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Modelling dispersal of juvenile krill released from the Antarctic ice edge: Ecosystem implications of ocean movement

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ABSTRACT

Sea ice retreat is a key event affecting Southern Ocean ecosystems during spring and summer. The impacts of this change can be seen in these ecosystems from primary producers to top predators, through biological, chemical and physical systems. We apply a Lagrangian particle tracking method to investigate transport processes from the retreating sea ice edge in the Southern Ocean during spring and summer. The resulting distribution of surface krill patches is used as a case study for our modelling approach. Antarctic krill (*Euphausia superba*), a secondary producer, plays a key role in the Southern Ocean ecosystems. Antarctic krill are highly abundant in the Southern Ocean with a complex distribution pattern both in the horizontal and vertical dimensions. Observations dating back to the 1930s show that juvenile krill often form surface patches – high density clusters of krill at the ocean surface – throughout the Southern Ocean during the spring and summer seasons.

We develop a hypothesis, based on historical observations, that surface krill patches composed of juvenile krill move passively with ocean currents after their release from the sea ice edge zone in spring. Applying this hypothesis and method to the Southern Hemisphere spring/summer, leads to results that indicate that the observed changes in distribution of krill patches from historical to contemporary records could be related to the southward shift of the sea ice edge over the last century.

1. Introduction

1.1. Importance of sea ice for primary and secondary production during the Southern Ocean spring and summer

Sea ice is a crucial driver for Southern Ocean ecosystems, strongly affecting productivity during both spring and summer seasons. In particular the marginal ice zone (MIZ) is known as a key area which enhances biological productivity (Smith and Nelson, 1985), with a modelling study suggesting that 15% of the yearly net primary production in the Southern Ocean is provided by MIZ blooms (Taylor et al., 2013). At the MIZ the input of fresh water from melting ice results in a shallow mixed layer, and together with nutrients released from the melting ice and increased sunlight, this provides ideal conditions for phytoplankton growth, resulting in a spring-summer bloom (Smith and Nelson, 1986; Sullivan et al., 1988). With sea ice retreat (i.e. a southward shift of the sea ice edge), as occurs between October and December, the phytoplankton bloom also moves southwards (Sullivan et al., 1988). Sokolov (2008) indicated a strong relationship between the level of chlorophyll concentration and the rate of decrease in sea ice concentration in a region. This primary production induced by sea ice is important for secondary production.

Antarctic krill (*Euphausia superba*), as a secondary producer, plays a key role in the Southern Ocean food web. Antarctic krill is the major prey for multiple top predators such as baleen whales, penguins and flying birds (e.g. Hunt et al., 1992; Veit et al., 1993; Takahashi et al., 2003; Santora et al., 2010; Nowacek et al., 2011). It is involved in recycling of the limiting nutrient iron (Nicol et al., 2010), and is economically important as a high demand fishery. Work by Saba et al. (2014) indicates that the positive relationship between krill recruitment and the level of primary productivity increases with sea ice extent, and the volume of sea ice in winter (that affects the speed of sea ice retreat in spring). Therefore, the effect of spring sea ice retreat on primary productivity determines feeding conditions for Antarctic krill. It should

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be noted that sea ice is not the only determinant of the fate of krill in the region. Ocean currents that advect krill also influence the survival of the population, in particular whether they encounter rich food, especially in their juvenile stage when they exhibit weak swimming ability. Particle tracking studies for Antarctic krill in the West Antarctic region indicate spring-summer sea ice retreat is important for the distribution of krill in summer (Murphy et al., 2004; Thorpe et al., 2007). Therefore, sea ice, ocean dynamics and primary production in spring are keys to the successful survival of Antarctic krill.

1.2. Composition of surface krill patches from historical in situ observations

Antarctic krill has been observed to form aggregations with varied vertical and horizontal structure (e.g. Marr, 1962; Miller and Hampton, 1989; Nowacek et al., 2011; Bernard and Steinberg, 2013). These aggregations are likely related to environmental conditions such as ocean currents and topography (e.g. Witek et al., 1988; Nicol, 2006), as well as schooling behaviour (e.g. Quetin and Ross, 1984; Kawaguchi et al., 2010). Krill aggregations at depth have been observed using hydroacoustic devices attached to ships since the 1970s. Prior to this, krill aggregations could only be observed at the ocean surface from a ship deck through direct observation (such as during the *Discovery* Investigations (Marr, 1962)). In this paper, we define an aggregation of Antarctic krill directly observed at the ocean surface as a "surface krill patch".

