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Antarctic krill recruitment in the south-west Atlantic sector of the Southern Ocean

by

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Abstract

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ANTARCTIC KRILL RECRUITMENT IN THE SOUTH-WEST ATLANTIC SECTOR OF THE SOUTHERN OCEAN

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Antarctic krill are a key component of the Southern Ocean ecosystem and support a variety of predators as well as an expanding commercial fishery. Yet, despite the ecological and economic importance of krill, crucial aspects of their recruitment are not understood. We need greater understanding of these processes in order to predict and model their population dynamics in the light of growing anthropogenic pressures. This thesis identifies three knowledge gaps in krill reproduction and, through mapping, modelling and laboratory experimentation, provides new insights into these research areas. The area of study is the south-west Atlantic sector as it contains the highest densities of krill, key krill spawning grounds and has supported the entire krill fishery since the mid 2000's. By generating distribution maps of six life stages of Antarctic krill, I identified key hotspots of egg production and nursery areas for larval krill along the Southern Scotia Arc. These maps showed that, although adult krill are widely distributed, the location of eggs, nauplii and metanauplii are mainly restricted to shelf and shelf-slope regions, partitioned spatially from the oceanic distributions of calyptopes and furcilia. By conducting a series of laboratory experiments, I identified the point at which temperature induces hatch failure and nauplii malformations in krill embryos. Hatching success decreased markedly above 3.0 °C, and the percentage of malformed nauplii reached 50 % at 5.0 °C. Furthermore, hatching success was variable and low (mean 27 %) between females. To further understand the whereabouts of spawning at the Antarctic Peninsula, and to test the hypothesis that krill migrate off-shelf to spawn, I conducted a seasonal analysis of adult krill size classes in relation to environmental variables. Contrary to the current paradigm, I found the adult krill population does not migrate on mass to off-shelf waters (>1000 m depth) to spawn their eggs. Instead all length categories of adult krill appear in reliably high concentrations ~ 75 km before the shelf break throughout the spawning season, where temperatures are lower and food availability is higher, potentially increasing growth and spawning potential. This information provides a more holistic view of krill spawning, reproduction and recruitment within the south-west Atlantic sector and provides policy makers with better information on which to base future krill fishery management decisions.

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Research Thesis: Declaration of Authorship

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I declare that this thesis and the work presented in it are my own and has been generated by me as the result of my own original research.

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Definitions and Abbreviations

Abbreviations	Definition/description of the term
ACC	Antarctic Circumpolar Current
AIC	Akaike Information Criteria
AMLR	Antarctic Marine Living Resources
ArcGIS	Arc Geographic Information System
BAS	British Antarctic Survey
BIOMASS	Biological Investigations of Marine Antarctic Systems
CAMLR	Conservation of Antarctic Marine Living Resources
CCAMLR	Commission for the Conservation of Antarctic Marine Living Resources
CDW	Circumpolar Deep Water
Chl-a	Chlorophyll-a
COG	Centre of Gravity
CPR	Continuous Plankton Recorder
CTD	Conductivity, Temperature, Depth
DVM	Diel Vertical Migration
ENSO	El Niño Southern Oscillation
FIBEX	First International BIOMASS Experiment
GAM	Generalised Additive Model
GEBCO	General Bathymetric Chart of the Oceans
GLM	Generalised Linear Model
GLOBEC	Global Ocean Ecosystems Dynamics
MIZ	Marginal Ice Zone
MPA	Marine Protected Area
OC-CCI	Ocean Colour Climate Change Initiative
RMT	Rectangular Midwater Trawls
RRS	Royal Research Ship
SAM	Southern Annular Mode
SCAR	Scientific Committee on Antarctic Research
SIBEX	Second International BIOMASS Experiment
SKAG	SCAR Krill Action Group
SST	Sea Surface Temperature
VIF	Variance Inflation Factors
WAP	Western Antarctic Peninsula

Chapter 1 Introduction

1.1 Introduction

The unique polar marine ecosystems in the Arctic and Antarctic are defined by cycles of sea ice, extreme changes in photoperiod and cold temperatures. Organisms adapted to these polar ecosystems are often stenothermal and have life cycles closely associated with sea ice. Consequently, these unique polar food webs are under increasing pressure from rapid ice loss and climate change (Moffat and Meredith, 2018). In both the Antarctic and sub-Arctic food webs, euphausiids are highly abundant and an important food web component (Mauchline, 1980). Euphausiids are a pelagic crustacean taxa with high grazing rates and lipid contents and with active behaviour, often involving horizontal and vertical migration. They are a pivotal prey item for many higher predators and are also key to biogeochemical cycling and carbon export in marine ecosystems (Everson, 2000; Pakhomov et al., 2002; Nicol et al., 2010; Hill et al., 2012; Atkinson et al., 2014; Schmidt et al., 2016; Siegel and Watkins, 2016b; Cavan et al., 2019). This is exemplified by the case of the euphausiid species *Euphausia superba* (Antarctic krill) in the Southern Ocean. The following introduction briefly summarises the biology of Antarctic krill (section 1.2), and some of the key impediments to understanding how climate change and fisheries management (section 1.3) may affect recruitment. This thesis particularly focuses on the process of recruitment (i.e. the year class strength) in Antarctic krill, defined as the degree of survival during the first year of life (Hjort, 1914). Section 1.4 describes the distribution of krill life stages and exemplifies the importance of the study area I have chosen for my thesis (the south-west Atlantic sector of the Southern Ocean (Figure 1)). Section 1.5 assesses how the environment influences the development of krill embryos. Section 1.6 outlines current knowledge regarding horizontal spawning migrations of krill and how they relate to krill recruitment. Finally, section 1.7 identifies the key outcomes of this thesis as framed by this introduction and the key questions that have been asked.

1.2 Antarctic krill and the Southern Ocean ecosystem

The Southern Ocean comprises ~32 million km^2 of habitat south of the 60 ^{o}S. Ecosystem services provided by the Southern Ocean include: fishery products, nutrient cycling, climate regulation and maintenance of biodiversity (Grant et al., 2013a). Many of the ectotherms within the Southern Ocean are stenothermal and their biological functions are extremely sensitive to temperature changes (Peck et al., 2004). Some of these species also have life cycle traits associated with sea-ice, an important habitat and a source of food, especially during the long austral winters (Smetacek et al., 1990; Eicken, 1992). However, global climate warming is causing complex ocean changes

(Doney, 2010; Hoegh-Guldberg and Bruno, 2010; Pörtner et al., 2019). During the past century, the Southern Ocean system has experienced rapid environmental change, including significant regional fluctuations in sea ice, decreases in ocean pH, ocean warming and variation in sea surface and air temperature (Orr et al., 2005; Stammerjohn et al., 2008, 2012; Whitehouse et al., 2008; Hobbs et al., 2016; Jones et al., 2016; Moffat and Meredith, 2018). Observations have shown a significant strengthening of Southern hemisphere westerlies (Saenko et al., 2005; Fyfe and Saenko, 2006) due to Antarctic ozone depletion. These strong westerlies and positive Southern Annular Mode (SAM) phases (Lovenduski and Gruber, 2005; Cai, 2006) have increased both the poleward transport of heat through the Upper Circumpolar Deepwater, and a southward migration of the ACC front (Gille, 2002). This has led to changes in circulation patterns in the Southern Ocean, a reduction in sea ice, and decreases of both water column stability, and phytoplankton biomass (Saba et al., 2014). Furthermore, there is an increasing trend for a positive SAM, which in turn is amplifying the effect of the El Niño Southern Oscillation (ENSO) at higher latitudes (Murphy et al., 2007; Whitehouse et al., 2008). Combined, these climatological factors are likely to have a strong impact on the biological components of this polar ecosystem (McGowan et al., 1998; Stenseth et al., 2003).

Antarctic krill (*Euphausia superba*) (hereafter “krill”) are a keystone species within the Southern Ocean ecosystem, in that they dominate pelagic biomass and are a major route through which energy passes from primary producers to higher trophic levels (Murphy et al., 1988; Loeb et al., 1997; Voronina, 1998). Originally described in 1850 by James Dwight Dana, krill is endemic to the Southern Ocean where it is predominantly found in the upper 200m over shelf-slope areas and in oceanic waters south of the Polar Front in the Southern Ocean. The northerly range limit of krill is the Polar Front, while to the south, krill are limited by the Antarctic coast (Cuzin-Roudy et al., 2014). There are five other species of euphausiid found within the Southern Ocean, namely *Euphausia crystallorophias, Euphausia frigida, Euphausia triacantha, Thysanoessa macrura* and *Thysanoessa vicina*. These species are associated with different primary habitats although there can be considerable overlap with the habitat of Antarctic krill.

