PEER REVIEWED:

FIRST PUBLISHED: 17 Oct 2022

DOI: https://doi.org/10.48361/b1vp-mt19

PRINT:

Author/s

So Kawaguchi (1, 2), Bettina Meyer (3, 4, 5), John A Conroy (6) , Haiting Zhang (7, 8, 9) , Emilce Rombolá (10, 11)

(1) Australian Antarctic Division, Kingston, Tasmania, Australia
(2) Australian Antarctic Program Partnership, Hobart, Tasmania, Australia
(3) Alfred Wegener Institute, Helmholtz Centre for Polar and Marine Research, Bremerhaven, Germany
(4) Helmholtz Institute for Functional Marine Biodiversity (HIFMB), University of Oldenburg, Oldenburg, Germany
(5) Institute for Chemistry and Biology of the Marine Environment, Carl von Ossietzky University of Oldenburg, Oldenburg, Germany
(6) Virginia Institute of Marine Science, William & Mary, Gloucester Point, Virginia, USA
(7) Shanghai Ocean University, China
(8) University of Tasmania, Australia
(9) Center for Polar Research, Shanghai Ocean University, Shanghai 201306, China
(10) Instituto Antártico Argentino, Buenos Aires, Argentina
(11) Consejo Nacional de Investigaciones Cientificas y Técnicas (CONICET), Buenos Aires, Argentina

Brief Overview

- The Antarctic krill is a dominant species of the Southern Ocean ecosystem, with possibly the largest biomass of any wild animal species on Earth. Krill play fundamental roles in marine food webs, including carbon cycling, and nutrient cycles. They are also the target for the largest fishery by tonnage caught in the Southern Ocean.
- The best estimate of circumpolar krill biomass is 379 million tonnes, but at regional scales krill biomass is highly variable from year to year.
- A krill abundance decline has been reported between the 1970s and the 2010s at the northern edge of krill habitat in the Atlantic sector. Farther south, summer seawater temperature remained below krill's upper thermal limit, and abundance remained stable. Multiple analyses suggest a southward contraction of krill distribution in the southwest Atlantic.
- The krill fishery is managed by the Commission for the Conservation of Antarctic Marine Living Resources (CCAMLR.org). The total fishery catch and the spatial concentration of that catch has been increasing due to recent technological advancement and commercial interest.
- New technology and coordination between scientists and the fishing industry can advance understanding of krill, particularly during winter and beneath sea ice. Sustained research support is important for improving management of the krill fishery under climate change.

Detailed Overview

What are Antarctic krill?

Antarctic krill (*Euphausia superba*, hereafter 'krill'), one of 85 euphausiid species, outnumbers the other six Southern Ocean euphausiids (Figure 1). Krill is a long-lived (5-6 years) pelagic crustacean of about 4-6 cm adult length and may have the largest biomass of a wild animal species on Earth (Siegel 1987, Tarling and Fielding 2016). Individuals can release more than 10,000 eggs in surface waters within a single summer spawning season (Kawaguchi 2016). The growing embryos sink to 700 – 1000 m where they hatch and then ascend as they develop (Ross and Quetin 1989). They develop through 12 larval stages, are classified as juveniles in their 2nd summer, reach sexual maturity in their 3rd or 4th summer, and continue to spawn up to three times or more depending on food availability each summer thereafter (Kawaguchi 2016).

Krill are generally associated with sea-ice habitat during their early life stages (Kawaguchi 2016). They have a circumpolar distribution south of the Polar Front (Marr 1962) that largely coincides with the seasonal ice zone (i.e., the area between year-round sea-ice coverage to the south and the northern edge of winter ice coverage to the north) but also includes the region around South Georgia where sea ice is absent (Siegel and Watkins 2016). Approximately 70% of the krill population is located in the Atlantic Sector of the Southern Ocean, from 0° to 90° W longitude (Atkinson et al. 2008). Krill is listed as "least concern" in the IUCN Red List of threatened species (Kawaguchi and Nicol 2015).

Figure 1. The Antarctic krill Euphausia superba. Credit: Simon Payne, Australian Antarctic Division.

