Quality of Sea-ice Habitat Traversed by Antarctic Krill Larvae Influences Recruitment Success

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Abstract

Antarctic krill are a key Southern Ocean species whose success is attributed to their adaption to the extreme polar seasonality. Overwinter sea-ice presence and characteristics exert a strong control on larval survival and subsequent recruitment. Our understanding of the mechanisms through which sea ice influences survival are mainly underpinned by small-scale observations, whereas planktonic larvae may be advected over large scales. Using a state-of-the-art sea-ice model we computed Lagrangian back-trajectories to simulate larval krill advection into three distinct recruitment regions and examined modelled sea-ice habitat characteristics along trajectories. From these results we identify potential overwintering habitats and present a conceptual model for explaining regional variability in sea-ice habitat drivers of recruitment. Crucially, many of these sea-ice habitats are currently under-sampled. This work can inform future sampling efforts that will improve our understanding of climate change impacts, and potential interactions with the krill fishery.

Introduction

Antarctic krill (*Euphausia superba*, hereafter krill) are one of the world's most abundant species by biomass^{1,2}, hence are a key species in the Southern Ocean ecosystem^{3,4}. The success of krill is due to their evolving a lifecycle tightly coupled to the extreme polar seasonality⁵. This involves maximizing growth and reproduction during the summer when phytoplankton (their main food source) is most abundant, while surviving the winter when phytoplankton growth is light limited⁶. Krill larvae are the stage most vulnerable to starvation^{7,8}, so larval overwinter survival likely exerts a strong control on their recruitment to the juvenile population the following spring⁹.

Variability in recruitment success is thought to be driven by the environment the preceding winter^{10–14}. Existing efforts to quantify environmental recruitment drivers generally involve correlations with simple indicators of sea-ice habitat availability, such as extent^{14–19}. This is due to krill recruitment processes being challenging to observe, occurring over large spatiotemporal scales^{5,20} and often under ice. Furthermore, the time series of remotely sensed sea-ice characteristics that influence these mechanisms is relatively short²¹. However, correlations with simple habitat indicators have limitations when being extrapolated beyond observed conditions.

Regional sea-ice environments will continue to change differentially in extent, timing and structure in response to climate change^{22,23}. Correlations with sea-ice extent indicate that habitat availability will decline in the future¹⁶, however changes in sea-ice quality, which underpin these correlations, may increase habitat availability²⁴. Explicitly quantifying sea-ice habitat quality is therefore important for understanding the impacts of changing environments on krill and on Southern Ocean ecosystems. An additional emphasis on winter processes emerges in relation to the krill fishery, as operations extend increasingly into the autumn/winter²⁵.

Variability in larval condition, survival and subsequent recruitment likely reflects larvae with differing life histories that have traversed different under-ice habitats²⁶. Here we hypothesize three drivers of variability in under-ice larval life histories:

1. overwinter transport
2. habitat presence and continuity, and
3. time-integrated habitat quality.

Using a state-of-the-art sea ice-ocean model, we compute overwinter larval back-trajectories and extract along-trajectory measures of sea-ice characteristics. We contrast our three drivers between recruitment success and failure events (1979-2016) across three distinct recruitment regions (Fig. 1):

1. the mid-west Antarctic Peninsula [wAP mid], which has shown clear relationships between recruitment and sea-ice dynamics^{27,28};
2. the Bransfield Strait [Bransfield], where complex oceanography²⁹ may obscure clear signals of environmental drivers^{30,31}; and
3. the eastern side of South Georgia [S. Georgia E.], which lies north of the sea ice zone and relies on inputs of krill from uncertain upstream source regions^{32,33}.

This analysis reveals potentially important overwinter habitats and spawning regions, many of which are currently under-sampled by observational programs. We also show that krill responses to sea ice environmental drivers are regionally variable and nonlinear, which may facilitate pockets of resilience to climate change while also carrying important implications for understanding environmental tipping points. These findings also support a conceptual model for explaining regional variability in sea-ice habitat drivers of recruitment.

