



Demographic and maturity patterns of Antarctic krill (*Euphausia superba*) in an overwintering hotspot

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Abstract

Overwinter environmental conditions are a major driver of larval survival, recruitment, and reproductive pre-conditioning in Antarctic krill (*Euphausia superba*). Few winter studies exist from which to infer impacts of changing environmental conditions on the biology of krill. Here demographic and maturity patterns of krill during five winters are examined at an overwintering hotspot in the northern Antarctic Peninsula. Two different recruitment pulses were present over the 5 years of the study. A large recruitment event was evident in winter 2012, followed by cohort growth tracked through winter 2014. A recruitment event also occurred in 2015, despite lower abundance of larvae in 2013 and 2014. The recruitment pulse in 2015 was correlated with the intrusion of high salinity water, characteristic of the Weddell Sea, during a positive El Niño–Southern Oscillation phase, suggesting recruitment was driven by advection of recruits into the northern Antarctic Peninsula. Despite the inter-annual environmental variability, most female krill were in resting reproductive stages in all years. The lack of variability in female reproductive status during winter may impose a developmental constraint to earlier spawning than previously considered; the time necessary to advance from resting stages to reproductive maturity may limit the ability of krill to adapt to trends in the timing and magnitude of the spring bloom. The observed patterns of recruitment and variation in maturity stages highlight the complexity of krill population dynamics and should be considered when projecting population responses of Antarctic krill to climate-driven changes in the Southern Ocean.

Keywords Antarctic krill · Recruitment · Maturity · Climate change · ENSO

Introduction

The northern Antarctic Peninsula ecosystem is a critical region of the Southern Ocean for populations of Antarctic krill (*Euphausia superba*; hereafter krill) serving as a major spawning and recruitment area (Siegel and Watkins 2016) and as an overwintering hotspot, especially within Bransfield Strait (Reiss et al. 2017). Over the last 40 years, climate-driven changes have resulted in warming waters (Swart et al. 2018), declines in seasonal sea ice extent and duration (Stammerjohn et al. 2008, 2012), changing phytoplankton community structure from large diatoms to smaller cryptophytes during summer (Montes-Hugo et al. 2009), and have driven a southward shift in primary production (Schofield

et al. 2010, 2018). Additionally, changes have impacted the population dynamics of krill, resulting in the contraction of the population in the southwest Atlantic Ocean toward the peninsula and increasing the mean length of krill, suggesting that recruitment events are declining (Atkinson et al. 2019).

Future climate scenarios suggest that the spring phytoplankton blooms in marginal ice zones will occur earlier because of the earlier seasonal decline in sea ice (Deppeler and Davidson 2017), but the magnitude of this shift is harder to predict (Henson et al. 2013). Seasonal variations in primary production affect the timing of krill spawning (Siegel and Loeb 1995) and the magnitude of the production of krill larvae during summer (Loeb et al. 2009) while recruitment the following year (Quetin et al. 2003; Loeb et al. 2009; Ross et al. 2014; Saba et al. 2014) has been correlated with overwinter sea ice dynamics (Loeb et al. 1997).

The variability in sea ice extent and longer-term declines in seasonal sea ice duration are correlated with the El Niño–Southern Oscillation (ENSO) and other long-term climatic patterns, including the Southern Annular Mode

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(SAM; Stammerjohn et al. 2008). Negative sea ice extent and duration are correlated with ENSO-positive conditions, and declining sea ice trends are correlated with the positive phase of the SAM, which is projected to remain in that state into the future (Lefebvre and Hugues 2008). The effects of physical variations in winter conditions (sea ice extent and duration) are apparent in the recruitment of krill (Atkinson et al. 2019), but given that waters around the northern Antarctic Peninsula winters are often now ice-free in winter (Reiss et al. 2017) adult krill may already be responding to these dynamic conditions.

Recent studies have shown the range of physiological and biochemical changes that comprise the overwintering strategies of krill (Meyer et al. 2012). Depressed metabolic activity (Meyer et al. 2012), down-regulation of gene expression related to reproduction (Seear et al. 2009), and changing metabolic pathways from lipids to protein (Meyer 2012) all suggest that krill undergo significant changes to successfully overwinter. Additionally, female krill can shrink in length during winter (Tarling et al. 2016) and regress to reproductively immature stages (Cuzin-Roudy and Labat 1992; Siegel 2012), a process that is partly cued by internal clocks (Teschke et al. 2011; Groeneveld et al. 2015), seasonal decreases in light intensity (Teschke et al. 2008; Höring et al. 2018), and reduced food availability below a concentration necessary to sustain vitellogenesis (Kawaguchi et al. 2007; Tarling et al. 2016).

Among the biological processes that could be impacted by changing winter conditions are the maturation schedules of krill, especially at lower latitudes where there is daylight throughout winter (Höring et al. 2018). In particular, changes in the timing or magnitude of the spring bloom (Montes-Hugo et al. 2008; Schofield et al. 2010) might have considerable impacts on krill population dynamics. Field studies from Cuzin-Roudy and Labat (1992) indicated that the cellular processes required to initiate spawning followed the spring bloom, as chlorophyll-*a* concentrations increased after the seasonal sea ice melts. Schmidt et al. (2012) showed that ‘superfluous’ feeding could fuel early spawning when primary productivity spikes were present, assuming that krill were physiologically ready to spawn. Höring et al. (2018) conducted a 2-year laboratory study that showed that the maturity schedule of krill, while under endogenous control, could be manipulated by changing light conditions. These authors suggested that at light levels typical of lower latitudes (~60°S), male krill, and to a lesser extent female krill, would not necessarily revert to immature or resting stages during winter, and that cellular processes may not always be turned off during winter. If so, krill may be able to readily adapt to changes in the spring bloom associated with seasonal environmental variability, such as the ENSO, and long-term climate change. For example, it is possible that krill may now begin to

mature earlier in some years in order to take advantage of the open water and earlier seasonal primary productivity.

Around the northern Antarctic Peninsula, krill aggregate in high numbers during winter within Bransfield Strait (Reiss et al. 2017). This overwintering hotspot is part of a seasonal migration from offshore to inshore in this region (Siegel 1988). Studies conducted during winter within large aggregations should help to elucidate the drivers of krill recruitment, population dynamics, and seasonal production that have historically been examined by studying inter-annual variability in life history characteristics observed during summer (Loeb et al. 1997, 2009; Siegel et al. 2002; Quetin and Ross 2003; Ross et al. 2014; Saba et al. 2014).

