmol m^{-2} day^{-1}. These processes drive substantial seasonal changes in DIC of up to -0.7 μmol kg^{-1} day^{-1} from winter to summer. Similarly to the blooms of Kerguelen and Crozet, the South Georgia bloom is likely to be fuelled by natural iron fertilisation. A DIC deficit of 2.2 ± 0.3 mol m^{-2} upstream of South Georgia suggested that the relative HNLC waters were more productive than indicated by satellites. The DIC deficit more than doubled downstream of South Georgia (4.6 ± 0.8 mol m^{-2}) to create the strongest seasonal carbon uptake in ice-free waters of the Southern Ocean to date.

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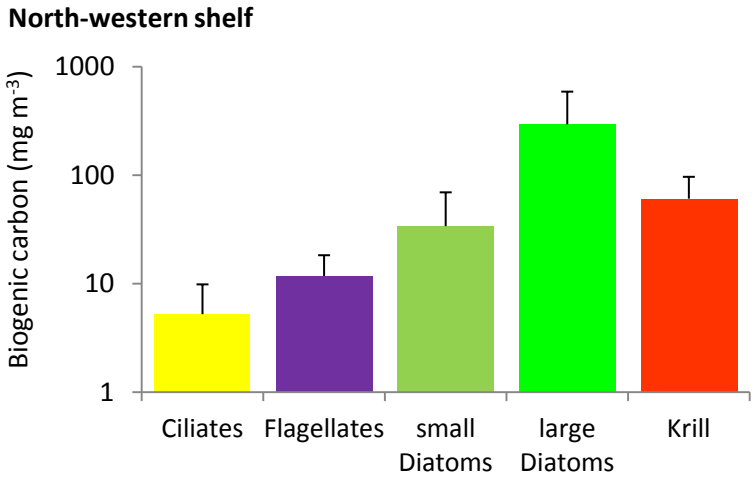
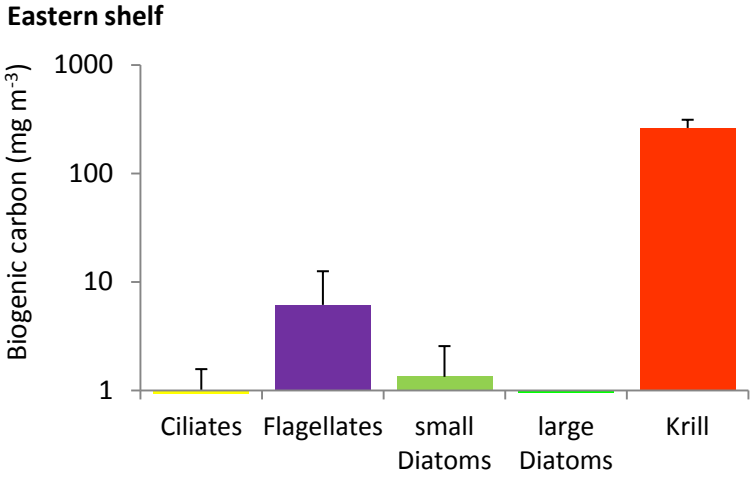
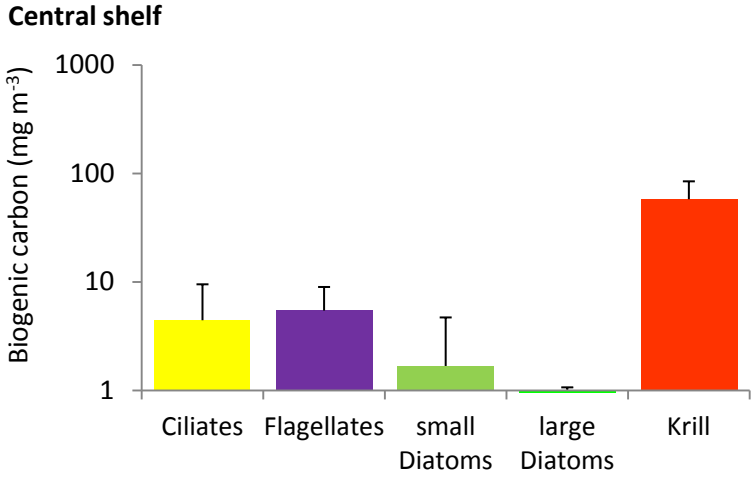
Antarctic krill can appear in very high abundances at the South Georgia shelf