In terms of dry mass, krill have the highest biomass of any species in the Southern Ocean, and are major filter feeders, second only to the total copepod group (Voronina, 1998). This high biomass, combined with their high lipid content, makes them an important food source for numerous predators (Grantham, 1977; Croxall et al., 1999; Reid et al., 2005; Trivelpiece et al., 2011; Braithwaite et al., 2015). Krill are flexible in their feeding habits and are an omnivorous species (Schmidt et al., 2014). Krill feeding strategies vary from zooplankton predation (Price et al., 1988; Huntley et al., 1994), to scouring algae from under-ice habitats (Marschall, 1988; Stretch et al., 1988) and feeding on the benthos (Kawaguchi et al., 1986; Gutt and Siegel, 1994) but they particularly thrive feeding on diatom blooms (Pond et al., 2005).

Krill have a complex multiyear life cycle (Siegel, 2000). This begins with gravid females spawning during the austral summer, from which their eggs sink to ~850 m whilst the embryo develops, a process known as the descent-ascent cycle (Marr, 1962; Quetin and Ross, 1984). Larval krill emerge from eggs roughly six days after spawning in the first nauplius stage and begin their ascent to surface waters (Quetin and Ross, 1984). Once at the surface, they reach the first feeding stage, calyptopes 1, and begin to feed on any available microplankton and continue to do so for the rest of summer and early autumn. During the autumn, the krill reach the furcilia stage, the state in which they spend their first winter. Krill larvae progress through 12 instars (larval stages) during their first year before moulting into post-larval juveniles at about one year (Jia et al., 2014). After spawning, both females and males regress to a less developed adult form (McWhinnie and Denys, 1980; Denys et al., 1981) in which state they spend the autumn and winter before re-maturing for the following spring and summer seasons (Ross and Quetin, 2001). In the natural environment, krill can reach up to six to seven years of age (Siegel, 2005).

Krill life stages must be able to exploit food sources when they are available as for much of the year, the pelagic Southern Ocean is oligotrophic. Adult krill have adopted multiple strategies to cope with reduced food availability including body shrinkage, protein catabolism and use of their lipid reserves laid down during periods of high food availability (Ikeda and Dixon, 1984; Quetin and Ross, 1991; Virtue et al., 1993; Hagen et al., 2001). During the spring, the melting ice edge (Marginal Ice Zone (MIZ)) creates conditions that allow elevated primary production (Arrigo et al., 1998). The timing of the sea-ice melt and resultant abundance of food fuels the maturation, mating and spawning behaviour in adults (Cuzin-Roudy and Labat, 1992; Ross and Quetin, 2001; Holm-Hansen et al., 2004). Krill larvae have low lipid contents compared to adults and therefore, must have access to food throughout their first year to avoid perishing (Quetin and Ross, 1984). The fitness of larval krill depends on their ability to over-winter in a suitable sea ice habitat. Initially, winter sea ice was thought to provide the required over-wintering conditions for larval krill (Quetin et al., 2003, 2007; Ross et al., 2004; Siegel, 2005). Meyer et al. (2017) have shown that, although the sea ice does provide shelter from predators for the over-wintering larvae, only the open MIZ provides a favourable food environment for high larval growth rates.

Krill habits and behaviour are critical to food acquisition. Specifically, krill are known for their schooling behaviour, which contributes towards successful food acquisition, as well as predator avoidance and reproduction (Priddle et al., 1990; Watkins et al., 1992; Olson et al., 2016). The nature of krill swarms varies from small densely packed aggregations to super swarms measuring >100 km^2 (Mathisen and Macaulay, 1983; Tarling et al., 2009). Tarling et al. (2009) suggest that young krill are predominantly found in large tightly packed swarms, and that, as krill mature, they are found in smaller less dense swarms. They also suggest that these patterns are modulated by food availability and light levels. The main entrainment cue for cycles of krill maturity and metabolic activity is photoperiod which can adapt to prevailing levels of food availability and temperature (Ikeda and Thomas, 1987; Kawaguchi et al., 2007; Teschke et al., 2007, 2008; Brown et al., 2011, 2013; Bahlburg et al., 2021).

Migration is also a key krill behaviour. Krill undertake three forms of vertical migration: the descent-ascent developmental cycle (see above), diel vertical migration (DVM), and seasonal vertical migration. The process of DVM is where organisms move deeper in the water during the day to avoid visually oriented predators in the day and move towards the surface at night to feed (Gliwicz, 1986). Within this cycle, they may also make vertical feeding forays (Tarling and Thorpe, 2017). Seasonally, krill in the late autumn have a tendency to swim down more than up (Kane et al., 2018) and overwinter at greater depth (Lascara et al., 1999). Krill use both DVM and swarming behaviour as a dual strategy of predator avoidance (Sainmont et al., 2013). Krill are also thought to undertake two types of horizontal migrations. Firstly, a winter contraction of their range so they are closer to the Antarctic continent, and second an off-shelf spawning migration so their eggs are released over deep water (Kanda et al., 1982; Siegel, 1988; Lascara et al., 1999; Atkinson et al., 2008., ; Venables et al., 2012).

1.3 Krill fisheries management, climate change and recruitment

The first experimental krill fishing occurred in 1962 and a commercial krill fishery began in earnest in the 1970’s (Nicol and Endo, 1999). In 1980, the Conservation of Antarctic Marine Living Resources (CAMLR) convention was signed by Antarctic treaty countries in response to international concerns about the rapid expansion of an unregulated Antarctic krill fishery, and its impacts on the health of the Southern Ocean ecosystem. Within the CAMLR convention, requirements were made for the sustainable harvesting of target species as well as the protection of non-target species which would be potentially impacted by harvesting (CCAMLR, 1982). Historically the Commission for the Conservation of Antarctic Marine Living Resources (CCAMLR) have managed the Antarctic krill fishery with a focus on the protection of the highest trophic levels such as penguins and other land breeding predators, and the Antarctic krill fishery, with little consideration given to the Antarctic krill population. However, the heterogeneous nature of the Antarctic krill population and the area intensive nature of the fishery means that the krill fishery could be having a greater impact on the Antarctic krill population than expected (Meyer et al., 2020; Watters et al., 2020). This is especially true if there is an overlap between the location of intense fisheries activity, and where the potentially spatially restricted proportion of Antarctic krill successfully spawn (Meyer et al., 2020).

To implement the CAMLR convention, CCAMLR uses an ecosystem-based management scheme. For the CCAMLR management strategy to work effectively in the future with a focus on protecting the

Antarctic krill population itself, it must be able to evolve with the growth and habits of the Antarctic krill fishery and the effects of global climate change (Zhang, 2007). Currently, the Antarctic krill component within the ecosystem-based management scheme is implemented using a Generalised Yield Model (Kinzey et al., 2013). Within this model, recruitment (i.e. the chain of events leading from reproduction to one-year-old post-larvae) is a key factor. However, present understanding of the process of recruitment in Antarctic krill is far from complete and requires further research, particularly with regards to the potential impact of climate change (Murphy et al., 2007; Atkinson et al., 2012; Flores et al., 2012; Hill et al., 2013; Meyer et al., 2020).

There is particular concern about how climate change will affect krill recruitment. Krill are known to have highly episodic recruitment, that can cause inter-annual oscillations in densities to fluctuate by over an order of magnitude (Quetin and Ross, 2003; Fielding et al., 2014; Ross et al., 2014). These variations in recruitment are thought to be driven by intraspecific food competition but modulated over large scales by climatological factors (Ryabov et al., 2017). Within the Atlantic sector of the Southern Ocean, years with positive SAM anomalies precede those of reduced recruitment (Atkinson et al., 2019). Whereas strong cohorts of krill larvae appear to be dependent on high summer phytoplankton biomass which, at the Antarctic Peninsula, occurs once every four to six years and is associated with negative phases of the SAM (Saba et al., 2014). Positive phases of SAM are associated with warmer temperatures, increased cloud cover, greater wind speeds and less sea ice, conditions that are less suitable for phytoplankton production, krill egg production and larval survival (Steinberg et al., 2015).

Further understanding of the spatial and temporal processes that affect recruitment will enable better predictions of how krill population dynamics will interact with increasing pressures from both the expanding fishery and ongoing climate change. This information will also help understand the current discrepancy between the number or larval recruits recorded from field observations and the numbers required to support the krill population (Kinzey et al., 2015). These discrepancies must be resolved for us to be able to calculate absolute recruitment from krill recruitment indices (Meyer et al., 2020).