Results

Overwinter transport

The overwinter environment encountered by krill larvae is likely highly influenced by advection. Larvae have minimal swimming capability³⁴ relative to the velocities of surface ocean currents and sea-ice drift, and the spatial scales over which these operate³⁵. These transport mechanisms demonstrate interannual variability, affecting the connectivity from productive source regions³⁶. To model the overwinter transport of krill recruits sampled during the Austral summer, we calculated Lagrangian back-trajectories for particles seeded at endpoints in each of the three recruitment regions. Following recent evidence³⁷, we advected particles using a combination of surface ocean and sea-ice velocities.

Over winter (Apr-Nov), particle locations differed in spatial extent and distribution between high and low recruitment years (Supplementary Fig. D.1), with differences being most evident at the beginning of winter. This highlighted concentrated “source regions” from which more particles originated in high

recruitment years compared to low (dark brown cells, Fig. 2). The most prominent source regions included the Amundsen Sea and continental shelf of the Bellingshausen Sea supplying the wAP mid region; the western Weddell Sea supplying the Bransfield region; and the Weddell-Scotia Confluence (WSC) and north-western Weddell Sea supplying S. Georgia E.

Habitat presence and continuity

Access to sufficient food is necessary for larval survival. Habitats characterised by distinct sea-ice qualities may play critical roles in this process by provisioning larval krill with adequate food over winter⁹. In the pack ice, food availability in the form of sea-ice algal communities at the ice-ocean interface is likely maximized in sea ice between 0.5-1 m thick³⁸. The marginal ice zone (MIZ) is also increasingly viewed as a food-rich habitat for larvae; here ocean swells perturb sea ice to release particulate organic matter and create horizontal slabs that facilitate larval feeding³⁷. The presence of the MIZ is represented by sea-ice concentration (between 9-92% for our model, as determined by a sensitivity analysis²¹). To model the availability sea-ice habitat along a trajectory, habitat presence was determined for each position of each advected particle using a conditional habitat filter: if either the condition for the presence of the MIZ (9-92% sea-ice concentration) or optimal sea-ice thickness (0.5-1 m) were met, habitat was determined to be present. Furthermore, we hypothesize that if a larva encounters habitat with sufficient continuity (Supplementary Appendix C), then they are less likely to starve (30-day starvation threshold).

Habitat covered a larger area in winters preceding high recruitment for all regions (Supplementary Fig. D.2), but habitat distribution varied depending on the timing of a particle's passage towards different recruitment regions (Supplementary Fig. D.3). For example, in the north-western Weddell Sea there was high probability of encountering habitat for larvae destined for S. Georgia E., but low probability for larvae that passed through the area later in the season destined for the Bransfield region.

The relative contributions of sea-ice concentration and thickness in driving habitat availability were explored (Supplementary Table D.1). For the wAP mid, high recruitment was preceded by an increase in habitat driven by both optimal MIZ and sea-ice thickness (from 8–30%). In the Bransfield region the same effect was observed, although the magnitude was less pronounced (from 18–23%). For S. Georgia E., the role of the MIZ in driving habitat declined slightly in favour of sea-ice thickness in high recruitment years (4% decrease and 3% increase, respectively). Spatially, habitat availability along the ice edge and Amundsen Sea appeared largely driven by the presence of MIZ, while optimal sea-ice thickness played a moderate role in determining habitat within the pack ice and along the shelf of the Bellingshausen Sea, and both drivers were important in the WSC (Supplementary Fig. D.4).

Sea-ice concentration (used to identify MIZ) diverged from optimal MIZ values when ice became too concentrated, while sea-ice thickness was often too thin to the west of the Antarctic Peninsula, and too thick to the east in the Weddell Sea (Supplementary Fig. D.5). High recruitment years occurred in the wAP mid and S. Georgia E. regions when sea ice in the Bellingshausen and Scotia Seas (respectively) became

thick enough. So, while sea-ice thickness may have moderate importance in overall habitat availability, thicker ice tends to create more habitat in high recruitment years.

Finally, examining habitat continuity (Fig. 3, Supplementary Table D.2) revealed that as the fate of particles was tracked through time, both the wAP mid and S. Georgia E. regions displayed higher proportions of continuous trajectories (larva remain within suitable habitat) in high recruitment years (Supplementary Fig. D.6). The origins of continuous trajectories (Fig. 3, Supplementary Fig. D.7) corresponded well to the source regions of particles in high recruitment years (Fig. 2), reinforcing the plausibility of these source regions as supplying viable larvae to their respective recruitment regions.