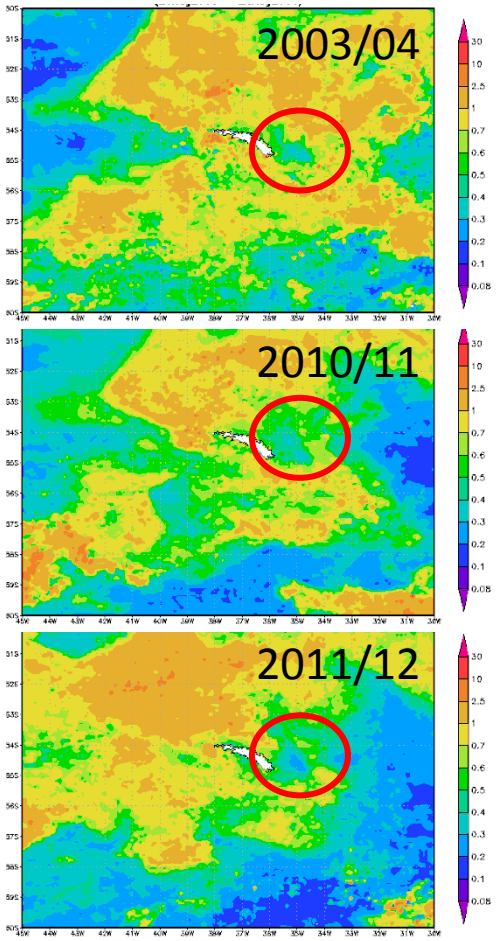
(data derived from a cruise in January 2011, note the logarithmic scale, Schmidt *et al.* unpublished)

Antarctic krill have been suggested to

exert a high **grazing impact** on phytoplankton

- especially on the eastern shelf of South Georgia where krill appear in highest abundances *(Whitehouse et al. 2009)*

low chl *a* concentrations might indicate grazing impact by krill



Chlorophyll *a* (µg L^{-1}) climatology derived from MODIS (August 2003-August 2004)

iron-fertilise the Southern Ocean

- due to Fe recycling from their food *(Tovar-Sánchez et al. 2007)*

- due to feeding at the seabed and subsequent introduction of iron into surface waters *(Schmidt et al. 2011)*

- due to storage of Fe in their tissues, and its release when ingested by predators *(Nicol et al. 2010)*

Our hypothesis:

Krill grazing and iron-cycling have a significant effect on the intensity and duration of the South Georgia phytoplankton bloom

Phytoplankton bloom dynamics were analysed using chlorophyll *a* concentrations from ocean colour radiometry (MODIS, 2002-2014, mid August – mid April, 9km standard product, 8-day composites, www.oceancolor.gsfc.nasa.gov).

Therefore the area of the South Georgia bloom (50°S-55°S, 34°W-42°W) was divided into 40 subareas of 1°Lat x 1°Long. For each of these subareas the median annual chl *a* concentration and bloom duration (chl $a \leq 1 \mu g\ L^{-1}$) were estimated, and correlated with the annual median krill body length. During the years 2006/7 and 2013/14 no phytoplankton bloom developed at South Georgia, and therefore these years were excluded from further analysis.

The **annual median krill body length** was used as an index of krill activity at South Georgia. A dominance of **small krill** indicates high metabolic activities and successful recruitment from krill-source regions further South (= high krill abundances), while a dominance of **large krill** indicates the lack of recruitment from source regions and lower metabolic activities (Murphy et al. 2007, Forcada et al. 2008).