Here, we report on maturity, demographic, and recruitment patterns from samples collected around the northern Antarctic Peninsula during five consecutive winters with varying environmental conditions. We examine likely sources for the recruitment events observed and relate them to ENSO conditions. We also examine whether mid- to late-winter maturity stages of krill vary at the lower latitudes of the Antarctic Peninsula, given long-term changes in the ecosystem, and the possibility that krill do not need to revert to immature stages under some conditions. We consider our results in relation to hypotheses regarding the links between krill productivity and climate change.

Materials and methods

At-sea sampling

Five annual surveys around the northern Antarctic Peninsula were conducted in mid- to late-winter (August and September from 2012 to 2016) (Fig. 1; Table 1) by the U.S. Antarctic Marine Living Resources (AMLR) Program, aboard the RVIB *Nathaniel B. Palmer*. The U.S. AMLR Program has defined four areas that have traditionally been used to examine spatial patterns in abundance (Fig. 1); The Elephant Island (EI) area, the West Area (WA), the Bransfield Strait (BS), and the Joinville Island area (JI). In each year, between 38 and 105 stations were sampled around the South Shetland Islands. In 2012, time constraints allowed us to sample only 38 stations, mostly around the EI area with a few stations within the BS and the JI areas. No samples were collected in the WA. In 2013, inclement weather and thick ice allowed us to sample only 88 stations, but all four areas were sampled. In 2014 and 2015, the entire survey area historically sampled by the U.S. AMLR Program was surveyed. In 2016, a few stations in the easternmost area of EI area and near the JI area were not sampled because of sea ice.

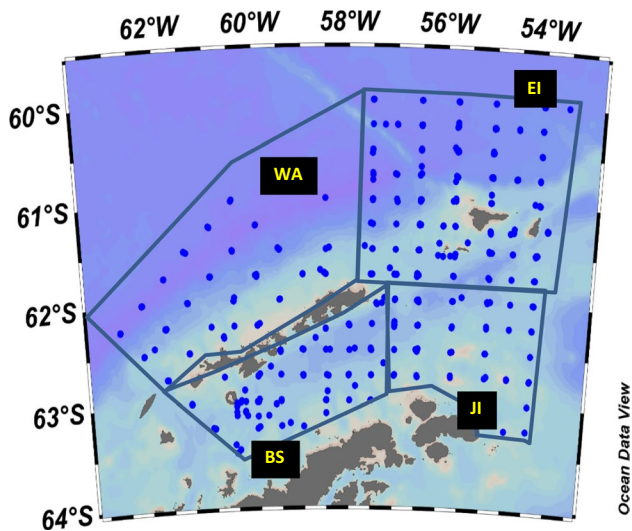


Fig. 1 Map of sampling locations around the northern Antarctic Peninsula during winter 2012 to 2016. Boxes define areas for the calculation of means. *BS* Bransfield Strait, *EI* Elephant Island, *JI* Joinville Island, *WA* West Area

Table 1 Survey dates and total number of stations occupied during winter surveys from 2012 to 2016

Cruise	Sampling start date	Sampling end date	Total number of stations
AMLR2012	8/6/2012	8/14/2012	38
AMLR2013	8/14/2013	9/5/2013	88
AMLR2014	8/22/2014	9/14/2014	112
AMLR2015	8/6/2015	8/27/2015	102
AMLR2016	8/6/2016	8/14/2016	87

Net sampling

Details of the sampling protocols used by the U.S. AMLR Program have been published elsewhere (Reiss et al. 2017). Briefly, krill were collected using a 1.8 m (2.54 m² mouth opening), 505 µm mesh size Isaacs-Kidd midwater trawl, towed obliquely from the surface to 170 m or 10 m from the sea floor, as estimated from a real-time pressure sensor attached to the wire. A flowmeter (General Oceanics Inc. Model 2030R) was mounted on the net frame to calculate the volume of water filtered per tow. Krill and krill larvae were enumerated at each station. A sample of up to 100 krill were measured (total length, mm), sexed (male, female, juvenile), and staged for maturity, according to Makarov and Denys (1981).

Abundance and proportional recruitment

The abundances of larval and post-larval krill were calculated for each station by dividing the number of krill sampled by the volume (m³) of water filtered in each tow, and then multiplying by 1000. Abundance is reported as no. 1000 m⁻³. For statistical analyses, the abundance data were $\ln(x+1)$ transformed to better approximate a normal distribution. To examine patterns of annual relative recruitment, we computed the proportion of krill less than 31 mm length to index the proportional recruitment strength (Reiss 2008). We chose this length class as an index of 1-year-old krill based on Siegel (1987). This index does not reflect absolute recruitment but provides an index of the relative success of spawning the previous summer.

Maturity

Maturity staging of post-larval krill was based on the classification scheme of Makarov and Denys (1981). Krill post-larvae with no petasma or thylecum were defined as juveniles. Male krill were defined using five stages of maturity. Immature males were classified as stage M2A when the petasma was present as a single simple lobe on the first pleopod, or stage M2B when the petasma was bi-lobed but had few other morphological characteristics. Males were classified as stage M2C when the petasma had an additional “wing” and morphological processes were visible. Mature male krill were defined as stage M3A when no spermatophores were present and stage M3B when spermatophores were present. No post-spawning definitions are defined using this schema for males.

Female krill were similarly staged. Immature females were classified as stage F2 based on the presence of a pale to light red thylecum. Fully mature female krill were defined based on five visual stages. Early maturation (F3A) was defined as no spermatophores attached to the thylecum, and normal body size (without enlarged ovaries). Stage F3B was defined as spermatophores attached to the thylecum and visible ovaries that did not fill the thoracic space. Stage F3C was defined as attached spermatophores and visible ovaries that filled the thoracic space, but with no swelling. Stage F3D was defined as a swollen thoracic space and distended carapace. Following spawning, maturity progresses to stage F3E, which was defined as an empty thoracic space and a distended carapace. For the analyses that follow, spawning potential was defined as the proportion of males in stage M3B and females in stages F3D and F3E relative to all krill in the samples.