1.4 Krill distribution and the importance of the south-west Atlantic sector

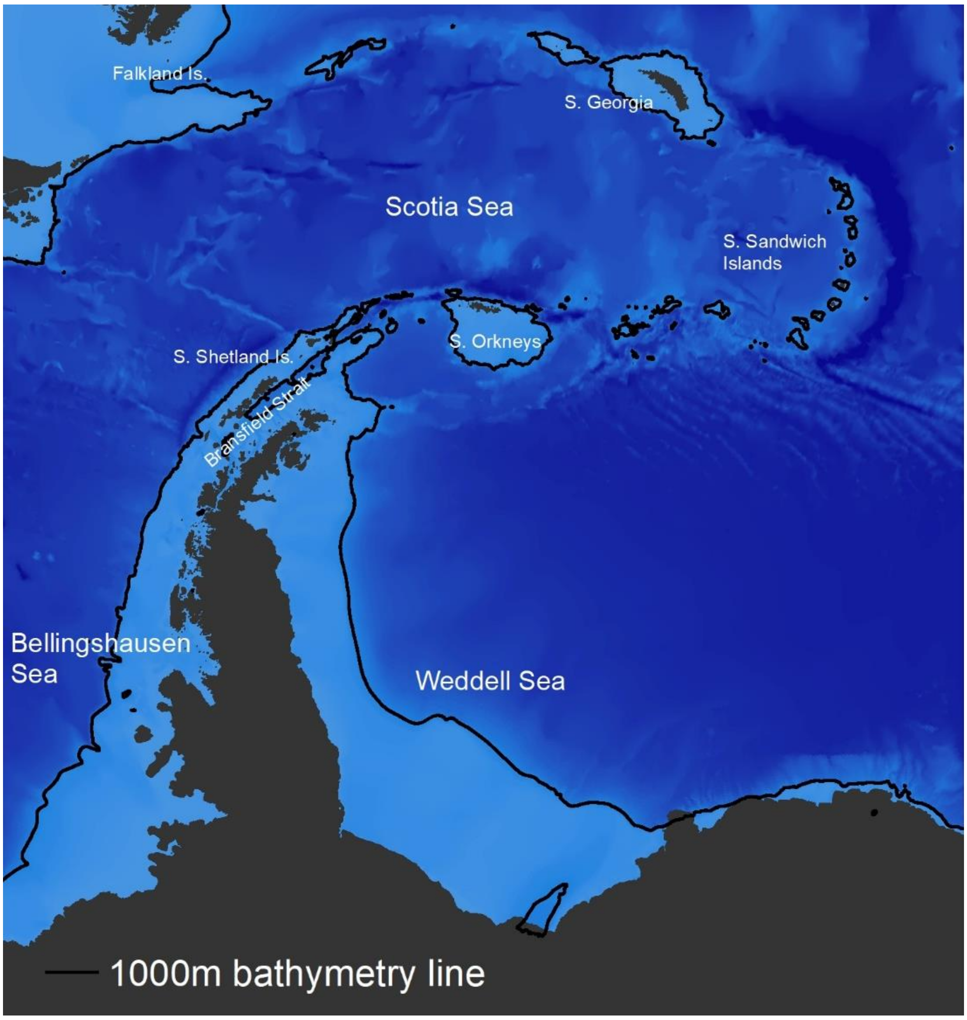

Figure 1. Map of the south-west Atlantic sector showing some of the major landmarks within this area.

The first sustained scientific efforts to understand krill ecology were the *Discovery Investigations*. These were a series of research cruises carried out mainly between 1926 and 1939 and were paid for by whaling levies. Much of the krill data collected from these cruises were published and continue to provide baseline knowledge of krill populations (Fraser, 1936; Marr, 1962; Mackintosh, 1972, 1973). Using the *Discovery Investigation* krill net data, Mackintosh (1973) mapped out suitable krill habitat within the Southern Ocean, which measured 19 million km^2. Subsequent acoustic surveys suggested that krill habitat was in fact much smaller in area (Nicol et al., 2000a; Siegel, 2005). Yet support for Mackintosh's (1973) original figure was later reinforced when 90 years' worth of net samples were summarised by Atkinson et al. (2009).

The first consideration of circumpolar density distributions of krill was made by (Marr, 1962) using net data collected during the *Discovery Investigations*. Maps were generated for each of the major life stages of krill and highlighted the pronounced asymmetry of all krill life stage distributions throughout the Southern Ocean. Since the 1960's, numerous surveys have created further distribution maps of krill life stages (Hempel, 1979; Hempel and Hempel, 1982; Hosie et al., 1988; Siegel, 1989; Daly, 1990b; El-Sayed, 1994; Ichii et al., 1998; Constable et al., 2000; Siegel et al., 2013; Skjoldal et al., 2013). However, the difficulty and expense of carrying out research in the Southern Ocean has meant that the distribution maps generated by these studies are either limited in space or time. Consequently, detailed, large scale maps updating Marr's initial distributions of larval life stages remain to be developed. On the other hand, post-larval distribution maps have been more recently updated firstly by Atkinson et al. (2004), and more recently by Yang et al., (2020).

Marr (1962) was the first to surmise that the main population centre of krill is found in the Weddell-Scotia Sea and that poor krill habitat is found east of 30 °E, and this was supported by findings of Mackintosh, (1973). Using post-larval data from 1926 - 2004, Atkinson et al. (2008) quantified this asymmetry, with three quarters of the stock calculated to occupy one quarter of the longitudinal extent of Antarctica. A more recent study by Yang et al., (2020) hypothesised that due to rapid deterioration of krill habitat suitability in the Atlantic sector, the circumpolar distribution of krill has become more even. The concentration of krill within the Antarctic-Bellingshausen sector was previously considered to be eight times that found in other areas of the Southern Ocean, but in this century, krill densities are only twice as high in this sector (Yang et al., 2020).

The concept of a krill decline in the south-west Atlantic sector has, however been a topic of debate (Cox et al., 2018, 2019; Hill et al., 2019) that is as yet unresolved. Nevertheless, there is no question that this sector is an important area for the krill population. It contains the highest population densities of krill throughout the Southern Ocean and supports the entire krill fishery (Grant et al., 2013b). The highest densities of krill in this sector occur around the main island groups: South Georgia, South Shetlands Islands, South Orkneys Islands, areas which also experience the most intense fishing (Grant et al., 2013b). High densities of krill are also associated with shelf break areas (1000m depth as defined by (Atkinson et al., 2008)) a trend reflected by the location of fishing vessels (Trathan et al., 2003). Yet, given the relatively small area of shelf waters in Antarctica, it was estimated that only 13% of the total krill population inhabit waters over shelf/shelf break areas with the remaining 87% found in deep oceanic waters (Atkinson et al., 2008).

While these overall distributions of post-larval krill in the Southern Ocean are well documented, that of the individual life stages is not. To gain a better understanding of the population dynamics of krill and the distribution of krill spawning, it is necessary to understand the distribution of the different life stages. The larval stages in the Southern Ocean appear in different quantities and in different places (Siegel, 2016). However, both calyptopis and furcilia tend to be found in higher densities within the south-west Atlantic sector. Once larvae reach the surface, they can be affected by surface currents (Siegel, 1988; Fach et al., 2002; Piñones et al., 2013) can be localised, or can be major large-scale flows such as the Antarctic Circumpolar Current Front (ACC) (Hofmann et al., 1998). The redistribution of krill larvae via transport by surface currents which can lead to increased or decreased connectivity between populations, an effect that can change with season and location (Piñones et al., 2016; Conroy et al., 2020). Yet, as outlined above our knowledge of the distributions of larvae and mature females within the Southern Ocean is limited compared to that of total post-larval distributions. Further detailed large scale distribution maps of multiple life stages must be generated in order to gain a better understanding of where the spawning populations are and where successful krill recruitment occurs.

Currently, only a series of single survey-based, localised maps are available for the distribution of gravid females (Hosie et al., 1988; Ichii et al., 1998; Flores et al., 2012) and early life stages (Hempel, 1979; Hempel and Hempel, 1982; Hosie et al., 1988; Daly, 1990a). This information is valuable from a management perspective as it provides detailed understanding of where spawning might occur in localised areas. However, to understand krill spawning at both a circumpolar level and within individual sectors, the distributions of gravid females and early larval stages must be synthesised across multiple surveys. This will ultimately provide a better understanding of krill reproduction and the mechanisms leading to a change in krill distribution from an asymmetric circumpolar distribution to the current more even circumpolar distributions, and how this may change in the future.

1.5 Female maturation, spawning and embryonic success

Spawning occurs when gravid females release their eggs. The number of eggs in each brood is proportional to female body length (Denys and McWhinnie, 1982; Cuzin-Roudy, 2000), and thus larger females are more fecund. Female krill can reproduce in their second year. However, females that are three years or older are larger, and more fecund (Ross and Quetin, 1983). The correlation between brood size and female length varies between regions (Jazdzewksi et al., 1978; Ross and Quetin, 1983). This is likely to be most affected by a combination of food availability and temperature (Atkinson et al., 2006). Post-spawn access to food is also important to female krill as it allows them to regain a normal weight-length ratio after the reproductive season, in time for the onset of winter (Siegel, 2000). During this time females lay down lipid reserves instead of gaining length (Siegel, 2016), to make up for lipid loss through egg production (Clarke, 1980).