Time-integrated habitat quality

Given habitat presence, it can be further quantified in terms of quality. This is ecologically relevant in terms of individual fitness. Individuals that encounter higher quality habitat may recruit with a larger body size, increasing their feeding capacity and allowing them to take better advantage of the spring bloom. Increased fitness may reduce vulnerability to other sources of natural mortality. Habitat quality may therefore be an important predictor of a strong recruitment class. To model this, habitat quality was represented through a set of model-derived sea-ice characteristics that describe the theoretical mechanisms of how sea ice functions as an overwinter habitat for larvae and were found to be correlated to krill recruitment²¹. These characteristics comprised sea-ice concentration, thickness, log(ridging rate) and its standard deviation (indicators of dynamism); and difference between the mean and modal values of sea-ice thickness (mean-mode SIT, an indicator of rugosity). Together, these characteristics are indicators of mechanisms influencing habitat quality, such as optimal sea-ice thickness for the growth of ice algal bottom communities³⁸, sea-ice rugosity for refuge³⁹, and dynamism for the increased release of food particles^{31,37}. Time-integrated habitat quality was calculated by extracting these sea-ice characteristics and integrating them along each particle back-trajectory.

We compared the time-integrated habitat quality of particles across high and low recruitment years and continuous vs fragmented trajectories, allowing us to separate individual drivers of differences in larval life histories (Fig. 4, Supplementary Table D3). Amongst the continuous trajectories, particles supplying the wAP mid displayed the largest differences in time-integrated habitat quality between high and low recruitment years. By the end of winter, particles in high recruitment years experienced significantly higher sea-ice concentration, thickness and duration, and lower log(ridging rate) when compared to low recruitment years. In contrast, particles supplying the Bransfield region experienced significantly less sea-ice duration in high recruitment years. There were also weaker differences in the mean and mean-mode sea-ice thickness. Particles supplying S. Georgia E. experienced only one significant difference in time-integrated habitat quality (log(ridging rate)), yet qualitatively the distributions were similar. The opposing trend appeared when comparing amongst the fragmented trajectories (Supplementary Fig. D.8), with particles supplying S. Georgia E. displaying significant differences between high and low recruitment years across all sea-ice habitat characteristics.

Discussion

Our study uniquely explored the influence of time-integrated sea-ice habitat quality on larval krill recruitment. To achieve this, we used a high-resolution model to represent the sea-ice environment, as satellite observations of key habitat parameters are still in their nascent stages^{40–44}. This approach has yielded promising relationships that can inform studies using emerging remote sensing products and mesoscale *in-situ* observations. Our findings show that the ice-related environmental drivers of overwinter larval life histories (simulated as passive particles) have regionally variable impacts on recruitment; these are summarised in Table 1. By synthesizing this information alongside emerging evidence, we present a conceptual model of the environmental drivers of overwinter survival and recruitment for three regions across the southwest Atlantic (Fig. 5).

Table 1

A synthesis of environmental drivers of high recruitment years across three recruitment regions. Columns 2-4 can be read as an answer to the question “Which differences in this driver result in high recruitment years within this region?”. Abbreviations used: Weddell-Scotia Confluence (WSC), north-western Weddell Sea (nwWS)

Region	Transport	Habitat Availability & Continuity	Integrated habitat quality	Conclusion: What are the environmental drivers of high recruitment in this region?
1. wAP mid	High concentrations of source particles from the Amundsen Sea and coastal Bellingshausen.	More continuous habitat availability. This is driven by an increased number of trajectories passing through marginal ice zone in the Amundsen Sea and sea ice thickening towards optimal values in the Bellingshausen Sea.	Higher integrated habitat quality amongst trajectories that experience continuous habitat.	Higher recruitment is likely driven by increased habitat continuity and habitat quality over winter, particularly for larvae coming from the Amundsen Sea and continental shelf of the Bellingshausen Sea. Habitat availability in high recruitment years is driven by optimal sea-ice thickness.
2. Bransfield	High concentrations of source particles from the western Weddell Sea.	Small increases in habitat availability and continuity, which may be driven by increased sea-ice thickness along the wAP.	Moderate/weak evidence of differences in habitat quality for all trajectories.	The relationship between overwinter sea ice and recruitment are not as tightly coupled. The immigration of larvae from Weddell Sea into the Bransfield may be influential.
3. S. Georgia E.	High concentrations of source particles from the WSC and nwWS. In low recruitment years the origins of trajectories are more diffuse, causing more particles to traverse the open ocean away from sea ice habitat.	Increased habitat continuity. In low recruitment years, habitat becomes more fragmented due to more trajectories passing through open ocean and experiencing less sea ice.	Habitat quality is consistent amongst trajectories that experience continuous habitat.	Higher recruitment years see more larvae originate from the WSC (a known spawning region) and the nwWS (insufficient observations). However, trajectories from the nwWS experience the most continuous habitat of consistent quality. Poor recruitment may be driven by differences in transport that disrupt connectivity to source regions, and cause more trajectories to traverse more fragmented, poorer quality habitat.