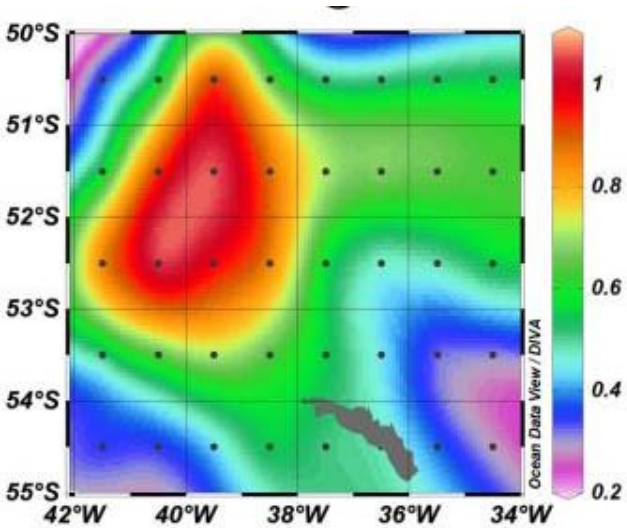
The krill body length data derived from a long-term dietary analysis of Antarctic fur seals based on scat samples collected weekly at South Georgia (Reid 1995). Here we calculated the median krill body length from samples collected between beginning of December and end of February for the Years 2002-2014. For each year about 1000 krill were measured.

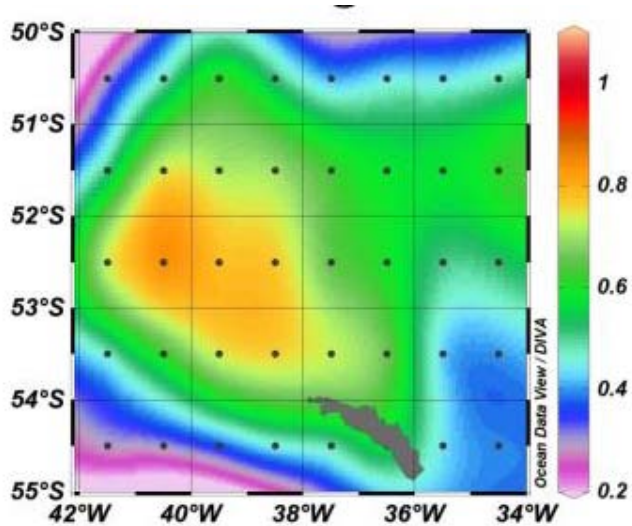
Years dominated by

Small krill

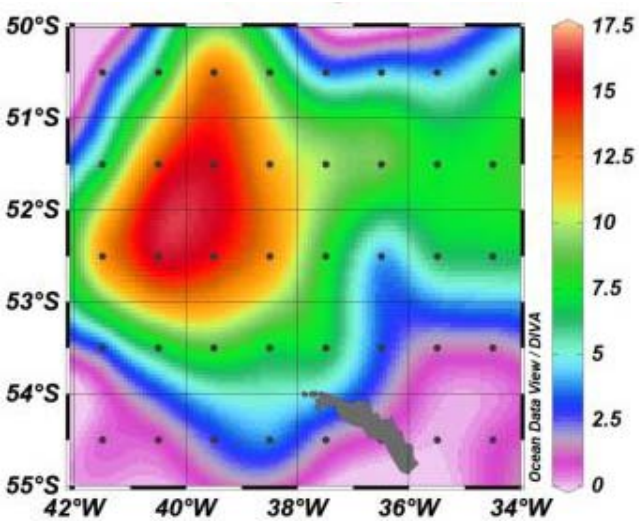
Large krill

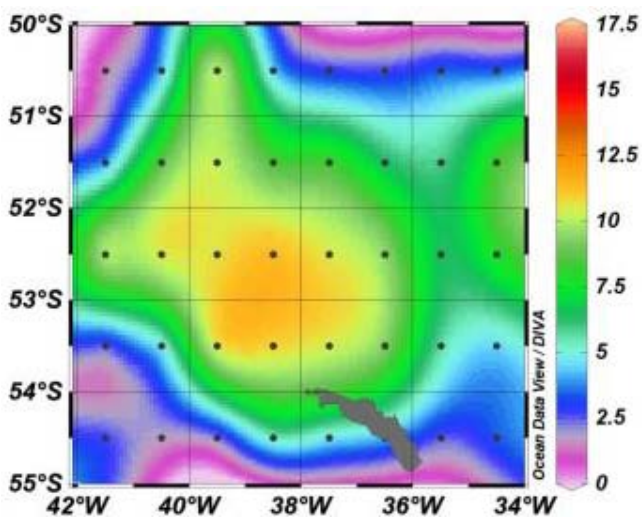
Median chl *a* concentration (20th August – 20th April) in *μg L*$^{-1}$