The maturation of female krill is controlled by an endogenous rhythm, as well as light levels and temperature (Thomas and Ikeda, 1987; Brown et al., 2010, 2011). However, the re-maturation process is energy expensive. Females that have greater lipid reserves at the end of winter may be able to mature faster (Teschke et al., 2007), and begin spawning earlier in the season when the spring phytoplankton blooms begin. The earlier in the season a female krill spawns, more spawning episodes, up to seven per season, become possible(Ross and Quetin, 1983; Cuzin-Roudy, 1987). For a long reproductive season with multiple spawning episodes, a female krill must be able to replenish her ovaries. High levels of primary productivity from late spring to summer have been correlated with long spawning seasons (Ross and Quetin, 2001). The variability of primary production in the Southern Ocean is linked to sea ice (Smith and Comiso, 2008) and is thought to affect spring maturation speeds and spawning in krill (Siegel, 2016). Other factors that affect the timing of krill spawning are; photoperiod (Brown et al., 2010), sea ice extent (Wiedenmann et al., 2009), and the presence of polynyas (Siegel, 2012). The krill spawning season can last from November through to April (Spiridonov, 1995). However, there is annual variability in both the beginning and the end of the spawning season, and the spawning season can be limited to only two months (Hosie, 1991; Spiridonov, 1995; Siegel, 2012, 2016).

Once eggs have been spawned they sink (Marr, 1962) and receive no parental care. However, maternal physiology and behaviour do continue to have an ongoing effect on embryonic success. Yoshida et al., (2011) found that a maternal diet with a higher percentage of unsaturated fatty acids, was reflected in the composition of embryos, thereby improving the likelihood of successful hatching . Both gravid females and eggs are nutrient rich and high in lipids, which makes them attractive to higher predators. Eggs are also potentially subject to cannibalism (Hempel and Hempel, 1986; Perry et al., 2019). Therefore, it is possible that certain behavioural adaptations have appeared in females to avoid these pressures, such as offshore migrations (Quetin and Ross, 1984; Siegel, 1988).

Embryos spawned in the top 50 – 200 m can reach depths of ~850 m before they hatch (Quetin and Ross, 1984). During this descent, embryos will encounter a variety of temperature conditions that will affect both their sinking and developmental speeds (Marschall, 1983; George, 1984; Ross et al., 1988; Yoshida et al., 2004). Embryonic development slows at temperatures < -1.5 °C (Ross et al., 1988; Yoshida et al., 2011). The upper temperature tolerance is considered to occur at 4.0 °C (George and Stromberg, 1985), however, these results are anecdotal and the upper temperature tolerances of embryonic development requires further attention. The effect of temperature on nauplii malformations remains unknown. Understanding the point at which temperature induces embryonic failure and nauplii malformations in krill is key to being able to model their distribution in a changing climate.

Further investigation into temperature effects on krill embryos may also provide further understanding of why there is such low larval recruitment at South Georgia. The waters around South Georgia contain high densities of sexually mature krill, yet, there is no reported larval recruitment in this area (Marr, 1962). Larval predation, and winter export of larvae and the effects of circulation and water mass distribution have all been suggested as reasons for the lack of larval recruitment (Ruud, 1932; Hofmann et al., 1992; Hofmann and Hüsrevoğlu, 2003; Tarling et al., 2007). However, the effect of the high summer sea surface water temperatures (>4.0 °C) at South Georgia have never been investigated as a factor contributing to the lack of larval recruitment.

1.6 Behavioural and environmental controls on krill distribution

The specific environmental conditions required by krill and the highly variable physical characteristics of the Southern Ocean are believed to be important factors leading to an uneven circumpolar distribution of krill (Everson, 2000). Relationships between krill distribution and environmental variables are difficult to identify and seem to differ regionally. The earliest studies into krill suggested that currents, specifically the West Wind Drift (now termed the ACC), were key to creating the large scale (100-1000s km) distribution of krill in the Southern Ocean (Marr, 1962). The advent of modelling techniques has provided further detail of how both post-larval and larval krill are transported within current systems within the Southern Ocean (Hofmann et al., 1998; Fach et al., 2002, 2006; Murphy et al., 2004; Piñones et al., 2013). Atmospheric circulation patterns cause fluctuations in ocean frontal positions and consequently annual distributions of krill (Priddle et al., 1988). The coupled atmosphere-ice system of the Southern Ocean may also play a key role in the distribution of krill (Murphy, 1995; Murphy and Reid, 2001), particularly the link between the life cycle and the seasonal expansion and shrinkage of the sea ice (Smetacek et al., 1990).

Krill distributions are not determined solely by ocean currents, but are moderated by krill behaviour (Daly and Macaulay, 1991). Post-larval krill are strong swimmers and can maintain swimming speeds of 1.5 - 3.5 body lengths per second (Kils, 1981, 1983). Observations of large krill schools have suggested that krill can maintain both swimming direction and velocities of 0.13 - 0.15 m per second for more than two weeks (Kanda et al., 1982). Tarling and Thorpe (2014) found evidence of directional movement in krill swarms against the prevailing flows of the ACC in the Scotia Sea. Nevertheless, whether these smaller scale movements result in larger scale migrations is yet to be established and an element of drifting with the prevailing flows may be as instrumental in determining larger scale patterns of distribution. Therefore, when considering krill distributions, both passive and active movement of krill must be taken into consideration (Hofmann et al., 1998; Fach and Klinck, 2006; Thorpe et al., 2007).

The horizontal distribution of krill also fluctuates seasonally (Mackintosh, 1973; Kanda et al., 1982; Siegel, 1988; Sprong and Schalk, 1992; Lascara et al., 1999; Atkinson et al., 2008). This annual change in distribution and density of krill is considered to be partly due to horizontal migrations of krill (Siegel, 1988; Lascara et al., 1999). The prevailing paradigm within the south-west Atlantic sector, specifically at the Antarctic Peninsula, is that krill undertake two forms of horizontal migration. The first being a seasonal migration, where krill utilise more of their habitat range during the summer, often extending northwards away from the Antarctic continent and often over the shelf break. This process then reverses in the winter. The second, superimposed migration is a spawning migration specifically of the spawning adult stages. This process is an extension of the first horizontal seasonal migration and contraction of krill distribution. This spawning migration creates a staggered distribution of post-larval krill. The largest and most fecund krill move the furthest off the shelf into deeper oceanic waters and smaller size categories are found closer to the shelf break (Siegel, 1988; Lascara et al., 1999). Again, the separation of the length categories breaks down after the spawning season when the post-larval krill move closer to the Antarctic continent during the winter (Cleary et al., 2016; Reiss et al., 2017). The summer migration of the reproductively active krill off the shelf break means that eggs are spawned over water where they will be able to complete their developmental descent without coming into contact with the sea floor (Hofmann et al., 1992; Hofmann and Hüsrevoğlu, 2003; Nicol, 2006). Winter surveys of very near-shore populations along the western Antarctic Peninsula (WAP) found high winter abundances indicative of an onshore seasonal krill migration during before or during this season (Cleary et al., 2016). Krill abundances in the Bransfield strait are consistently found to be an order of magnitude greater in the winter compared to the summer (Reiss et al., 2017). Both acoustic and net sample surveys have reported seasonal changes in krill densities that, on occasion, can be greater than an order of magnitude (Siegel, 1988; Kim et al., 1998; Lascara et al., 1999; Fielding et al., 2012). However, there are also several surveys that did not find an increase in on-shelf krill density in winter (Stepnik, 1982; Zhou et al., 1994), and krill vertical movements, including to the seabed (Schmidt et al., 2011; Kane et al., 2018) may also drive large changes in abundance in surface waters. To date, no studies have taken data from long term composite krill databases to look at average positions of seasonal off-shelf migrations of different length categories of adult krill (≥30 mm). Although Marr's (1962) life stage distribution maps indicated habitat partitioning between different life stages of adult krill, adults have always been treated as a single group. A further understanding of where the spawning stock of krill are during the spawning season, and how this may be affected by environmental conditions, will increase our understanding of the process of recruitment in this species as well as inform the fishery to avoid targeting the spawning stock.

1.7 Aims and layout of my thesis

A better understanding of krill recruitment is required for the CCAMLR management strategy to evolve with the expanding fishery and ongoing climate change. There is currently a discrepancy between recorded densities of larval recruits and the numbers of these recruits required to maintain the krill population (Kinzey et al., 2015). Identifying the causes of these differences will enable us to create realistic indices of krill recruitment (Meyer et al., 2020) and will improve both the modelling of krill distributions at a level appropriate for effective fisheries management (Hill et al., 2006) and our ability to predict how krill recruitment may change in the future.

For this to happen we must improve our understanding of key krill recruitment processes. This thesis focuses on three key knowledge gaps in krill recruitment, specifically:

- The distribution of all life stages of krill in the south-west Atlantic sector, so that spawning hotspots and nursery areas can be identified.

- How temperature affects hatching failure and nauplii malformation in krill embryos in order to understand the controls on spawning across their full distributional range.

- Patterns of off-shelf spawning migrations and the consequent distribution of adult krill at the WAP to identify where the spawning population are located in the summer spawning season.

These knowledge gaps have been repeatedly identified by krill experts as areas requiring further attention (Flores et al., 2012; Meyer et al., 2020). Using a combination of approaches, including spatial analysis of krill databases, laboratory experiments and statistical modelling, I have addressed each of these points in the following data chapters.