In the wAP mid region, higher recruitment was preceded by an increase in particles originating from the Amundsen Sea and continental shelf of the Bellingshausen Sea. While the sparse sampling coverage in these regions limits validation from observations, our findings are corroborated by other modelling studies. A previous particle tracking study using ocean advection concluded that krill along the wAP have

local and remote origins, with the latter coming from the Bellingshausen Sea²⁷. The Amundsen Sea is located farther upstream, but is also a plausible source region, as including sea-ice transport can increase transport distance^{36,37}. The continental shelf of the Bellingshausen Sea has also been identified as potential spawning habitat^{45,46}, along with the Amundsen Sea³³. Therefore, the Amundsen and Bellingshausen Seas represent potential source regions for krill downstream along the wAP.

We also found that habitat availability, continuity and quality may drive both high and low recruitment years in the wAP mid region. Increased habitat availability was driven by the Amundsen Sea MIZ and a thickening of the Bellingshausen Sea pack ice towards optimum values to support ice algae. The importance of sea ice in the Amundsen and Bellingshausen seas is supported by correlations between large-scale physical forcings in these upstream areas, such as sea-ice timing and extent (and its governing climate modes), and wAP recruitment success^{27,28,47,48}. However, there are intriguing implications considering the context of sea-ice compaction events, where persistent north-westerly winds push sea ice towards the coastline resulting in extreme sea-ice thickening and ridging⁴⁹. During a compaction event, anomalously low krill growth rates were observed⁴⁹, which alongside our findings indicates that deviations from optimal conditions are likely very influential in this system. Indirectly, the associated lower sea-ice extent may exert a multi-year influence on recruitment, reducing summer phytoplankton availability^{50,51} for spawning krill and deteriorating the environment that pre-conditions a successful recruitment event¹³.

In the Bransfield region, we found weak connections between transport, habitat continuity and recruitment, and these two drivers highlighted different regions as providing larval habitat. Years with increased transport of particles from the north-western Weddell Sea to the Bransfield region demonstrated high recruitment. This agrees with another modelling study⁵², but does not match observations of low larval concentrations in water parcels originating from the Weddell Sea⁵³. Conversely, the Bellingshausen Sea supports particles with more habitat continuity in high recruitment years. Overall, findings in the Bransfield region are ambiguous, with few clear environmental drivers of recruitment success.

These weaker relationships could result from one or a combination of several processes. Firstly, our particle tracking simulations may not accurately capture the local retention of larvae in the Bransfield region, which possesses complex topography coincident with hydrographic fronts²⁹ that may act to retain larvae^{54,55}. Local larvae may furthermore be less reliant on sea-ice habitats for food, as recent observations and modelling studies show little influence of sea-ice extent or characteristics on abundance and recruitment in this area^{21,30,31}. This may be because the Bransfield region is located at a moderately-low latitude and receives sufficient wintertime light to sustain adequate pelagic primary productivity as well as heterotrophic food sources in the water column and benthos^{31,56}. Secondly, the Bransfield region may receive larvae with western and eastern origins due to the convergence of the Antarctic Slope Current in this area, which causes an influx of larvae regardless of ice cover³⁰. Larvae in

the Bransfield may therefore have a diverse set of life histories making it difficult to disentangle clear signals in environmental drivers.