Results

Variation in the abundance of post-larvae

Post-larval krill exhibited considerable spatial structure in their abundance across the northern Antarctic Peninsula region (Fig. 2; Table 2). The variability in the abundance of post-larvae was compared among the four areas (EI, WA, BS and JI) and for the 4 years (2013–2016) when there were data from all areas. We found no significant differences among years (two-way ANOVA, $F_{3,356} = 1.53$, $p = 0.207$) and no interactions between area and year (two-way ANOVA, $F_{9,356} = 0.76$, $p = 0.654$). In general, krill were several orders of magnitude more abundant within Bransfield Strait every year compared to areas north of the South Shetland Islands (ANOVA, $F_{3,356} = 61.08$, $p < 0.0001$).

Length distributions

Krill length–frequency distributions showed a progression in lengths over years typical of this species' recruitment pattern (Reiss 2016; Siegel and Watkins 2016). Over the first 3 years of this study (Fig. 3) a distinctive modal progression was observed. In 2012, the length–frequency distribution was dominated by a single mode centered at 22 mm, representing more than 70% of all krill collected during that survey. Larger krill occurred with lower frequency, with no single length class representing a secondary length mode. In winter 2013, we observed another single mode centered at 32 mm. In 2014, the length–frequency distribution was skewed and

bimodal with a large mode that consisted of a broad peak between 35 and 45 mm, and a much smaller mode between 17 and 20 mm. The last 2 years of the study, another progression of krill lengths is apparent (Fig. 3). In winter 2015, a single broad peak was found centered at around 30 mm and ranged from 25 to 35 mm, suggestive of another recruitment event. There was little evidence of a larger (> 45 mm) length class, as might be expected to follow the skewed distribution observed in winter 2014. In 2016, a bimodal distribution was observed with one mode centered at 35 mm and a second mode centered at 42 mm.

Sex ratios

Additional detail regarding the length–frequency distributions was resolved by examining length distributions by sex (Fig. 4). In 2012, the large peak of small animals dominating the catch was composed of juveniles. There was no obvious pattern in the prevalence of female or male krill in 2012 given the low occurrence of sexually mature animals in the samples. In all other years, krill were sexually differentiable by 27 mm. Females dominated the length compositions at intermediate lengths, but two emergent patterns were present in the data. In 2013 and 2015, when the length–frequency distributions were skewed towards smaller krill, male and female krill decreased in frequency of occurrence at relatively similar rates after about 37 mm. In contrast, in 2014 and 2016 when the modal length was greater than about 35 mm, male krill were relatively more abundant compared to females after about 40 to 45 mm. In general, male krill were about 5 mm longer than females during 2014 and 2016.

Maturity distributions

The distributions of maturity stages collected over the 5-year period also showed significant variability with some evidence for the initiation of spawning in both males and females in some years (Fig. 5). In 2012 and 2013, most female krill were stage F2 and most male krill were stage M2B or M2C. As noted previously, the vast majority of krill in both years were small. However, in 2014 and 2015, while the majority of female krill were still classified as F2, a few individuals were stages F3A and F3B. Although no females were stage F3C, observations of animals in stages F3A and F3B suggest that there was some reproductive activity in 2014 and 2015.

Male krill exhibited considerably more variability in their reproductive stages over the study period (Fig. 5). In 2013 and 2014, more than 25% of all krill sampled were males in stage M2C, whereas in 2015 and 2016, males were predominantly stages M2A, M3A, and M3B. In contrast to the paucity of mature female krill across all years, we found high proportions of mature male krill in every year except in 2012 and 2013,

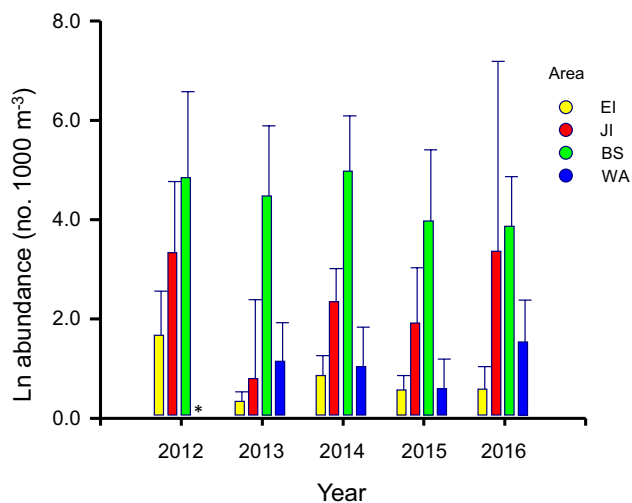


Fig. 2 Abundance ($\ln(x+1)$) and standard error (± 1) of post-larval Antarctic krill (*Euphausia superba*) from four sampling areas around the Antarctic Peninsula during five winters from 2012 to 2016. BS Bransfield Strait, EI Elephant Island, WA West Area, JI Joinville Island

Table 2 Number of stations, means and standard deviation (SD) for physical and biological samples collected in four areas around the northern Antarctic Peninsula over five winters from 2012 through 2016