Chapter 2 uses data extracted from three composite krill databases to map the distribution of six life stages of krill within the south-west Atlantic sector of the Southern Ocean. This chapter updates life stage distribution maps created by Marr (1962) with data from the modern era (1976 - 2016) and tests the hypothesis that there is habitat partitioning between different life stages of krill. The results identify hotspots of successful krill spawning and nursery grounds. This chapter has been published in PLoS ONE (Perry et al., 2019). Outputs from this chapter have also been published in Communications Earth & Environment (Meyer et al., 2020), a recent paper on which I contributed as an author.

Chapter 2 shows that spawning is largely unsuccessful in the northern reaches of krill's range, so Chapter 3 investigates the upper temperature tolerance of krill embryos through a series of field and laboratory-based experiments. I specifically tested the hypothesis that temperatures approaching the warm distributional limit have a negative impact on egg hatching success and naupliar development. My results show that krill embryonic hatching success decreases markedly above 3.0 ˚C, the percentage of malformed nauplii reaches 50 % at 5.0 ˚C, and that hatching success of embryonic batches varies enormously, from 0 – 98 %. This chapter has been published in Frontiers in Marine Science (Perry et al., 2020).

Chapters 2 and 3 raise questions about where successful spawning occurs in the south-west Atlantic sector stronghold of krill. Chapter 4 therefore makes a finer scale analysis of the seasonal off-shelf spawning migration of adult krill during the austral spring-summer-autumn seasons. The location of the relatively small percentage of the krill population that make up the spawning stock is vitally important to understanding where krill eggs are spawned. Therefore, I wanted to test the hypothesis that adult krill migrate off-shelf to spawn. This work also contributes to our understanding of what regions need further protection from the fishery to ensure that the spawning stock are avoided so preventing any negative impacts on consequent krill recruitment. This chapter has been prepared as a manuscript for submission to Marine Ecology Progress Series at the same time as this thesis.

Finally, in Chapter 5, the findings of chapters 2 - 4 are discussed in the context of how they update current knowledge of krill recruitment, the implications this has with regards improving krill fishery management and a prognosis for future climate change and data collection relevant to krill recruitment. In considering future work, I also identify knowledge gaps that have been further revealed by my present investigations.

Chapter 2 Habitat partitioning in Antarctic krill: spawning hotspots and nursery areas

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FAP led the analysis, created the figures and wrote the original draft of this paper. Help with data aquisition and guidance on visualisation were provided by AA, SLH, SFS and GAT. Supervision, review and editing were provided by AA, SFS,GAT, SLH, CHL, and DJM.

2.1 Abstract

Antarctic krill, *Euphausia superba*, have a circumpolar distribution but are concentrated within the south-west Atlantic sector, where they support a unique food web and a commercial fishery. Within this sector, our first goal was to produce quantitative distribution maps of all six ontogenetic life stages of krill (eggs, nauplii plus metanauplii, calyptopes, furcilia, juveniles, and adults), based on a compilation of all available post 1970s data. Using these maps, we then examined firstly whether hotspots of egg production and early stage nursery occurred, and secondly whether the available habitat was partitioned between the successive life stages during the austral summer and autumn, when krill densities can be high. To address these questions, we compiled larval krill density records and extracted data spanning 41 years (1976-2016) from the existing KRILLBASE-abundance and KRILLBASE-length-frequency databases. Although adult males and females of spawning age were widely distributed, the distribution of eggs, nauplii and metanauplii indicates that spawning is most

intense over the shelf and shelf-slope. This contrasts with the distributions of calyptope and furcilia larvae, which were concentrated further offshore, mainly in the Southern Scotia Sea. Juveniles, however, were strongly concentrated over shelves along the Scotia Arc. Simple environmental analyses based on water depth and mean water temperature suggest that krill associate with different habitats over the course of their life cycle. From the early to late part of the austral season, juvenile distribution moves from ocean to shelf, opposite in direction to that for adults. Such habitat partitioning may reduce intraspecific competition for food, which has been suggested to occur when densities are exceptionally high during years of strong recruitment. Understanding the location of krill spawning and juvenile development in relation to potentially overlapping fishing activities is needed to protect the health of the south-west Atlantic sector ecosystem.

2.2 Introduction

Antarctic krill (*Euphausia superba*), hereafter "krill", provide a key link between primary production and a suite of predator species (Everson, 2000; Hill et al., 2012; Atkinson et al., 2014; Siegel and Watkins, 2016b). Krill are an important grazer species in the Southern Ocean (Voronina, 1998) with an estimated biomass of between 300 and 500 million tonnes (Atkinson et al., 2009). Their importance in the diets of vertebrate predators is well documented (Grantham, 1977) with populations of penguins, whales, seals, and albatrosses all exhibiting a dependence on krill (Croxall et al., 1999; Reid et al., 2005; Trivelpiece et al., 2011; Braithwaite et al., 2015). Krill also play an important role in iron cycling (Nicol et al., 2010; Schmidt et al., 2016) and carbon export (Pakhomov et al., 2002) and support a commercial fishery, managed by the Commission for the Conservation of Antarctic Marine Living Resources (CCAMLR) (Everson, 2000; Siegel, 2016).

Of the total area in the Southern Ocean (32 million km^2), the total suitable krill habitat is considered to be approximately 18 million km^2 (Siegel, 2016). The first circumpolar distribution maps of krill were compiled from data collected during the *Discovery Investigations* during the 1920s and 1930s which have been been fundamental to our understanding of krill (Marr, 1962). These maps revealed that the circumpolar distribution is assymetric, with higher concentrations in the south-west Atlantic, the sector where the current fishery now operates. More recent studies have added further detail, showing that the sector 0 ° - 90 °W contains 70 % of the total stock (Atkinson et al., 2008).

While the heterogeneous distribution of adult krill in the Southern Ocean is now well documented, differences in the relative distribution of the life stages within the south-west Atlantic sector are not so well known. Krill have a complex ontogeny and a lifespan of up to seven years (Ikeda and Thomas, 1987). The larval stage lasts for the first twelve months and comprises of: the descent ascent development cycle which begins with egg sinking and the nauplii swimming back to surface waters; the short non-feeding metanauplii stage; the calyptope stages during which the larvae feed for the first time; and finally the furcilia stages at which the larvae will spend their first winter. After the furcilia stages the krill moult to post-larval juveniles, continuing to grow to adulthood in subsequent years. A better knowledge of the relative distribution of these different life stages would help us to understand the regional distribution of spawning and recruitment (Mackintosh, 1973), identifying hotspots that may be sensitive to influences such as climate change and fishing.

The ground-breaking studies of krill life stage distribution were based on data collected over 80 years ago (Marr, 1962; Mackintosh, 1973) during the *Discovery Investigations*. These studies produced maps, typically presented as a series of overlain bubble plots of abundance, based on a composite of surveys spanning over a decade. Although these composite maps are hard to draw quantitative insights from, they are still valuable, and continue to be used as a source reference for the distribution of each life stage (Siegel, 2016). However, since then the system has changed, with warming and a changing suite of krill predators, and furthermore a wealth of data has been collected in the modern era since the 1970s. These include a series of large-scale, semi-synoptic surveys that have been used to determine the distributions of krill, including FIBEX 1981 (El-Sayed, 1994), SIBEX 1984-85 (Siegel, 1986a), CCAMLR 2000 (Constable et al., 2000), Southern Ocean GLOBEC 2001-2005 (Skjoldal et al., 2013), and US AMLR 2011. In addition, a series of maps of krill life stage distributions (some including larval stages) have been produced from single surveys (Hempel, 1979; Hempel and Hempel, 1982; Hosie et al., 1988; Daly, 1990a; Ichii et al., 1998; Siegel et al., 2013). All of these studies are valuable to our understanding of krill but, being based on one or a few surveys, they are spatially and temporally limited and provide only snapshots of krill life stage distribution, each of which can vary substantially between surveys (Atkinson et al., 2004; Siegel et al., 2004). There has been no attempt, so far, to map the relative distribution of each krill life stage using all available modern era data, equivalent to the old *Discovery* approach.

The overall aim of this paper is therefore to quantify and compare the distributions of all the life stages of krill within the south-west Atlantic sector during the modern (post 1970s) era. The approach is similar to that of the *Discovery Investigations* in combining all available data for each life stage from multiple surveys to produce a climatology map of mean distribution. However we benefitted from the much greater volume of data available since the 1970s and instead of overlain bubble plots of distribution, we plotted the data quantitiavely as mean densities within grid cells. To achieve this we compiled all available egg and larval krill abundance data from the modern era into a single database. For the postlarvae we integrated the data provided from two existing databases, namely KRILLBASE-abundance and KRILLBASE-length-frequency. Our first objective was to identify krill spawning hotspots to highlight potential source regions for krill recruitment. The second objective was to compare the relative distributions of the life stages to investigate whether the habitat was partitioned during the summer season. Distributions of both krill and krill sampling are heterogeneous, so in addition to the gridded maps we included simple "habitat analyses" based on water depth and mean temperature to provide alternative visualisations of the distribution of each life stage.