In the S. Georgia E. region, high recruitment years were characterized by an influx of particles from two source regions: the WSC and the north-western Weddell Sea. For the former, analyses of net-sample data^{57–61} and habitat modelling^{33,46} provide strong evidence for suitable spawning habitat. Furthermore, forward-trajectory particle tracking shows that the WSC spawning grounds can be an important source of small krill observed at South Georgia^{62,63}, however this connectivity is highly variable^{36,64,65}. In some years, the smallest cohort arriving at South Georgia may reflect the influx of larger and potentially older krill that have spent a further winter under the sea ice in southern regions around the Antarctic Peninsula or in the southern Scotia Sea/Weddell Sea^{32,66,67}. Further south in the north-western Weddell Sea, limited observational data⁵⁷ suggests that it is not a major spawning region⁶⁸. In summary, our transport analysis supports the existing view that years of low recruitment at South Georgia may result from a disruption in the connectivity to source regions. We find that the WSC likely represents an important supply of recruits to South Georgia, while more validation is needed further south in the north-western Weddell Sea.

When along-trajectory sea-ice habitat continuity and quality are considered, our modelling results highlight the north-western Weddell Sea. This region represents the principal source of continuous trajectories reaching South Georgia, amongst which there was a striking lack of interannual variation in time-integrated habitat quality. This could be indicative of survivor bias, where krill arriving at South Georgia from the north-western Weddell Sea have all experienced consistently good habitat quality. This indicates that there is some ecological benefit to starting a journey to South Georgia from the north-western Weddell Sea, although this area may not support spawning krill. In contrast, our analysis did not detect continuous trajectories originating from the WSC – a known spawning habitat (see above). While continuous trajectories originating from the north-western Weddell Sea do pass through the WSC *en route* to South Georgia, particles originating from the WSC lack continuity due to differences in the timings of passage resulting from differences in points of origin. The lack of habitat continuity coming from the WSC may represent a type II error due to more influential sources of larval mortality occurring outside the time window when our habitat continuity rules were imposed, or sea-ice dynamics that would increase habitat continuity but are not captured in the model. Alternatively, this result may reflect real processes. Larval survival in the WSC may be decoupled from sea-ice habitat drivers due to alternate survival mechanisms⁵⁶, allowing them to successfully reach South Georgia regardless of habitat continuity. Larvae spawned in the WSC may also be locally-retained by fine-scale oceanographic processes over their first winter. This would enable them to capitalize on the ecological benefit of transiting to South Georgia via the north-western Weddell Sea the following winter.

Identifying environmental drivers of krill population dynamics is key to furthering our understanding of climate change impacts on Southern Ocean ecosystems. By integrating environmental conditions along back-trajectories, we are able to characterize the over-winter habitat encountered by an advected larva.

This individualized detail is important as it allows us to understand the spatially and temporally variable impacts of climate change in the Southern Ocean²³. Therefore our approach gives us insights at the scale necessary to investigate environmental drivers of larval krill overwinter survival and recruitment. Future studies could extend this work by exploring sensitivity to inter and intra-annual variability *e.g.*³³.

Our results indicate that recruitment responses to future changes in sea ice are likely to be regionally-variable and nonlinear. In the wAP mid region, high recruitment showed the strongest relationship to sea-ice variability. There is high uncertainty in how sea ice in the wAP mid and its upstream regions will change in the future, due to the interplay between counteracting thermodynamic forces causing sea ice to thin²⁴, as well as dynamically thicken²³. However recruitment in the wAP appears linked to sea ice that is “just right”, which would indicate that nonlinear relationships between habitat descriptors and their biological responses will be a critical consideration when extrapolating future responses to climate change. Recruitment in the S. Georgia E. region may have an altogether different response to climate change, as recruitment has been related to the connectivity with areas farther south^{10,32}, specifically the WSC and north-western Weddell Sea. Sea-ice habitat continuity along these trajectories is influenced by sea-ice extent and date of retreat in the Weddell Sea^{10,32,62}, but continuity may be less essential for the survival of larvae spawned in the WSC. Similarly, the Bransfield region may be less responsive to changes in sea-ice habitats, supporting previous suggestions that this region may provide a pocket of resilience to climate change²¹. Similar pockets of resilience may be occurring in other regions across the circumpolar range of krill^{69,70}. All these considerations are highly relevant to informing strategies for the sustainable management of the krill fishery in the context of climate change.