Year	Area	CTD Stations	UML (m)	UML (SD)	Salinity	Salinity (SD)	Temperature (°C)	Temperature (SD)	Tempera- ture (SD)	Net stations	Krill post-larvae (no. 1000 m ⁻³)	Krill post-larvae (SD)	Krill larvae (no. 1000 m ⁻³)	Krill larvae (SD)
2012	EI	14	100.8	65.2	34.05	0.08	-1.55	0.34	0.34	23	261.7	954.8	6.6	9.4
2012	Jl	6	100.0	39.7	34.12	0.05	-1.84	0.03	0.03	6	64.9	85.5	6.6	10.1
2012	BS	4	95.0	30.0	34.09	0.06	-1.85	0.01	0.01	3	266.6	364.7	39.7	58.9
2013	EI	34	79.3	46.2	33.93	0.13	-1.74	0.12	0.12	35	1.4	4.8	1.8	5.1
2013	Jl	1	60.0	**	34.23	**	-1.84	**	**	1	3.9	**	0.3	**
2013	BS	14	113.6	30.4	34.16	0.05	-1.73	0.14	0.14	15	2584.7	8002.4	6.8	9.8
2013	WA	22	62.6	48.9	34.00	0.10	-1.82	0.04	0.04	22	103.4	424.6	9.7	20.2
2014	EI	43	61.1	35.7	33.92	0.19	-1.70	0.13	0.13	44	12.3	53.0	16.7	33.4
2014	Jl	23	75.3	90.4	34.35	0.17	-1.75	0.10	0.10	23	31.3	54.0	18.7	29.6
2014	BS	18	82.0	82.6	34.27	0.14	-1.77	0.07	0.07	24	1570.1	2914.2	51.8	159.0
2014	WA	21	79.1	66.3	33.96	0.15	-1.81	0.05	0.05	21	43.2	148.7	23.4	54.0
2015	EI	39	112.9	46.3	34.16	0.12	-1.71	0.13	0.13	45	2.7	6.9	334.5	816.5
2015	Jl	14	141.8	157.2	34.43	0.09	-1.77	0.10	0.10	18	134.0	392.5	174.3	259.4
2015	BS	17	160.8	97.3	34.37	0.11	-1.79	0.07	0.07	19	1173.8	2356.1	145.5	219.4
2015	WA	14	56.9	70.4	34.11	0.15	-1.83	0.02	0.02	18	12.3	49.7	112.2	324.3
2016	EI	28	91.8	101.4	34.09	0.22	-1.66	0.21	0.21	28	6.4	23.8	129.3	240.0
2016	Jl	2	179.5	75.7	34.36	0.04	-1.74	0.07	0.07	3	262.2	428.0	38.9	40.3
2016	BS	27	158.7	139.4	34.39	0.11	-1.72	0.16	0.16	34	490.0	766.1	27.8	35.6
2016	WA	21	64.6	110.8	34.11	0.21	-1.79	0.06	0.06	22	47.5	146.7	72.9	238.0

The number of samples for each of the physical (upper mixed layer depth (UML), UML temperature (°C), UML salinity), and biological (net tows) of larvae and post-larvae of Antarctic krill (*Euphausia superba*) vary depending on sampling conditions in the field

EI Elephant Island, Jl Joinville Island, BS Bransfield Strait, WA West Area. Note that the WA was not sampled in winter 2012

**Too few samples to calculate a standard deviation

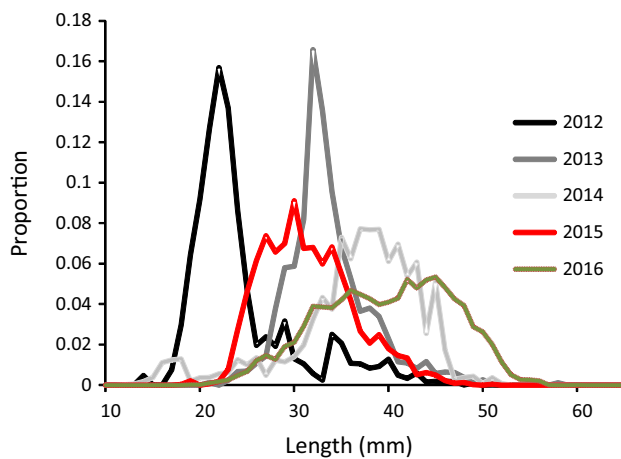


Fig. 3 Length–frequency distributions of Antarctic krill (*Euphausia superba*) collected around the Antarctic Peninsula during five winters from 2012 through 2016

when most krill were small. Krill in stages M3A and M3B ranged from just under 1% of those sampled in 2014, when krill were relative large, to approximately 3% of those sampled in 2015, when the mean length of male krill was about 35 mm, to more than 25% in 2016, when most krill were longer than 40 mm (Table 3).

Larval abundance and distribution

The abundance of larval krill varied both inter-annually and spatially (Fig. 6; Table 2) in ways that were unrelated to patterns for post-larvae. For the 4 years (2013 to 2016) with data collected in all areas, larval abundance showed a significant interaction between year and area (two-way ANOVA, $F_{9,356}=2.62$, $p=0.006$). This result indicates that krill larvae were neither found consistently in a single area over the study, nor were they consistently abundant. On average, fewer larvae were found in 2012 and 2013 (Fig. 6; Table 2) and were most abundant in 2015.

Proportional recruitment

The proportion of small krill varied over the survey period, and high (> 0.5) proportional recruitment was only observed in 1 year (Fig. 7). Proportional recruitment was 0.87 in 2012 and was lower in 2013 and 2014. The only other relatively large proportional recruitment occurred in 2015, when 44% of all krill were less than 31 mm in length.

Discussion

The marine ecosystem surrounding the northern Antarctic Peninsula is among the most impacted by climatic changes over the last 40 years. Declines in sea ice extent and duration around the Antarctic Peninsula have occurred (Stammerjohn et al. 2008; Parkinson 2019), concurrent with increases in water and air temperatures (Vaughan et al. 2003; Swart et al. 2018) and potential changes to the timing, magnitude, and composition of the spring bloom (Montes-Hugo et al. 2008; Schofield et al. 2010). These environmental changes all suggest that krill populations could be impacted greatly by climate change (Murphy et al. 2007; Quetin et al. 2007; Flores et al. 2012; Hill et al. 2013; Piñones and Fedorov 2016; Klein et al. 2018). However, plasticity of the life history of krill makes it difficult to make predictions about krill and the pelagic ecosystem with any certainty (Hill et al. 2013; Melbourne-Thomas et al. 2016; Piñones and Fedorov 2016; Atkinson et al. 2019). Because winter conditions are the most rapidly changing, understanding the condition of krill during this season is critical for projections about the future (Flores et al. 2012). In this study, we showed that despite the changes occurring around the Antarctic Peninsula, female krill maturity schedules continue to reflect regression to resting stages during winter, while male krill experience considerable variability in their maturity stages at the same time. Additionally, demographic patterns showed that krill length–frequency distributions reflected two recruitment events over the 5-year study period, a somewhat unexpected result given the normal 5- to 6-year cycle commonly observed (Reiss 2016). Together, these findings suggest that understanding the impact of climate change on krill populations, especially in areas that are ice-free more often, and where spring bloom dynamics may be more muted as a result, will require an understanding of the flexibility in the machinery that influence the maturity schedules of Antarctic krill.