Why are krill important?

Krill have a central role in energy flow from primary producers to apex predators in most of the Southern Ocean (Everson 2000).

Their high biomass and production of rapidly sinking faecal pellets play an important role in the biological carbon pump, the suite of processes by which living organisms transfer carbon from surface waters to depth (Gleiber et al. 2012; Belcher et al 2019). Krill also play a prominent role in the cycling of nutrients (e.g., iron and nitrogen) that are essential for phytoplankton growth in the Southern Ocean (Nicol et al 2011; Cavan et al 2019).

Krill form large aggregations spanning up to 100 km^2 (Tarling and Fielding 2016) and are an economically important target species for the Southern Ocean's largest fishery. The krill fishery has the potential for further sustainable increase with an improved management scheme (Kawaguchi and Nicol 2020).

What is the population size of krill, and how are they sampled?

Estimates of the circumpolar biomass of krill vary between 60-500 million tonnes (e.g. Ross and Quetin, 1988; Nicol et al., 2000; Siegel, 2005). A re-examination of krill biomass based on combinations of net sampling and acoustic data provided a best estimate of mean total biomass of 379 million tonnes (Atkinson et al., 2009).

Acoustic surveys are the preferred method to estimate absolute krill biomass and to provide the basis for setting fishery catch limits by the Commission for the Conservation of Antarctic Marine Living Resources (CCAMLR) (Atkinson et al 2009; Krafft 2021; Hewitt et al. 2004; Nicol et al. 1996; Jarvis et al 2010) (Table 1). Acoustic transect surveys are supported with biological information derived from associated net samples (e.g., species composition and krill length) to inform which echo targets should be identified as krill and to allow conversion from echo signals to krill biomass (Watkins et al. 2004). The 2019 biomass estimate for the main krill fishing grounds, the southwest Atlantic Sector, was 62.6 million tonnes with a sampling coefficient variation of 13% (Krafft et al 2021) and was similar to the previous estimate of 60.1 million tonnes during CCAMLR's synoptic survey in 2000. The results of annual regional surveys within the area suggest high interannual variability in krill biomass.

Krill flux between neighbouring regions could have large effects on the degree of biomass variability. Krill are active swimmers, and therefore flux cannot simply be approximated with the motion of ocean currents. This creates challenges in understanding regional krill population dynamics and complicates the spatial distribution of fishery catch to minimise impacts on regional ecosystems.

Table 1. Area-scale krill biomass and catch limits in CCAMLR Divisions

CCAMLR Area/Division	Total area surveyed (10^6 km^2)	Year surveyed	Biomass (10^6 tonnes)	*Precautionary catch limits (10^6 tonnes)	*Trigger limits (Conservation Measure in Force 2021/22)	Reference
Subarea 48.1, 48.2, 48.3, and 48.4 (Antarctic Peninsula to Scotia Sea)	2.065	2000	60.3	5.61	48.1: 155,000 48.2: 279,000 48.3: 279,000 48.4: 933,000 All combined catch shall not exceed 620,000	SC-CCAMLR-2010 Report Krill Fishery Report 2020
Subarea 48.1, 48.2, 48.3, and-48.4 (Antarctic Peninsula to Scotia Sea)		2019	62.1	**Not applicable	*Not applicable	Krafft et al (2020)

Division 58.4.1	West: 0.453 East: 0.420 Entire: 0.873	1996	West: 3.046 East: 1.799	West: 0.277 East: 0.163	Trigger not set in this Division	Nicol et al. 2000
Division 58.4.1	Entire: 0.909	2019	4.325	**Not applicable		SC-CAMLR 2021
Division 58.4.2	West: 0.680 East: 0.537 Entire: 1.314	2006	West: 15.34 East: 11.47 Entire: 28.43	West: 1.448 East: 1.080	West: 260,000 East: 192,000	Cox and Kawaguchi 2012 CCAMLR Conservation Measure in force (2020)
Division 58.4.2	East: 0.776	2021	East: 6.477	**Not applicable		SC-CAMLR 2021

*Precautionary catch limits and Trigger limits from Conservation Measure in Force 2021/22 (CCAMLR 2021)

**These recent estimates were agreed as best available by CCAMLR Members (SC-CAMLR 2020; 2021) but yet to be used for updating Conservation Measures for these Subarea/Divisions.