Our results reinforce the need to increase our observational capacity in key areas, particularly improving sampling coverage in potentially important spawning regions²⁵, as well as process studies targeting the nuanced relationship between larvae and sea-ice habitats in complex regions such as the Bransfield Strait³¹. Using high-resolution model output, we demonstrate how considering spatial and temporal changes in habitat can provide novel insights into larval habitat quality. This comes as many new environmental data projects are emerging, including models incorporating sea-ice biogeochemistry⁷¹, novel satellite observation products^{40–44} and mesoscale sampling methods of the sea ice zone *e.g.*^{72,73–76}. Furthermore, our capacity to sample krill population dynamics and distribution is improving with novel methods and technologies^{77–79}. As both observational and analytical approaches continue to improve, we are at the verge of quantifying environmental drivers of krill recruitment at ecologically relevant scales, which will be instrumental in projecting future krill population dynamics in a changing Southern Ocean.

Methods

Study area

This study focuses on the southwest Atlantic sector of the Southern Ocean and its oceanographic upstream regions (130° W to 25° W and 75° S to 50° S, Fig. 1). This area is ecologically relevant as a population centre for krill² and their dependant predators³. This sector also has the best sampling coverage of krill acoustics and net tows, most of which occur along the western Antarctic Peninsula (wAP) and South Georgia. Our study area extends to upstream regions including the Amundsen and Bellingshausen Seas, as previous analyses have indicated that sea ice in these regions may be linked to recruitment of krill along the wAP²¹.

Data description

Regional recruit density

To compare between years that experienced high vs low krill recruitment, time series of regional recruit density were obtained from²¹. These were calculated from the KRILLBASE density⁸⁰ (see <https://www.bas.ac.uk/project/krillbase/>) and length measurement databases, as well as krill length measurements from the Palmer LTER study region spanning 2009-2016⁸¹. Briefly, these density and length measurements were filtered and binned into nine hexagonal regions across the southwest Atlantic see Fig. 1 from²¹. For each region and sampling season (October 1st of previous calendar year to May 31st), Gaussian mixture distribution models were fit to the length frequency data to determine the proportion of 1-year-old krill in the population (R_1). R_1 was then weighted by the average density to yield recruit density.

We focussed our analysis on the three best-sampled regions: wAP mid, Bransfield and S. Georgia E. These regions also represent three different regional types across the range of high-krill density areas in the southwest Atlantic, where we expect different processes to be driving recruitment variability. The wAP mid region encompasses the Palmer LTER study region within which many links between recruitment and sea ice dynamics have been found^{27,28}, whereas the Bransfield region is characterised by complex oceanography²⁹ which could influence larval advection, causing signals between environmental drivers and biological processes to be less clear. The S. Georgia E. region on the other hand is north of the sea ice zone. Krill here are thought to rely on inputs of krill from upstream source regions^{32,68}, however the precise mechanisms behind this are unclear⁶⁶. Therefore, we expect to find different drivers of recruitment variability across our different recruitment regions. The time series of regional recruit density within these regions were then nominalized into high and low recruitment years using a cluster analysis for a more robust approach (see Supplementary Appendix A).

Ocean-sea ice model

We selected an ocean-sea ice model "COCO" v4.0⁸² (hereafter "the model") with an ice shelf component⁸³. The spatial resolution varies with latitude from 5.5 km at 75° S to 14.5 km at 50° S and output is at a daily temporal resolution. The hindcast simulation is run from 1979-2018 forced by atmospheric surface boundary conditions from the global atmospheric reanalysis ERA-Interim⁸⁴. The model has been tuned to

the Southern Ocean, and reproduces trends and sea-ice variability⁸⁵⁻⁸⁷ as well as spatial patterns of sea-ice thickness^{21,87} consistent with satellite observations. Therefore, this model is highly suited to simulate the physical ocean-ice environment within our study area.

We used model-derived sea ice and ocean variables from 1979-2016. To support our calculation of particle back-trajectories (Analysis step 1), modelled values of sea ice and near-surface ocean (depth averaged from 0-22.5 m) velocities were extracted in both daily and monthly timesteps. To estimate along-trajectory habitat presence and quality (Analysis steps 2-3), daily model outputs of sea-ice concentration, sea-ice thickness, and ridging rate were also used.