Maturity variability

Despite significant changes in the physical and biological environment around the Antarctic Peninsula over the last 40 years (Schofield et al. 2010), and the plasticity in krill life history (Schmidt et al. 2014), there appears to be no evidence for advancement of the maturity schedules of female krill. Most female krill were in stage F2, and males had highly variable maturation states among years. These results are similar to those from other studies (Cuzin-Roudy and Labat 1992; Ross et al. 2000) conducted over the last 30 years and across a broad latitudinal gradient

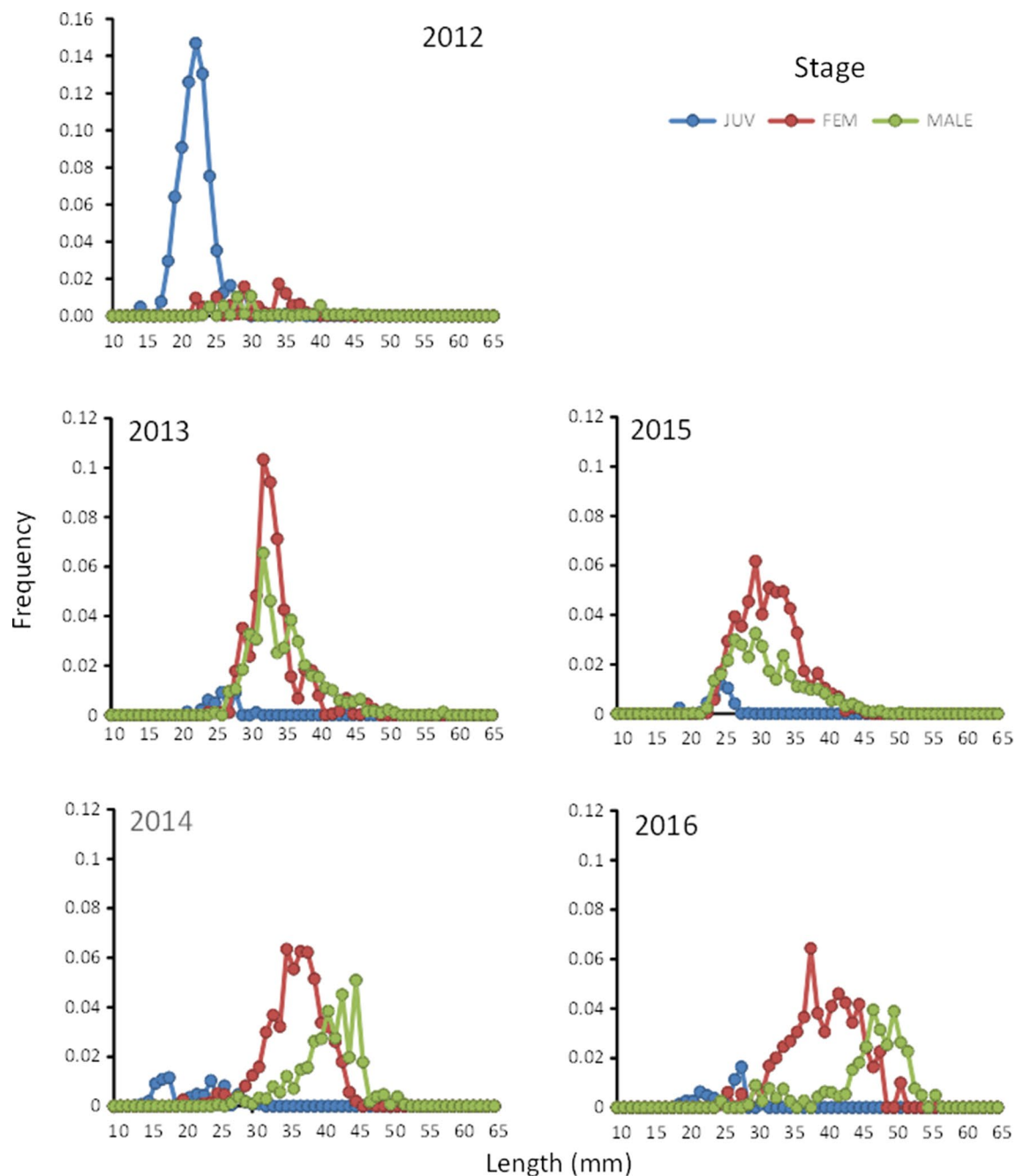


Fig. 4 Length–frequency distributions of juvenile (blue), male (green) and female (red) Antarctic krill (*Euphausia superba*) collected around the Antarctic Peninsula during five winters from 2012 through 2016

(Ross et al. 2000). Thus, despite laboratory studies that document potential for krill to partially regress under seasonal light conditions like those found in the northern Antarctic Peninsula (Kawaguchi 2016; Höring et al. 2018), at present female krill continue to regress to resting stages in this region. This has implications for changing ecosystem dynamics in this region. For example, Kawaguchi et al. (2007) showed that the maturation of female krill takes a number of months and moults (dependent on

sea ice algal biomass, water temperature, and growth) to complete (see Fig. 6.2 in Kawaguchi 2016). The intermoult period for krill is on the order of weeks, suggesting that the progression from stage F2 to stage F3C could take up to 2 to 3 months. Thus, if continued moderation of the climate occurs at the peninsula, it is likely that the timing, magnitude, and duration of the spring bloom will vary as well. Further advancement of the mean dates of sea ice melting may create a mis-match between krill maturation

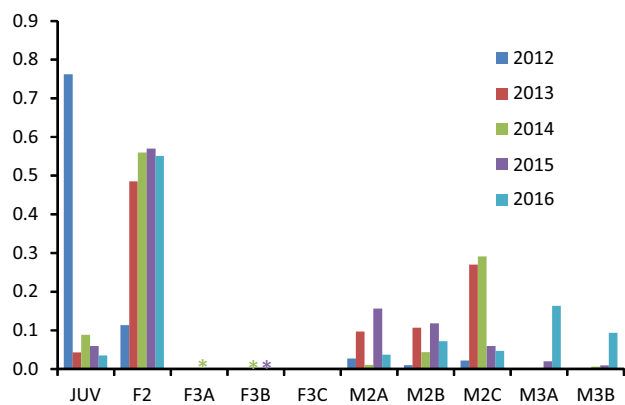


Fig. 5 Proportion of reproductive maturity stages of Antarctic krill (*Euphausia superba*) collected around the Antarctic Peninsula over five winters from 2012 through 2016. F represents female maturity stages; M represents male maturity stages; *positive occurrence but too few to visualize