2.3 Methods

2.3.1 Overview of the krill databases used for this study

In this analysis we combined two existing post-larval krill databases, entitled KRILLBASE-abundance and KRILLBASE-length-frequency and compiled an additional database on density of the eggs and larval stages specifically for this study. The source data compiled for this new larval dataset is detailed in Supplementary Table 1. Each of the three databases is a large, multi-national composite of net sampling data, summarised in Table 1.

All three of the databases have been compiled in a similar manner, with information gathered from a variety of sources ranging from paper logbooks to published reports and institute records that were sent to us. Since the 1920s and 1930s of the main *Discovery* era there is a long gap in data available to us and the first record of what we define in this paper as the "modern era" was in 1976. This modern era of data comprises 41 years spanning 1976 - 1916.

Table 1. Summary of the three composite databases that were used for this study.

Attribute for each database	**KRILLBASE-abundance**	**KRILLBASE-length-frequency**	**KRILLBASE-larvae**
Source data	DOI: 0.5285/8b00a915- 94e3-4a04-aa903-dd4956346439	Held at the UK Polar Data Centre at the British Antarctic Survey, Cambridge	Compiled for this study
Reference on data source for further information	Atkinson et al., 2017	Atkinson et al., 2009	see Supplementary Table 1
Summary of database	All available un-targeted scientific net catches. Measured in density (no. m^{-2})	Length, sex and maturity stage data of post-larval krill	Densities of eggs, nauplii, metanauplii, calyptopes and furcilia larvae
Years of coverage after screening	39	40	21

The specifics of screening of the individual databases are described in the following sections. For all three databases the data were pre-screened to include only the south-west Atlantic sector of the Southern Ocean, defined as between 20 ° and 80 °W. The northern limit of data extracted from the three databases was determined by the position of the Antarctic Polar Front. Its position is based primarily on Orsi et al., 1995 see Figure 2. The Southern limit was determined by the coast of Antarctica. All data were plotted using ArcGIS version 10.2.2. A few data points in the length frequency database plotted on land and were removed. Table 2 summarises the data coverage provided by the three databases after all of the screening procedures and Supplementary Table 2 shows the data coverage of the three databases by year.

Allocation of data into early and late season

The large majority of the KRILLBASE datasets were from the austral spring-summer-autumn season (i.e. from November to March). Only a few records were in October or April, and only the larval database had any records in May (29 stations). For this paper we defined year as austral season, such that, for example the year 1980 spanned October 1979 to May 1980. Within each year we further divided all data as being either “early season” (defined here as 1 October to December 31) or “late season” (1 Jan to 31 May). We divided the data like this because the majority of the larvae were recorded in the late season, thus providing a natural division for our analysis of habitat partitioning, while retaining large sample sizes.

Table 2. Summary of KRILLBASE data used. The number of stations, per approximate 10 year period, provided by each of the data sets after screening. Supplementary Table 2 provides further breakdown of stations into early and late austral season coverage for every sampling year.

Number of stations	**1976-1985**	**1986-1995**	**1996-2005**	**2006-2016**	**TOTALS (after screening)**
KRILLBASE-abundance	1682	1522	3153	1270	7627
KRILLBASE-length-frequency	1745	1040	1425	184	4394
KRILLBASE-larvae	776	11	524	312	1623

2.3.2 KRILLBASE-abundance database

KRILLBASE-abundance (https://www.bas.ac.uk/project/krillbase) is an open access database of net-based post-larval Antarctic krill and salp densities (Atkinson et al., 2017). Because the database is a composite of multiple sampling methods with variable efficiency in catching krill, all densities (nos. m^{-2}) used in this analysis have been standardised to account for variation in sampling method. This procedure is detailed in Appendix 1 of (Atkinson et al., 2008) and its rationale is further explained in (Atkinson et al., 2017). In brief, we used the KRILLBASE-abundance dataset to derive a series of conversion factors based on the net mouth area, sampling depth, time of day and time of year of sampling. These factors were used in an empirical model to multiply the catch values for the nonzero krill densities to those of a single and relatively efficient net sampling method; namely a night-time RMT8 net sampling from 0 - 200 m on 1 January. Prior analyses (Atkinson et al., 2017) have showed that this standardisation procedure yields a very similar geographic pattern of krill distribution to that based on un-standardised krill densities, although mean values were overall higher.

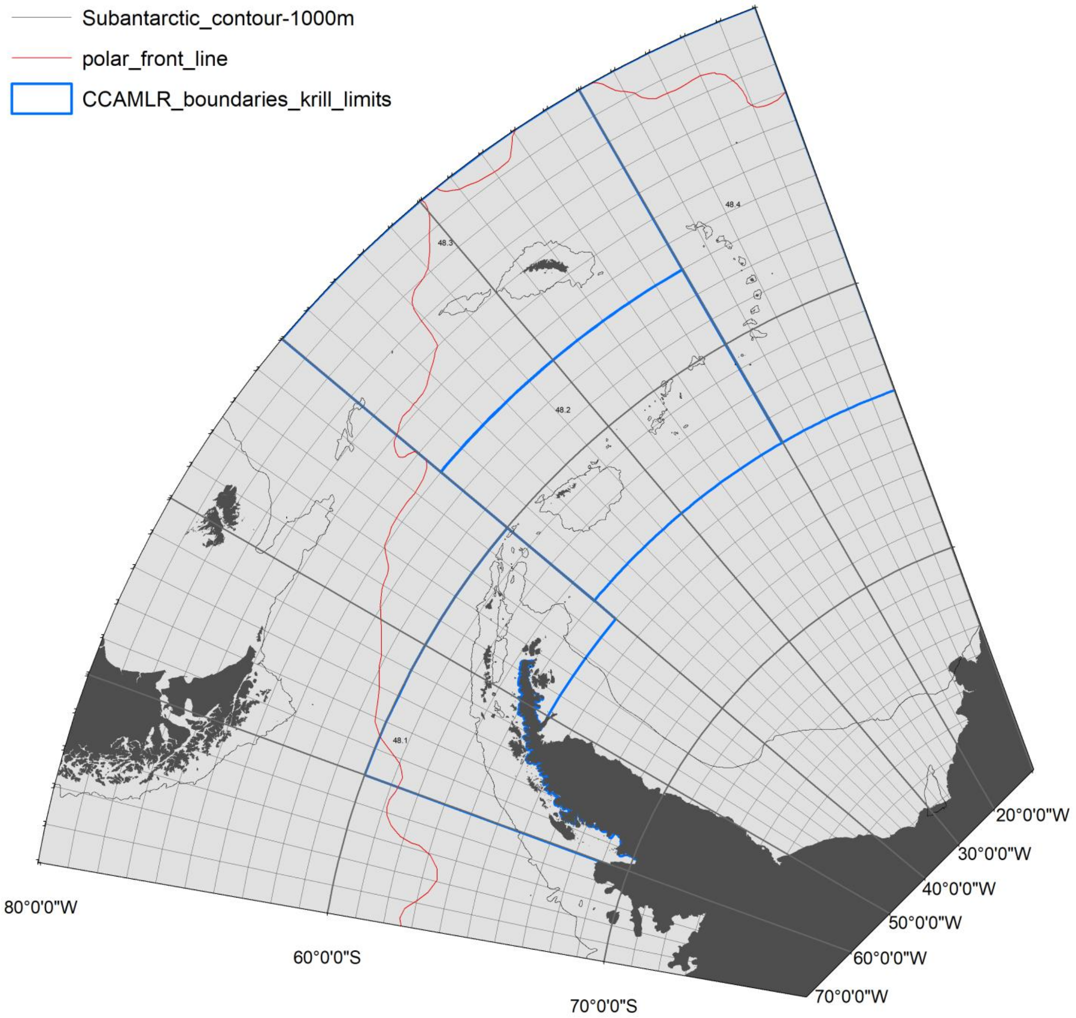


Figure 2. The study area. Also depicted are CCAMLR management subareas (each of which has its own catch limit), 1000 m bathymetry line, Antarctic Polar Front and the 1 ° latitude by 2 ° longitude grid cells used for this study.

For our study, we filtered the database for standardised numerical densities of post-larval krill that fell within the previously outlined spatiotemporal parameters, with additional filtering on sampling depth following Atkinson et al., (2008). Namely, the upper sampling depth was within the topmost 20m and the bottom sampling depth was at least 50 m depth. This resulted in a total of 7,627 usable stations out of a possible 12,758.