Analysis

Our analysis consisted of three steps that map directly to our aims. To test the robustness of our results to our analytical choices, sensitivity analyses were performed (Supplementary Appendix B).

Step 1: Simulating larval transport over winter

A total of 421 particles were seeded across the three recruitment regions. The locations of the seeded particles corresponded to the model's native grid. As the grid had a finer resolution towards the coast, particles were seeded every fourth grid cell for the WAP mid and Bransfield regions, and every third for the S. Georgia E. region. This resulted in a comparable number of particles (176, 122 and 123 respectively) in each region. For each winter from 1979-2016, Lagrangian back-trajectories were calculated for each particle following the method of ⁸⁸, starting on Julian day 330 and ending on day 90. The simulation was updated in 12h timesteps, with one timestep being advected with monthly-averaged sea ice velocity fields, and the second advected with monthly-averaged ocean surface current velocity fields. When sea ice was not present the particle was advected with ocean surface currents for both timesteps. The position of each particle was recorded every 10 days to thin the data. Short trajectories that ran aground before Julian day 182 were removed (30% of all trajectories over all the years).

Step 2: Quantifying along-trajectory sea-ice habitat presence and continuity

To model the availability and continuity of sea-ice habitat along a trajectory, we applied a conditional habitat filter with continuity rules designed to represent the sea-ice characteristics that support food availability for larvae (summarized in Supplementary Fig. B.2). Habitat was determined to be present if either of the following habitat conditions were met: (1) if the sea-ice thickness was between 0.5-1 m thick to support the growth of ice algal bottom communities³⁸; or (2) if the MIZ was present, as previous observations indicated that the MIZ supports higher larval growth through increased food availability compared to the open ocean and pack ice³⁷. The MIZ was defined by ²¹ for the model as between 9-92% sea-ice concentration using a sensitivity analysis to match passive microwave sea-ice concentration observations. The presence or absence of habitat was then determined for each recorded particle position.

Using this conditional habitat filter to determine habitat presence, we applied a set of continuity rules to assess which trajectories possessed sufficient habitat continuity to support a larva's survival. Observations of low larval growth rates indicate that the early winter may be less critical for providing food (Supplementary Table 1 in ³⁷, and ⁸⁹), as light remains too low to support photosynthesis^{9,38}. Therefore after an initialization period preceding Julian day 182, trajectories that experienced an absence of habitat for more than a 30-day starvation threshold⁸ were classified as "fragmented" after that event. This habitat filter coupled with continuity rules allowed us to mechanistically incorporate the biological importance of habitat continuity into our analysis. Special exemptions to the continuity rules were made for particles destined for South Georgia, which are detailed in Supplementary Appendix C.

Step 3: Time-integrated habitat quality

The explicit comparison of differences in particle life histories requires estimating the along-trajectory environment of each particle and inferring habitat from that environment. To obtain estimates of the environment, for each recorded particle position (*i.e.* 10-day interval) we extracted model estimates of sea-ice concentration, sea-ice thickness and log(ridging rate) for that day and location. Sea-ice concentration was also used to calculate duration, represented as the number of days since ice advance as defined by ⁹⁰ at the time the particle passed through that grid cell. We also calculated additional variables from the surrounding 3x3 matrix of model grid cells for each position: the standard deviation of the log(ridging rate); and mean-mode sea-ice thickness. To summarise the habitat quality experienced by a larva over winter, for each trajectory we integrated each sea-ice characteristic with respect to time. For each region and sea-ice characteristic, we tested whether there was a significant difference in the time-integrated values between high and low recruitment years using a permutation test. For each permutation, the group allocations of each value were randomly resampled, and the resulting absolute difference between the new group means was recalculated. For each test, 500 permutations were run.

All analyses were carried out in the R statistical computing environment⁹¹. The *SOMap* package⁹² was used to produce Fig. 1, *Inkscape: Open-Source Scalable Vector Graphics Editor* (<https://inkscape.org/>) was used to produce Fig. 5, and the *ggplot2* package⁹³ was used for the rest of the manuscript and supplementary figures unless otherwise indicated.