Table 3 Proportional maturity stage of Antarctic krill (*Euphausia superba*) collected around the Antarctic Peninsula during five winters from 2012 through 2016

Year	2012	2013	2014	2015	2016
JUV	0.762	0.043	0.088	0.059	0.034
F2	0.113	0.485	0.559	0.570	0.551
F3A	0.000	0.000	*	*	0.000
F3B	0.000	0.000	0.000	*	0.000
F3C					
M2A	0.026	0.097	0.010	0.155	0.036
M2B	0.010	0.106	0.043	0.117	0.072
M2C	0.021	0.270	0.291	0.059	0.046
M3A	0.000	0.000	0.002	0.019	0.163
M3B	0.000	0.000	0.005	0.009	0.093

*Less than 0.001

and primary productivity peaks, negatively influencing krill productivity. The few females in more advanced stages of maturity from 2014 and 2015 were caught north of Elephant Island, where primary production is consistently higher during winter than in the Bransfield Strait, where krill aggregate during winter (Reiss et al. 2017). This suggests that females overwintering in the Bransfield Strait will need to migrate to these offshore areas to take advantage of winter primary production. The large spatial separation between the main overwintering habitat and winter production indicates that krill would be unable to use this early production to fuel the maturation and growth processes (Kawaguchi et al. 2007; Schmidt et al. 2012).

In this study, we used visual indicators of maturity stage to derive our conclusions about the reproductive status and

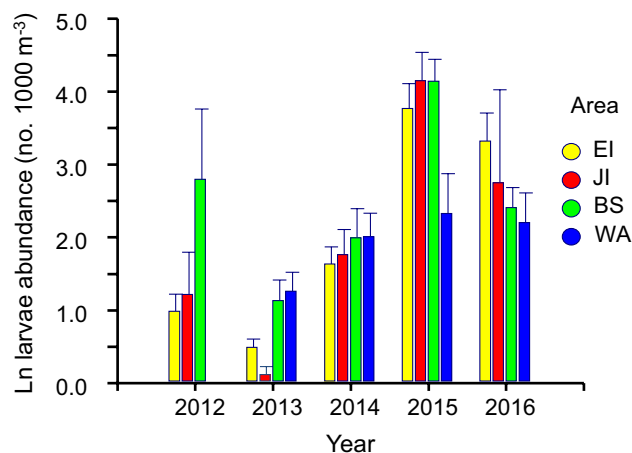


Fig. 6 Abundance of Antarctic krill (*Euphausia superba*) larvae from four sampling areas around the Antarctic Peninsula during five winters from 2012 to 2016. BS Bransfield Strait, EI Elephant Island, WA West Area, JI Joinville Island

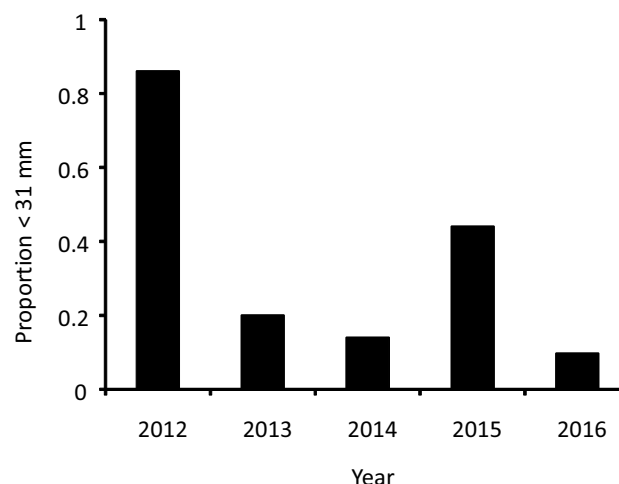


Fig. 7 Proportional recruitment of Antarctic krill (*Euphausia superba*) around the Antarctic Peninsula during five winters from 2012 through 2016. Proportional recruitment is defined as the proportion of Antarctic krill less than 31 mm in length

flexibility of krill. It is possible that at the cellular level, the machinery and processes that are necessary to initiate re-maturation may have been active (Kawaguchi et al. 2007; Kawaguchi 2016). However, re-maturation also requires that krill go through an indeterminate number of moults to progress from fully immature to fully mature, and the inter-moult period is limited by temperature and food availability (Kawaguchi 2016). The visual staging methods used here indicate that female krill were a number of moults away from maturing. Thus, the biases introduced by using this visual method, rather than histological methods, are probably not large. However, it would be useful to collect histological,

and biochemical data from the same location in multiple, consecutive winters in the future to determine whether the visual indicators of maturation are consistent with cellular processes that might indicate greater flexibility than is suggested by our data.

Demographic and recruitment dynamics

The progression of length modes over time can be used to infer the ages of krill if mostly unimodal patterns of krill are present in samples (Siegel 1987; Reiss 2016). Krill spawn from November to March, so a January “hatch date” is often assumed for ageing purposes (Siegel 1987). Krill larvae spawned in January develop and grow throughout the autumn and winter such that by late winter (September), furcilia VI are about 10 mm in length while age-0 juveniles (recently transformed larvae) are 10–12 mm (Frazer et al. 2002; Schaafsma et al. 2016). As the spring progresses, these juveniles grow rapidly (0.02 to 0.082 mm days⁻¹; Ross et al. 2000), and by age-1 (January) recruits at the northern Antarctic Peninsula are between 25 and 30 mm (Siegel 1987, 1988), having grown 15–20 mm between September and January. Examining the length–frequency distribution of krill over the first 3 years of the study showed some discrepancies relative to the normal model for the recruitment and growth of krill. The 22 mm post-larval krill present in the survey area in August 2012 were clearly not recently metamorphosed furcilia VI animals because they were about 10 mm too long. It is unlikely that krill spawned in January grew from early larvae to 22 mm in just 8 months, as that would require a doubling of growth when food resources are most limiting. If the krill that were 22 mm in length in August were not 8 months old, then it is more possible that these 22 mm animals were at least 1.75 years of age, and were spawned in January of 2011. If true, then the modal lengths of krill in the following two winters were consistent with growth from 22 to 33 mm in 2013 (2.75 years) and then to 39 mm in 2014 (3.75 years).