Bloom duration (≥1μg chl *a* L^{-1}) in *weeks*





Left:
Small krill (= young krill, <50mm) indicates high abundances and intensive metabolism (see 'Method').

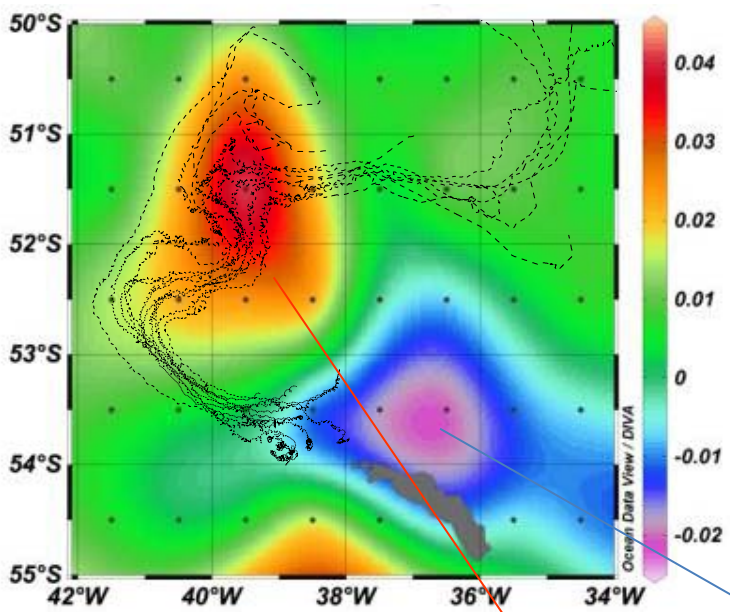
During years where **small krill dominated** (2005/6; 2007/8; 2009/10; 2011/12) , median chl *a* concentrations were low and bloom durations were short across the South Georgia shelf, but high in an area about 150-450 km downstream of the island.

Right:
Large krill (= old krill, >50mm) indicates low abundances and less intensive metabolism (see 'Method').

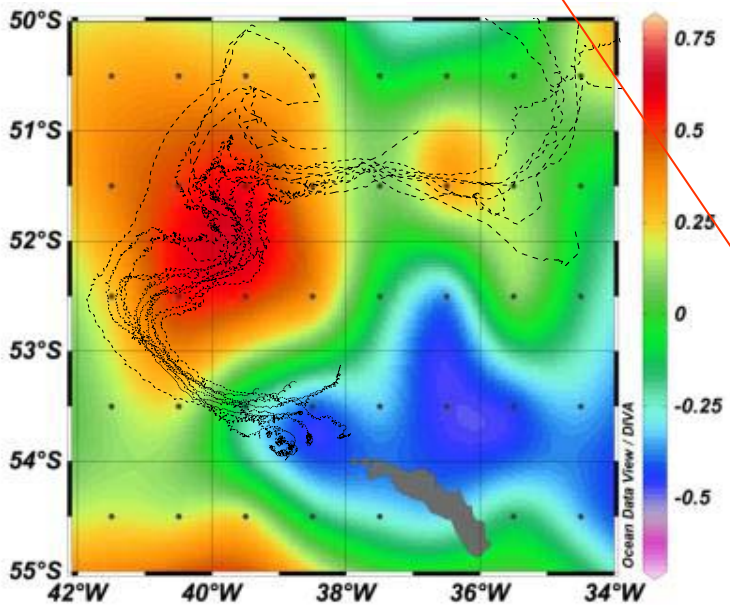
During years where **large krill dominated** (2002/3; 2003/4; 2004/5; 2008/9; 2010/11; 2012/2013) the chl *a* gradient between shelf and downstream of South Georgia is less pronounced and the bloom occurs closer to the island.