According to Marr (1962), surface krill patches are krill aggregations with a sufficiently high density to result in visible changes to the local ocean colour (red or pale straw yellow depending on weather, water conditions, krill pigmentation and depth of aggregation). Surface krill patches are generally observed at depths of 1–4 m, occupying areas ranging from a few square metres to $> 200\ \mathrm{m}^2$ in various shapes such as circles, belts and ovals. They are mainly observed during the summer season and have been reported across multiple historical field observations (e.g. Marr, 1962; Suisancho, 1980, 2001). Combined observations including (hourly) changes in the size class composition of krill at the surface layer (1.5 m depth) from net catches and visual sightings of surface krill patches in the East Antarctic region indicate that surface patches are dominated by larval-juvenile stages (around 25 mm length) (Matuda et al., 1979; Nemoto, 1983). Net catch data from Pakhomov (2000) and Kawaguchi et al. (2010) also support the idea that surface krill patches generally consist of juveniles in the upper 10 m of the water column. The study of Daly and Macaulay (1991) also found that juveniles (20 mm - 35 mm) were dominant in surface patches. This study collected krill from the ship's engine tank filter and results indicate there were high concentrations of juveniles at the surface layer in open water. Moreover, the eighth Japanese Antarctic Investigation program operated by the Kaiyo-maru (Suisancho, 2001) reported surface krill patches were composed mainly of juveniles (18 mm - 25 mm, indicating first-year krill). From these combined findings we assume that surface krill patches are mainly composed of juvenile krill.

1.3. Understanding transport of surface krill patches to illustrate juvenile distribution during spring and summer

Understanding these surface krill patches is important to improve our knowledge of the krill-based ecosystem through prey-predator interactions in time and space, the spring-summer distribution of juveniles in relation to recruitment processes, and consequently stable stock assessment (Santora et al., 2016). However, the mechanisms that drive the formation of surface krill patches are poorly understood, mostly due to the very limited availability of observations. Conventional hydroacoustic surveys are limited in their ability to observe krill patches at the surface, there are no recorded remotely sensed observations of surface patches (aerial or satellite), and direct sightings of surface krill patches are limited to a few ship tracks. As a consequence, only very sparse data sets on the distribution of surface krill patches exist.

Using a Lagrangian particle tracking method developed by Mori et al. (2017), this paper investigates biological/ecological processes driven by sea ice retreat and ocean dynamics during spring-summer in the Southern Ocean, focusing on transport of surface krill patches composed of first-year (juvenile) krill as a case study. Surface krill patches demonstrate the direct effects of sea ice retreat and ocean dynamics as juvenile krill can be treated as passive particles (as opposed to adults that are active swimmers). Our model examines the general transport and distribution of juveniles interacting with sea ice retreat by analyzing i) connectivity between sea ice sources and open ocean destinations and ii) the effect of different monthly sea ice retreat speeds by considering transport times and the resultant spatial distribution. We apply our model results to historical observed circumpolar distributions of surface krill patches to explain the mechanism of transport from present day back to the 1930s and how this is may be related to changes in sea ice extent in the Southern Ocean. We also analyze monthly sea ice retreat and chlorophyll concentration from spring to summer to determine the fate of juvenile krill.

This study does not attempt to predict the location of specific surface krill patches, nor explain the mechanism of formation of each surface patch. Instead, our approach is intended as a starting point towards a mechanistic explanation of the general properties of surface krill patch formation in the Southern Ocean at circumpolar and regional scales. Our approach can also be applied to increase understanding of transport processes in the vicinity of the ice edge during the Antarctic spring and summer more generally, for example modelling the diffusion of iron and phytoplankton.

2. Methods

To investigate the observed distribution of surface krill patches during spring and summer we use the Lagrangian particle tracking method developed by Mori et al. (2017). This method uses the Ssalto/Duacs gridded absolute surface geostrophic velocity fields derived from AVISO, distributed through the Copernicus Marine Environment Monitoring service (CMEMS) (`https://www.aviso.altimetry.fr/en/data/products/sea-surface-height-products/global/madt-h-uv.html#c5129`). This data is available at a daily time step with a spatial resolution of 1/4° × 1/4° from 1993 to present. As opposed to Mori et al. (2017), where passive particles were released on a regular grid, in this study we released particles at the sea ice edge. To define the sea ice edge zone we use daily sea ice concentration data with 25 km × 25 km resolution from 1993 to 2016, available through the National Snow and Ice Data Centre (NSIDC) (Cavalieri et al., 1996, updated yearly).

The observed distribution of surface krill patches is derived by the reports from the *Discovery* Investigations and Japanese Antarctic Investigations (see Table 1). The digitized spatial positions of actual krill patches observed in these cruises are plotted in Fig. 1. The total number of observed surface krill patches is 135 for the Japanese observations and 122 for the *Discovery* Investigations (all in the spring-summer season). While we have reasonable confidence that the spatial coverage of the data sets are comparable (based on sampling stations shown in the reports from the *Discovery* Investigations and ship tracks from the Japanese Antarctic Investigations), it is not possible to directly compare the sampling intensities for the two available data sets. As such our results are constrained by possible differences in spatial effort between the two studies. We also used 8-day chlorophyll concentration at 9 km resolution obtained from 1997–2003 SeaWiFS level-3 Mapped Chlorophyll datasets and 2004–2016 MODIS-Aqua Level-3 Mapped Chlorophyll datasets (NASA Goddard Space Flight Center et al., 2018a, 2018b). The particle tracking and all analyses are implemented in the software package R (R Development Core Team, 2018).