Historical changes in krill population

Historical changes in krill abundance have been studied extensively in recent years using KRILLBASE (a database compiling historical and modern circumpolar net sampling data, see Atkinson et al. 2017). Sampling methods and gear differ among vessels, and survey designs changed over time. Therefore, standardising data to reduce uncertainty is necessary but inherently challenging (Candy 2021). A circumpolar analysis of KRILLBASE data spanning the 1920s to 2010s found that krill abundance declined in the Atlantic sector but remained steady or increased elsewhere (Yang et al. 2021). This finding suggests krill are now more evenly distributed throughout the Southern Ocean compared to previous decades.

The Atlantic Sector, where the krill population and data collection is concentrated, is the subject of particular research focus (Johnston et al. 2022). Recent KRILLBASE studies suggest an abundance decline since the 1970s in the northern region of krill habitat where warmer waters present a physiological challenge for this species (Atkinson et al. 2019, 2022; Candy 2021). In contrast, the same studies found that krill abundance was relatively more stable in colder southern areas. Together, these analyses support a southward contraction of krill distribution since the 1970s in the southwest Atlantic sector. Spatial variability obscures any region-wide abundance trend, and there is not strong evidence for a significant abundance decline across the entire southwest Atlantic sector since the 1970s (Cox et al. 2018, 2019; Hill et al. 2019). Meso-scale surveys in this region do not indicate directional trends in krill biomass since 2000, but they do demonstrate high interannual variability in biomass (Siegel and Watkins 2016; Fielding et al. 2014).

Drivers of the changes in the krill population

Recruitment is a result of survival through the first year to join the post-larval population and is therefore an important determinant of the trends and patterns of year-to-year population change. The magnitude of annual recruitment is affected by phytoplankton productivity and regional physical processes including seasonal sea-ice dynamics and variability in ocean circulation, which affect larval survival, growth, dispersal and transport (Reiss 2016). The marginal ice zone is a favourable overwintering environment for larval krill because complex under-ice habitat provides protection from predators and access to food (Meyer et al. 2017).

Climatic forces such as fluctuations in the El Niño Southern Oscillation (ENSO) and Southern Annual Mode (SAM) influence sea-ice dynamics and the position of frontal systems that drive ecosystem conditions and affect krill recruitment (Saba 2014; Loeb and Santora 2015; Atkinson et al. 2019; Johnston et al. 2022).

The krill fishery and its management

The krill fishery started as an Antarctic summer fishery in East Antarctica from the 1960s to 1970s, moved further into the Atlantic Sector in 1980s and early 1990s, and since the mid-1990s the catch has been almost exclusively from the Atlantic sector, although some sparse fishing occurred in the Indian Ocean Sector in 2016. The annual total catch peaked in the early 1980s at excess of 500 thousand tonnes when the Soviet Union was the major fishing nation. Catch declined to around 120 thousand tonnes after dissolution of the Soviet Union but then gradually increased again after 2000 with a more rapid increase since 2010; the catch reached 450 thousand tonnes in 2020 (Figure 3). Recent catches have been increasingly concentrated in a small number of localised fishing grounds in the southwest Atlantic sector near the northwest Antarctic Peninsula, the South Orkney Islands and South Georgia (Watters and Hinke 2022). The recent main fishing season is from the Austral autumn to early winter, and the current largest catches are made by Norway followed by China and Korea (CCAMLR 2022).

CCAMLR manages the fishery and strives to employ an ecosystem-based approach by taking account of krill-dependent predators (CCAMLR 2022). CCAMLR currently has 26 Member states.