Declarations

Data Availability

Regional recruit density time series are available from the corresponding author upon request. The KRILLBASE density data are freely available (<https://www.bas.ac.uk/project/krillbase/>). KRILLBASE length frequency data are available from the British Antarctic Survey by request (contact: Simeon Hill, sih@bas.ac.uk), and the Palmer LTER length frequency data are available online (<https://doi.org/10.6073/pasta/be42bb841e696b7bcad9957aed33db5e>). Ocean-sea ice model output

are available from K.K. upon request (kazuya.kusahara@gmail.com). The code relating to this study is available from the corresponding author upon request.

Code Availability

The code relating to this study is available from the corresponding author on request.

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Contributions

All authors contributed to conceptualization, formal analysis, interpretation of results and writing. S.C., S.B., S.K., K.M. and E.M. contributed to the supervision of D.V.. K.K. developed the sea-ice ocean model used in the analysis.

Competing interests

The authors declare no competing interests

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Figures

Figure 1

Map of study area and recruitment regions. Red hexagons indicate the regions for which indices of krill recruitment were calculated²¹, and are labelled internally with their region name as referred to in the main text. Black text indicates seas (standard font) and geographical features (*italics*).

Figure 2

Difference in particle locations at the start of winter between high and low recruitment years. For each region, year and particle, the location of the particle on April 1 (*i.e.* the beginning of winter and end of the back-trajectory simulation) was binned to an equal-area 150 km by 150 km grid. The spatial average of the binned counts was taken over all the years classified as high or low recruitment, yielding an annual average. The map displays the difference, with cells coloured in brown indicating that more particles originated from that cell on April 1 in high recruitment years as opposed to low. The binned counts were capped at their 5th and 95th percentiles. Red hexagons indicate the recruitment region where the particles for the back-trajectories were seeded.

Figure 3

Maps display average duration of continuous habitat for simulated larvae trajectories. For each trajectory, the duration of continuous habitat was calculated according to the continuity rules (Supplementary

Appendix C). This value was assigned to the trajectory location at the start of winter on April 1 (*i.e.* the end of the back-trajectory). All start locations were binned to an equal-area 150 km by 150 km grid and for each grid cell, the average continuous habitat duration for all trajectories was calculated. The purple-orange colour ramp shows this average duration if this was less than the duration of the simulation. Yellow cells indicate that on average, habitat remained continuous for the entire simulation (*i.e.* over the entire winter from day 90 to 330). Conversely, black cells indicate that trajectories immediately became fragmented as soon as continuity rule 1 was enacted. Red hexagons indicate the recruitment region where the particles for the back-trajectories were seeded.

Figure 4

The distributions of time-integrated habitat quality for continuous trajectories. Panel a provides an example of the integration of sea-ice characteristics with respect to time; here for sea-ice thickness in the wAP mid region. Each individual trajectory is represented by a line. The distributions of the resulting

cumulative values of the trajectories at the end of the simulation (violin plots) are then displayed in Panel **b** for all regions and sea-ice variables, and the relationship between the two figures is indicated by the red arrows. The differences between the distributions for high and low recruitment years was tested using permutation tests (500 permutations for each test). Significant differences are indicated by the horizontal bars, with increasing numbers of asterisks indicating increasing confidence. Results from the permutation tests can be found in Supplementary Table D.3. Abbreviations used are as follows: sea-ice concentration (SIC), sea-ice thickness (SIT), ridging rate (RR) and standard deviation (sd).

Figure 5

Conceptual model of sea ice overwinter habitat driving high krill recruitment. This conceptual model synthesizes our novel findings and hypotheses for how overwinter habitat influences larval overwinter survival and recruitment. Here we depict environmental drivers of recruitment for three recruitment

regions (red hexagons, Fig. 1) as described in Table 1. Transport pathways (yellow arrows) connect sources regions (salmon) to recruitment regions (red hexagons) along regions with habitat continuity (translucent orange). Habitat availability is driven by a combination of MIZ (stippling) and optimal sea-ice thickness (vertical stripes). High pelagic chlorophyll ($>1 \text{ mg chl m}^{-3}$) north of South Georgia (reproduced from Supplementary Fig. C.1), allows us to infer larval survival if larvae emerge from the sea ice on or after Julian Day 210 (habitat continuity rule 3, Supplementary Appendix C).

Supplementary Files

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