Satellite data:
MODIS (2002-2014)

Slope values for regressions between **median chl *a* conc.** and the inverted anomaly of the **median krill body length** for years 2002-2013



Slope values for regressions between **bloom duration** and the inverted anomaly of the **median krill body length** for years 2002-2013



The black lines are 11 drifter trajectories (Meredith et al. 2003), which show that the current flow links the area of high grazing to the downstream-area dominated by fertilisation.

Regressions between chl *a* concentrations and the inverted anomaly of the median krill body length for the years 2002-2013 show **negative slope values** near the South Georgia shelf (blue area, ~58500 km^2), but **positive values** downstream (red area, ~53400 km^2).

The same pattern exists for the bloom duration .

This indicates that high krill abundances and their high metabolic activity have a **two-fold effect** on the South Georgia system:

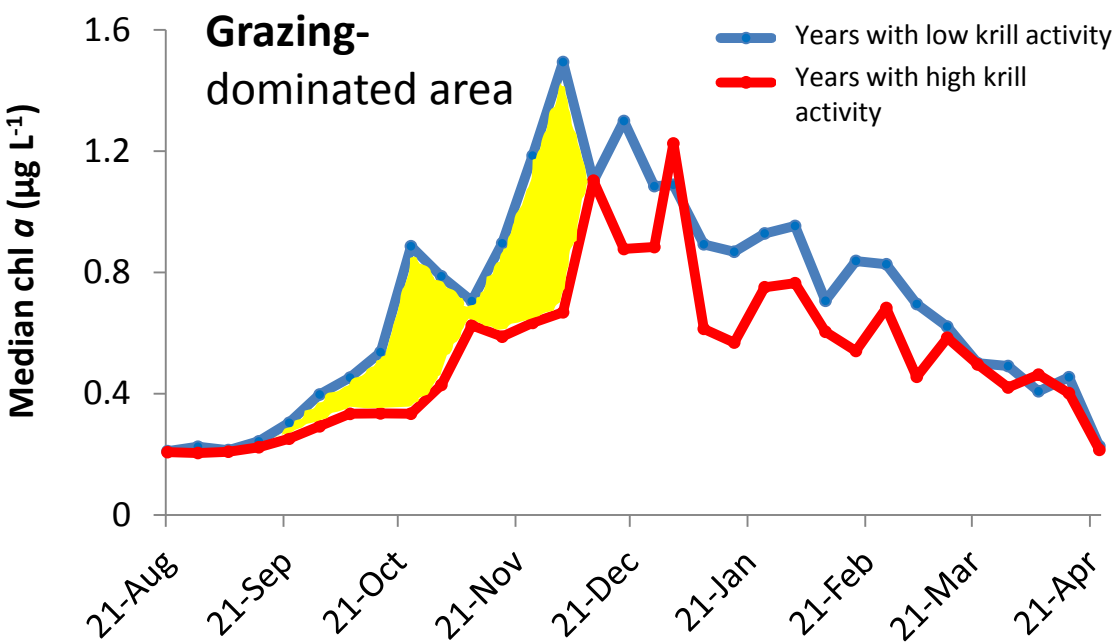
(1) **phytoplankton loss** due to intensive grazing on the northern shelf **(grazing > fertilisation)**

(median chl *a* concentrations **reduce from 0.8 to 0.5 µg L^{-1}** and bloom duration s from **6 to 3 weeks** during years with small krill)