Precautionary catch limits are estimated for CCAMLR Statistical Areas and Divisions where krill biomass is agreed upon by Members. Trigger limits are used to limit catch in some Subareas and Divisions. These will be updated through the krill management approach as it evolves to account for finer-scale spatial and temporal variation in distribution and the risks to krill-dependent predators. Fixed annual catch limits at coarse spatial scales risk negative impacts on the krill stock and krill-dependent predators (Meyer et al. 2020; Watters and Hinke 2022). Details of the conservation measures for the krill fishery are available on the CCAMLR Website, as are historical reports of fishery performance.

Market demand was not the primary determinant of krill fishing in the 1970s and 1980s when a heavily subsidised fleet from the Soviet Union dominated operations (Kock 1994). The current krill catch is directed toward meal production or frozen whole krill due to increasing demand in the aquaculture industry (Aker BioMarine 2021). Less than 1,000 tonnes of krill oil are produced annually using about 10% of the annual catch (Kawaguchi and Nicol 2020), but recent increases in the demands for high-value krill products (e.g. eicosapentaenoic acid (EPA) and docosahexaenoic acid (DHA) for human and pet nutrition) is driving the industry (Aker BioMarine 2021). Estimates of sale revenues for the combined fleet operating in 2019 (total catch of 390 thousand tonnes) was US $223 million, with the total global market for the two main krill products (meal and oil) for the same year valued at US $435 million (ASOC 2021). Investment into this fishery is expanding (Stupachenko 2020), including an increasing number of new krill fishing vessels being launched in recent years (Aker Biomarine 2020; Wärtsilä Corporation 2020).

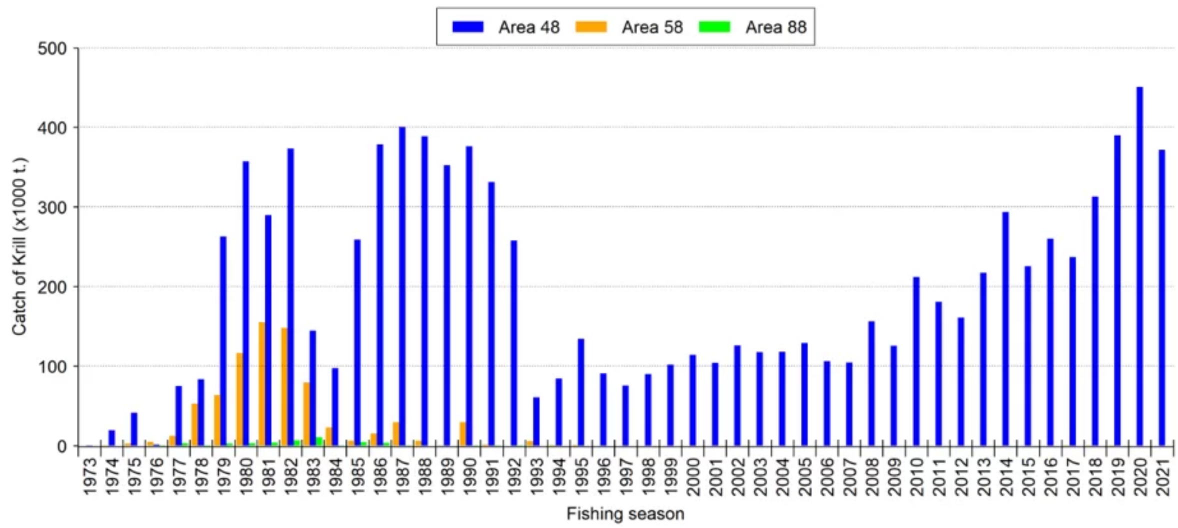

Figure 3. Year-to-year chart of Antarctic krill catch by CCAMLR area (Source: CCAMLR 2022)

Table 2 Relative proportion of krill product (Data Source: Kawaguchi and Nicol 2020)

Product type	Average %
Whole frozen	43.5
Meal	38.5
Paste	4.7
Oil	4.5
Lipid	2.9
Meat	0.7
Peeled	1.2
Boiled	4.0
Total	100.00

Challenges

Knowledge gaps in population dynamics and connectivity

Successful krill spawning and recruitment appear to be localised processes that occur in distinct areas (Perry et al. 2019; Conroy et al. 2020). Thus, only a relatively small portion of the adult population may contribute to effective recruitment (Meyer et al. 2020). Larvae and juveniles are transported by sea ice and ocean currents such that krill sampled at a given location may have been spawned hundreds to thousands of kilometres away (Thorpe et al. 2007). Population connectivity between regions as well as between epipelagic and benthic populations are not well understood. Addressing this knowledge gap is fundamental for revealing the response of krill population to climate change and improving management of the expanding krill fishery so that fishing effort can be redistributed optimally in space and time (Meyer et al. 2020).