2.3.3 KRILLBASE-length-frequency database

The full KRILLBASE-length-frequency database contains the individual length measurements for >1,000,000 krill, with sex and maturity stage as additional variables for a portion of these. These values were obtained from both scientific hauls and commercial fisheries. Most of these were oblique or targeted hauls (often towed horizontally) within the top 200 m layer. Unlike the other two databases we included horizontal hauls in this study to enhance sample sizes, based on prior analyses that showed that the trends in krill length were congruent between the two sampling methods. After filtering for the spatiotemporal criteria stated in section 2.1, we ensured that any records outside of the following parameters were removed; Krill <15 mm were excluded, since krill this size would likely be furcilia, counted in the larval database. Records sampled with a >6 mm mesh were excluded due to the possibility of net mesh selection and under-representation of the smaller krill. This removed both commercial trawl data and some of the scientific trawls. Data from some scientific nets were further excluded where mesh size was not stipulated, including nets described as trawls. This left 530,018 measured krill from 4,394 stations.

2.3.4 Larval database

We collated the larval database for this study, and it contained density estimates for eggs and individual larval stages. The component surveys and sampling details are described in Supplementary Table 1. These data were not standardised in the same way as the post-larval density data, given the decreased net escape responses of the small larvae. Further, the nets compiled were restricted to those that provided a reasonable estimation of egg and larval densities. An important difference in the screening compared to the post-larval data was the requirement for the top depth to be the surface and the bottom depth to be at least 200 m, to ensure that the densities of calyptopes and furcilia, known to undergo extensive diel vertical migrations, were included. We stress that sampling even in the whole of the top 200 m layer will under-sample eggs and nauplii due to the deep developmental cycle and discuss this issue in section 2.4.1.

Our compiled larval database contains detailed information on densities of a range of early life stages and includes depth distributions of life stages from stratified hauls. We simplified the depth distributions to provide densities (no. m^2) within the whole sampled water column, and for four larval stages; eggs, nauplii plus metanauplii (hereafter referred to as “nauplii”), calyptopes, and furcilia. Low data availability and the fact that larvae were relatively rare before January meant that we could only provide late season distributions for these four larval stages. For our analysis we extracted 1,623 usable stations out of the total 3,449 in this database.

2.3.5 Producing grid maps of krill life stage densities

Baseline maps of land masses were plotted using the WGS 1984 Antarctic Polar Stereographic co-ordinate system using Arc GIS v 10.2.2. To these maps, a grid of cells, 1° latitude × 2° longitude, and the Antarctic Polar Front position was overlaid (Figure 2). By joining each of the three databases separately to this grid, we derived a series of mean krill indices for each grid cell, both for early and late season where data allowed. These indices included densities for each of our four larval groups (eggs, nauplii plus metanauplii combined, calyptopes and furcilia), total post-larval density, fractions of juvenile and adult krill (defined respectively as 15 - 30 mm and > 30 mm following Kanda et al., (1982) and the sex ratio for these adult krill. KRILLBASE-length-frequency provided the source of these fractions and the adult sex ratio. By multiplying the appropriate indices for each cell we calculated the mean density of female and male adult krill, juvenile krill, and of the four larval stages. Calculations for these juvenile and adult densities could only be made if there were values from both the density and length-frequency databases in any given grid cell. This led to 389 grid cells being excluded due to lack of length frequency data, and 41 grid cells being excluded due to lack of post-larval density data. These exclusions obviated the need to interpolate between grid cells.

2.3.6 Selection of environmental data

We should stress that krill life stage distribution has been linked to a wide range of environmental factors such as sea ice, phytoplankton concentration, fronts, eddies, bathymetry and temperature (reviewed recently in Siegel and Watkins, 2016). It is beyond the scope of this paper to attempt an analysis of how all of these the factors influence the distribution of each life stage. In any case, the timespan of the data pre-date the satellite era, and matching environmental data are unavailable for most of the 41 sampling years. The aim of this paper is instead to use environmental descriptor data, alongside the plots themselves, simply to illustrate the degree of habitat partitioning among the life stages. For this we selected both mean water depth and mean water temperature within each grid cell as our habitat descriptor variables. While water depth is clearly invariant across the 41-year timespan of observations, mean water temperature changes both seasonally and over longer timescales. The purpose of this temperature index was therefore to provide an internally consistent index to portray the radically different distribution patterns of the life stages across the sector.

To derive these two habitat descriptors, ocean bathymetry was sourced from the GEBCO data series. The most up-to-date GEBCO data available was version GEBCO_2014 grid (The GEBCO_Grid, www.gebco.net). These data were used to create isobaths and to derive mean water depth for each of the grid cells used for analysis in ArcGIS. To derive mean sea surface temperature (SST) for each grid cell, data from 1 January 1979 to 1 December 2014 were downloaded from the European centre for medium-range weather forecasts, specifically the European re-analysis interim dataset. An average February value was taken for our study area, as described in (Atkinson et al., 2017).

2.3.7 Environmental habitat analysis

As described in section 2.3 there are numerous variables which may influence the distribution of Antarctic krill (Hofmann and Hüsrevoğlu, 2003; Atkinson et al., 2008; Piñones and Fedorov, 2016; Silk et al., 2016). We sought to summarize key physical habitat characteristics with a simple index which combines water depth and climatological mean temperature to assess the broad habitat of each krill life stage. For our water depth and temperature analyses, we first obtained mean water depths and temperatures for each cell of our 1° latitude by 2° longitude grid. For each sampling station we then related each available life stage density to its grid mean temperature and depth value. This matrix of linked krill and physical data was then divided into broad categories of temperature (-2 - 0 °C, 0 - 2 °C, 2 - 4 °C, > 4 °C) and of depth (0 - 1000 m, 1000 - 2000 m, 2000 - 3000 m, 3000 - 4000 m, >4000 m). While other finer divisions were trialled, these broad categories preserved relatively large sample sizes, while still being able to depict the large differences in habitat that we found between the life stages. Within each of these combinations of temperature and depth we calculated the arithmetic mean krill density for each of the life stages.

2.4 Results

2.4.1 Overview of sampling coverage and life stage distribution

Temporally, the most intensively sampled period in our analysis was 1996 - 2005 (5,102 stations), with the least sampled being 2006 - 2016 (1,766 stations) (Table 2). Spatially, sampling was widespread across the south-west Atlantic, albeit with most emphasis in shelf and oceanic waters surrounding the Scotia Arc, particularly for the length frequency data (Figure3). We have compared the relative distributions of the life stages both during the early season (Oct-Dec) (Figure 4) and the late season (Jan to May) when larvae were abundant (Figure 5). The most striking features of the maps were first, the general northward and simultaneous horizontal spread of the larval stages, from eggs to furcilia; second the relatively restricted and off-shelf distributions of calyptopes and larvae; third, the highly restricted shelf distribution of juveniles, particularly in the late season; and fourth the much more extensive distributions of the older (adult) males and females. Thus for example, 58% of all grid cells had an average density of zero for late juveniles, while the late season males and females had respective values of only 14 % and 11 %.

2.4.2 Distributions and habitat analysis

Given the fundamental differences in bathymetric distributions of the stages evident in Figures 4 and 4, we have plotted their mean depth distributions in Figure 6. We then illustrated the distribution patterns in terms of depth and temperature combined (Figure 7). The patterns derived from these various depictions of distribution are described in detail below, in the sequence from spawning females, through larvae to juveniles.