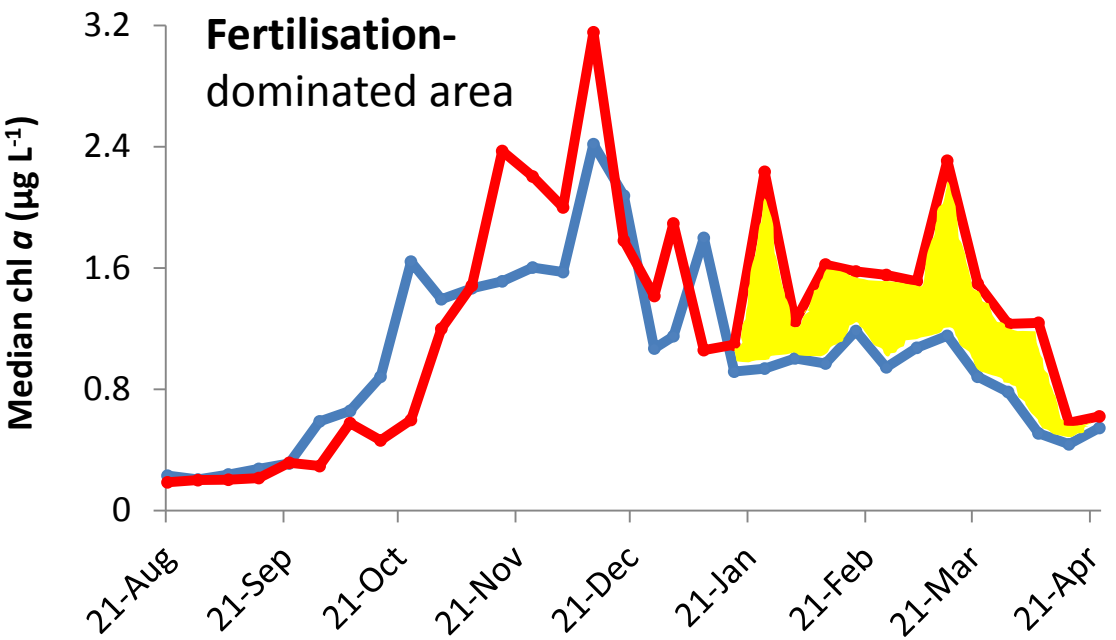
BUT

(2) **enhanced phytoplankton abundance** downstream of the island due to fertilisation **(fertilisation > grazing)**

(median chl *a* concentrations **increases from 1.0 to 1.3 µg L^{-1}** and bloom durations from **11 to 14 weeks** during years with small krill).



In the area on the South Georgia shelf, the phytoplankton bloom starts later and is less intensive in years with small, highly abundant krill. This might indicate **bloom suppression due to grazing.** However, at the same time, unselective feeding of krill on glacial flour (common on the South Georgia shelf, see first slide) introduces a new source of iron into the food web. We found very high Fe:C ratios of 3600±330 µmol mol^{-1} in diatom-dominated particulate matter north-west of the island. This is 2-3 orders of magnitude more iron than commonly found in diatom cells (Boyd et al. 2012) and might sustain numerous cell divisions (Marchetti et al. 2009).



In the area downstream of South Georgia, **high chl *a* values** are restricted to spring and summer in years with few large krill, but **extend into autumn** when krill are small and abundant. This suggests that fertilisation by krill counter-acts potential iron limitation later in the season (Nielsdóttir et al. 2012). Additional iron might be transported to this region when incorporated in to phytoplankton biomass (see 'grazing dominated area'). The pattern of seasonal phytoplankton development along the current flow indicates that the summer bloom in the shelf-region might seed an autumn bloom in the fertilisation–dominated area downstream 1-2 months later.

Usually it is difficult to separate zooplankton grazing effects from those of fertilisation, as they counteract each other. However, at South Georgia there is some spatial displacement of the two zooplankton roles, due to krill being mainly restricted to the shelf-area of the island while water masses move northwards. Thus, across the shelf, krill exert a strong grazing impact on phytoplankton, which is channelled into the foodweb and supports abundant wildlife and fisheries. However, nutrient release during krill grazing helps to condition the water for a phytoplankton bloom that extends hundreds of kilometres downstream of the island, creating the strongest carbon uptake in the ice-free Southern Ocean.

Our study shows that a combination of rate process measurements and satellite data provides insights into how small-scale processes propagate up to the scale of major phytoplankton blooms.

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