The growth progression of this cohort was also evident in summer surveys conducted in the region. In summer 2013, Siegel (2013) found a single mode of krill that was 33 mm in the Bransfield Strait, while Reiss and Espino-Sanchez (2014) found a principal mode of about 40 mm in Bransfield Strait during summer 2014. Given the progression of these length modes and the coherence between winter and summer observations, it is clear that there was growth from winter to summer in each year, and little growth from summer to winter. Between winter (August) 2012 and summer (January) 2013 (4 months), and between winter (September) 2013 and summer (January) 2014, modal length–frequencies changed from 22 to 33 mm (11 mm of growth) and 32 and 40 mm (8–9 mm of growth), respectively. In contrast, there was little growth between consecutive summer to winter

periods (e.g., 33 mm length in summer (January) 2013 and winter (September) 2013).

These findings are consistent with studies that have examined seasonal growth patterns in other areas. For example, Kawaguchi et al. (2007) modeled krill growth and showed that post-larval growth declines between late summer (0.2 mm days⁻¹) and winter (0.011 mm days⁻¹) and that krill do not exhibit much growth in winter, with instantaneous growth rates near zero or negative (Quetin and Ross 1991; Meyer et al. 2010). The lack of growth in post-larvae from late summer through winter has been explained in part by the tradeoff between continuing growth versus storing lipids for use during winter (Hagen et al. 2001; Schmidt et al. 2014). Thus, we can conclude that for smaller krill (40 mm; Fig. 7) that do not shrink in winter, most growth occurs during spring to summer, and less growth occurs in autumn.

After winter 2013, tracking krill cohorts in our length–frequency data was complicated by two factors that suggest other dynamics impact inferences about recruitment in this region. First, in 2014 and 2016, there was a substantial difference in the length–frequency distributions of male and female krill that was not apparent when krill lengths were, on average, less than 35 mm, as they were in 2012, 2013, and 2015. In both 2014 and 2016, male krill dominated the largest length groups and were about 5 mm longer than female krill. The differences in growth, and the dominance of male krill during these two winters, are consistent with the findings of Tarling et al. (2016) that showed mature female krill shrunk between 3 and 5 mm in length as they regressed to overwintering resting stages, while male krill did not shrink during winter. Thus, the skewed length–frequency distributions in 2014 and 2016 do not reflect multiple cohorts of krill, but rather, the skewed distribution reflects sexual differences in shrinkage during winter. For length–frequency distributions marked by smaller modal lengths (e. g., 2013 and 2015), female and male krill overlap in length, making it easier to discern annual growth.

Second, the decrease in the mean lengths of krill observed in 2015 suggests that there was recruitment of smaller animals to the region in that year (Fig. 3). These 33 mm animals should have also been reflected in a larger number of small (1 year old) krill in 2013 and 2014, which was not the case. Moreover, there were relatively few larvae found in the waters around the Peninsula in those years. Advection of krill produced in other areas has often been argued to be occasionally important (Siegel et al. 2013). However, there are few studies that have demonstrated that the abundance of krill around the peninsula are derived from elsewhere.

During winter 2015 and 2016 we found evidence that water masses within the northern Antarctic Peninsula varied in a manner consistent with the changes in observed recruitment, suggesting that water-mass movement and recruitment may be linked. Both upper mixed layer (UML)

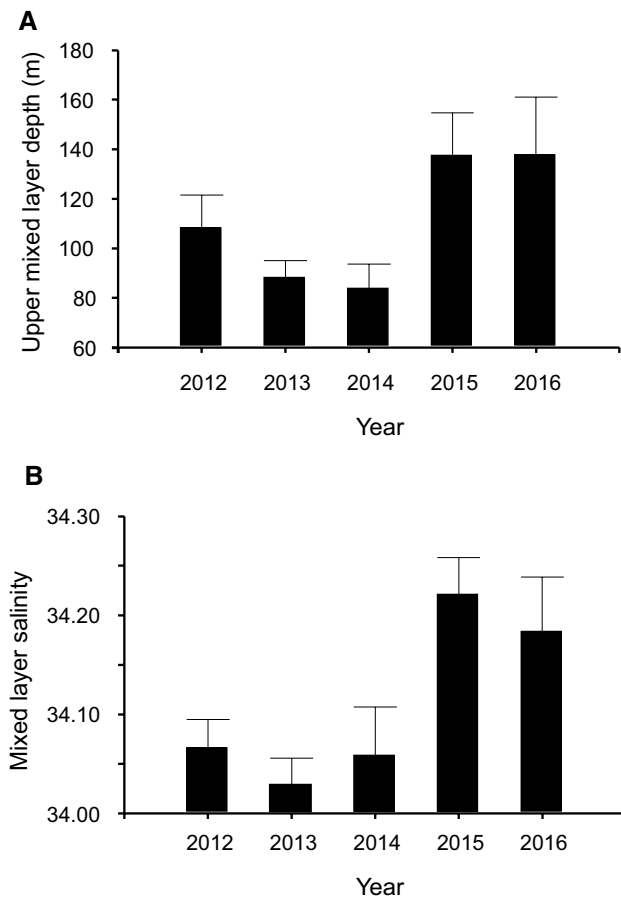


Fig. 8 Inter-annual variability in the **a** Upper Mixed Layer (UML) depth (m) and **b** mean UML salinity around the Antarctic Peninsula in five winters from 2012 through 2016

salinity and depth increased significantly in 2015 and 2016 (Fig. 8; Table 2). UML depth increased from an average of about 80 m in 2012, 2013, and 2014 to an average of more than 120 m in 2015 and 2016. UML salinity also increased greatly over the same years. Increased salinity can occur for two reasons: (1) sea ice formation that rejects brine and results in salinification of the water column; and (2) from the advection of higher-salinity water into the region. There was relatively little sea ice in the survey area during 2015 and 2016 (Reiss in prep.), so it is unlikely that brine rejection was responsible for the observed increase in salinity. In contrast, climate conditions during 2015 and 2016 were dominated by an ENSO that began in early 2015 and extended into 2016 (Armitage et al. 2018). Under ENSO conditions, higher-salinity water from the Weddell Sea enters the basins and shelves of the northern Antarctic Peninsula (Hellmer et al. 2011). Thus, it is plausible that both the higher-salinity water and the krill observed in 2015 and 2016 were transported from the Weddell Sea, and were not the result of local production or recruitment. If so, then our