Addressing climate change impacts

Krill life history is adapted to the Antarctic seasonal cycle. Winter sea ice provides nursery and feeding habitat, and the spring phytoplankton bloom supports rapid growth and reproduction (Kawaguchi et al. 2007). Changing environmental conditions such as sea-ice decline, ocean warming, and ocean acidification could therefore impact krill abundance, distribution, and behaviour as well as allowing increased access to fishing vessels (Flores et al. 2012; Kawaguchi et al. 2013). More frequent area-scale surveys to update understanding of population abundance and structure as well as process studies to understand mechanistic relationships between krill and their environment should be conducted hand-in-hand (Meyer et al. 2020). Controlled laboratory experiments are critical for understanding effects of multiple stressors (Ericson et al. 2018). The following outstanding questions are important to address.

- What drives krill distribution and recruitment success?
- How will overall krill distribution be affected by changing habitat conditions?
- How will the location and timing of spawning and recruitment change?
- How will the prey demand of krill-dependent predators shift in time and space?

Opportunities for coordination between the research community and fishing industry

Our view of krill is changing rapidly with increasing research capabilities using remote sensing, autonomous underwater vehicles, remotely operated vehicles, deep-sea cameras, and moorings that allow observation at various scales in time and space that were previously not possible. Such technology is shedding new insights into krill habitat and dynamics, as well as improving efficiency of data collection. One important challenge is ensuring data continuity. There needs to be an overlapping calibration period when transitioning to new technologies. Importantly, traditional net sampling and acoustic surveys from research vessels remain difficult to replace for understanding long-term population trends and recruitment (SKAG 2021) including year-round variability in population dynamics.

Securing dedicated time on research vessels is becoming increasingly difficult, thus coordination with fishing vessels as research platforms is logical and becoming important as they are now equipped with scientific-grade echosounders. The 2019 synoptic acoustic survey for krill biomass coordinated transects by six ships (four fishing vessels and two research vessels) and is a possible model for regular area-scale krill surveys in the future (SC-CAMLR 2019). As krill fishing vessels conduct year-round operations, they also could serve to support deployment and recovery of autonomous platforms in coordination with the research community. Some recent studies (e.g. Ericson et al. 2018; Zhu et al. 2019) have shown promise in the use of fishing vessels as platforms for studying krill biology and ecology, particularly in the winter.

Conclusion

Antarctic krill is a large, long-lived pelagic crustacean that is widely distributed around Antarctica and is among the most abundant wild animal species on Earth by biomass. Krill form dense swarms, are the main food source for many predators, and play important roles in biogeochemical cycles.

However, crucial gaps remain in our understanding of krill population dynamics. Resolving these uncertainties will be fundamental to improving management if the fishery targeting this species is to expand sustainably while fulfilling CCAMLR's conservation goals.

In the southwest Atlantic sector since the 1970s, there are indications of a localised decline in krill abundance at the northern edge of the species' range. Combined with relatively stable abundance patterns farther south, this resulted in a southward shift in krill distribution over forty years. Evidence for a region-wide decline in krill abundance is less consistent. Climate change will further impact krill habitat by way of sea-ice loss, warming, and uncertain shifts in prey availability. A holistic research approach is essential to advance predictions about krill and krill-dependent systems.

Recent technological advancement is starting to provide us with new insights on krill. Coordination between the scientific community and the fishing industry will accelerate data acquisition and holds potential to improve the ecosystem-based approach to managing the krill fishery.