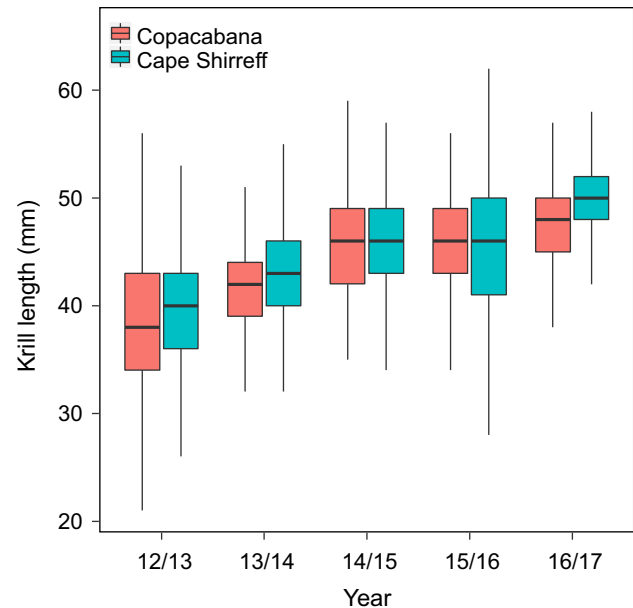


Fig. 9 Antarctic krill (*Euphausia superba*) lengths in the diets of penguins at Copacabana field stations (King George Island; Bransfield Strait) and Cape Shirreff (Livingston Island; West Area) over five austral summers from 2011/2012 through 2016/2017

study was fortuitously timed to capture a major oscillation in the sources of krill to the northern Antarctic Peninsula.

There may be other reasons that could potentially bias krill length–frequency or maturity patterns, and these might have some impact on the interpretations we make here. For example, behaviorally, krill may occupy deeper waters during winter and may exhibit larger diel vertical migrations (Cleary et al. 2016; Bernard et al. 2018) than during summer. In Bransfield Strait, vertical migrations exceed 300 m during winter, while in other regions krill migrate to the seafloor to feed on phyto-detritus (Cleary et al. 2016; Kane et al. 2018). The potential for deep vertical migrations may result in the under-sampling of some krill length categories or maturity stages, if krill segregate vertically. Our study, which only sampled the upper 170 m of the water column, may have missed some fraction of the population that has different attributes (length, sex ratio, and maturity) potentially affecting our interpretations. However, given the strong diel migration signal (Bernard et al. 2018) and migration into surface waters at night, and the fact that about 67% of samples were collected at night, we do not believe that our sampling strategy substantially biased our findings.

Ecosystem effects

The patterns of krill recruitment and growth resulting from potentially different sources of krill around the northern Antarctic Peninsula were also reflected in diets of

krill-dependent predators (Fig. 9). Analysis of diets from penguins monitored by the U.S. AMLR Program at King George and Livingston Islands (Hinke et al. 2007) were consistent with the patterns derived from the surveys. Mean krill lengths in penguin diets at both locations increased from 2012 to 2014 and followed the same pattern observed during our winter cruises. Furthermore, in 2015 and 2016, when krill lengths in the surveys also changed, these changes were reflected in the krill lengths from penguin diets during those summers (Fig. 9). That the length compositions of krill consumed by predators reflect those in the environment is well known (Miller and Trivelpiece 2007), but what is more important, and an additional source of uncertainty, is that our findings suggest that krill-dependent predators in this region were consuming krill derived from two different source areas over the 5 years of our study. This has important implications for understanding the future dynamics of predator populations in this region because a variable source of krill, independent of, but in addition to recruitment fluctuations, would suggest a further layer of uncertainty that requires knowing when different sources of krill are contributing to predator diets in this region. Further, such a pattern also suggests that, during these years, the krill fishery was catching krill derived from two different regions. Current management strategies for krill do not include consideration of different sources of krill to this area. But if our data are correct then it is important to account for this variability in management strategies, especially if krill are continued to be harvested in winter. Clearly, understanding the relative contributions of alternative source populations of krill to predators and the krill fishery is fundamental to conserving resources and projecting future impacts of climate change and environmental variability on this ecosystem.

Implications for climate-based projections

Various studies have provided different projections regarding the extent to which krill will be either negatively or positively impacted by climate change in the Southern Ocean (Hill et al. 2013; Melbourne-Thomas et al. 2016; Piñones and Fedorov 2016). Many of these studies have looked at the impacts of the changing physical structure like sea ice dynamics that are correlated with recruitment (Loeb et al. 1997; Quetin and Ross 2003; Loeb et al. 2009; Saba et al. 2014). There has also been considerable effort to document the changes in phytoplankton community structure and production along the peninsula (Montes-Hugo et al. 2008; Schofield et al. 2018), because it drives the seasonal production of krill (Siegel and Loeb 1995) and the survival of first feeding larvae (Loeb et al. 2009). The projections about the changes to the timing and magnitude of the spring bloom in different areas of the Southern Ocean vary (Henson et al. 2013; Deppeler and Davidson 2017), but it is possible that

areas like the northern Antarctic Peninsula that are more likely to be ice-free in the future may see smaller spring bloom peaks that may start earlier.

The plasticity in krill life history that is exhibited in the varying and successful overwintering strategies (Meyer 2012) does not seem to translate to the maturation schedule, as female krill in this study showed little variability in their maturity schedule across highly variable winters. The nutritive condition of post-larvae emerging from winter is largely dependent on the amount of lipids accumulated in autumn (Meyer 2012), as well as the potential to forage opportunistically in some areas (Schmidt et al. 2014). By storing lipid for winter, rather than investing in growth during autumn (Cuzin-Roudy and Labat 1992), krill must exploit the spring bloom to initiate maturation prior to spawning. A future where the spring bloom is smaller and earlier, or occurs away from the overwintering areas, means there may be a seasonal constraint on the flexibility of krill to take advantage of early seasonal phytoplankton blooms or changing bloom dynamics either because krill must locate areas with high primary production that may occur away from the overwintering grounds, or because krill are physiologically constrained, and their cellular machinery cannot respond to seasonally variable bloom dynamics.

Thus, projecting the impacts of climate change on krill populations will require a better understanding of the potential physiological and developmental bottlenecks that could impact productivity of krill over management time scales, and a better understanding of the sources of krill that form the populations on which predators depend and fisheries exploit.

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Compliance with ethical standards

Conflict of interest The authors declare no conflict of interest.

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