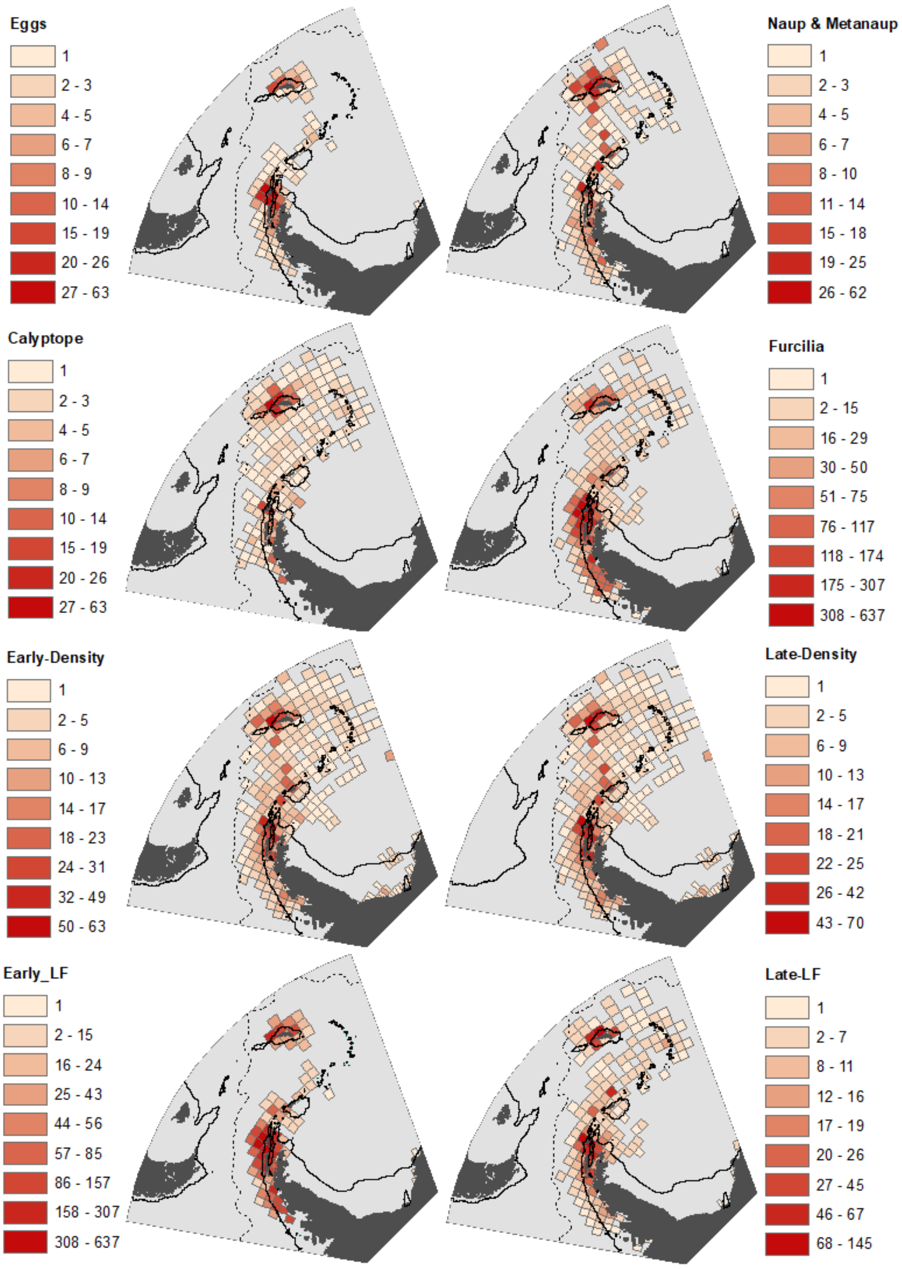


Figure 3. Density of sampling coverage for each krill life stage. Natural breaks have been used for the scale division of number of stations per grid cell: note the difference in scale between life stages. Eggs, nauplii, calyptopes, and furcilia are depicted here and in the rest of this paper only for the late (January to May inclusive) part of the survey season due to lack of stations and low abundances in the early part of the season. Sampling intensity plots for combined juveniles and adults male and female density and length-frequency (LF) are shown both for the “early” (October to December inclusive) and “late” (January to May inclusive) parts of the survey season. Both the 1000m isobath (continental shelf edge; solid black line) and the Antarctic Polar Front (dashed black line) are shown.

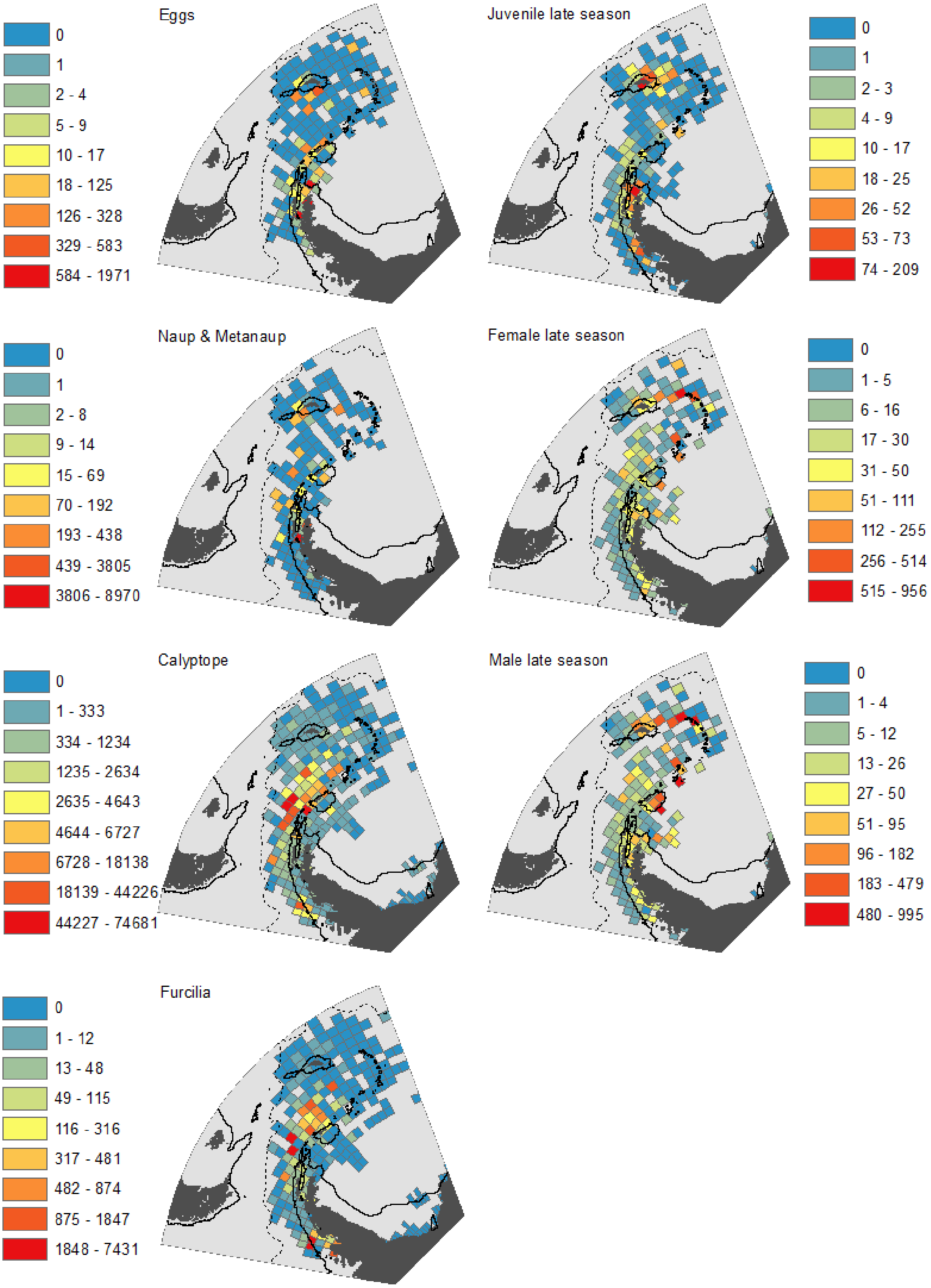


Figure 4. Distribution of krill life stages in “late” season (January to May). Scale bars of mean density (no. m^{-2}) in each grid cell differ between the life stages. Natural breaks are used for scale divisions. Grey represents un-sampled areas. Both the 1000 m isobaths and Antarctic Polar Front are the same as Figure 2.

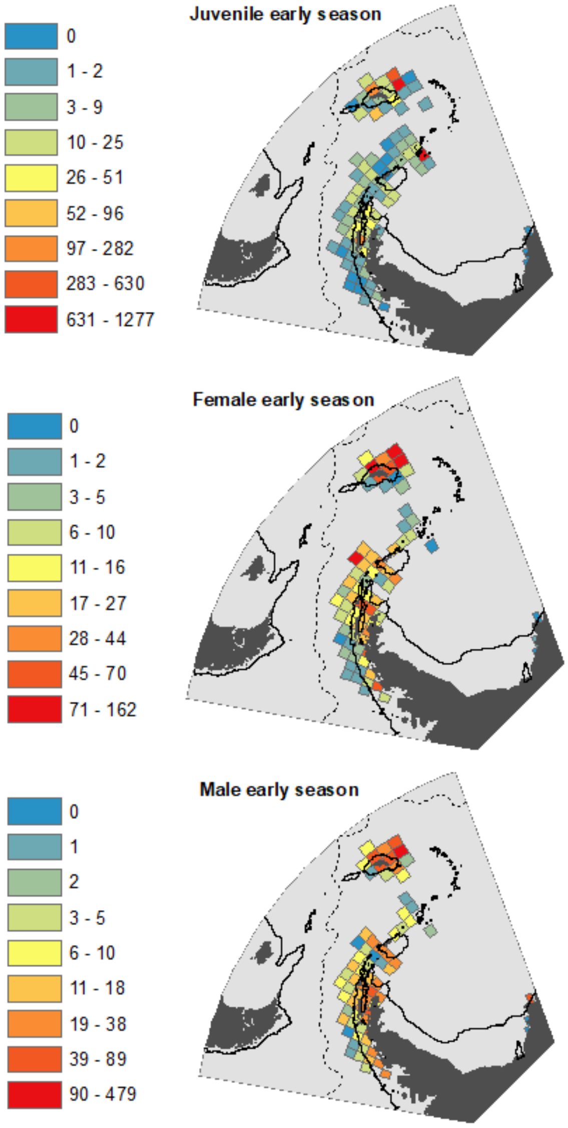


Figure 5. Distribution of krill life stages in “early” season (October to December). The map layout is identical to that in Figure 4.

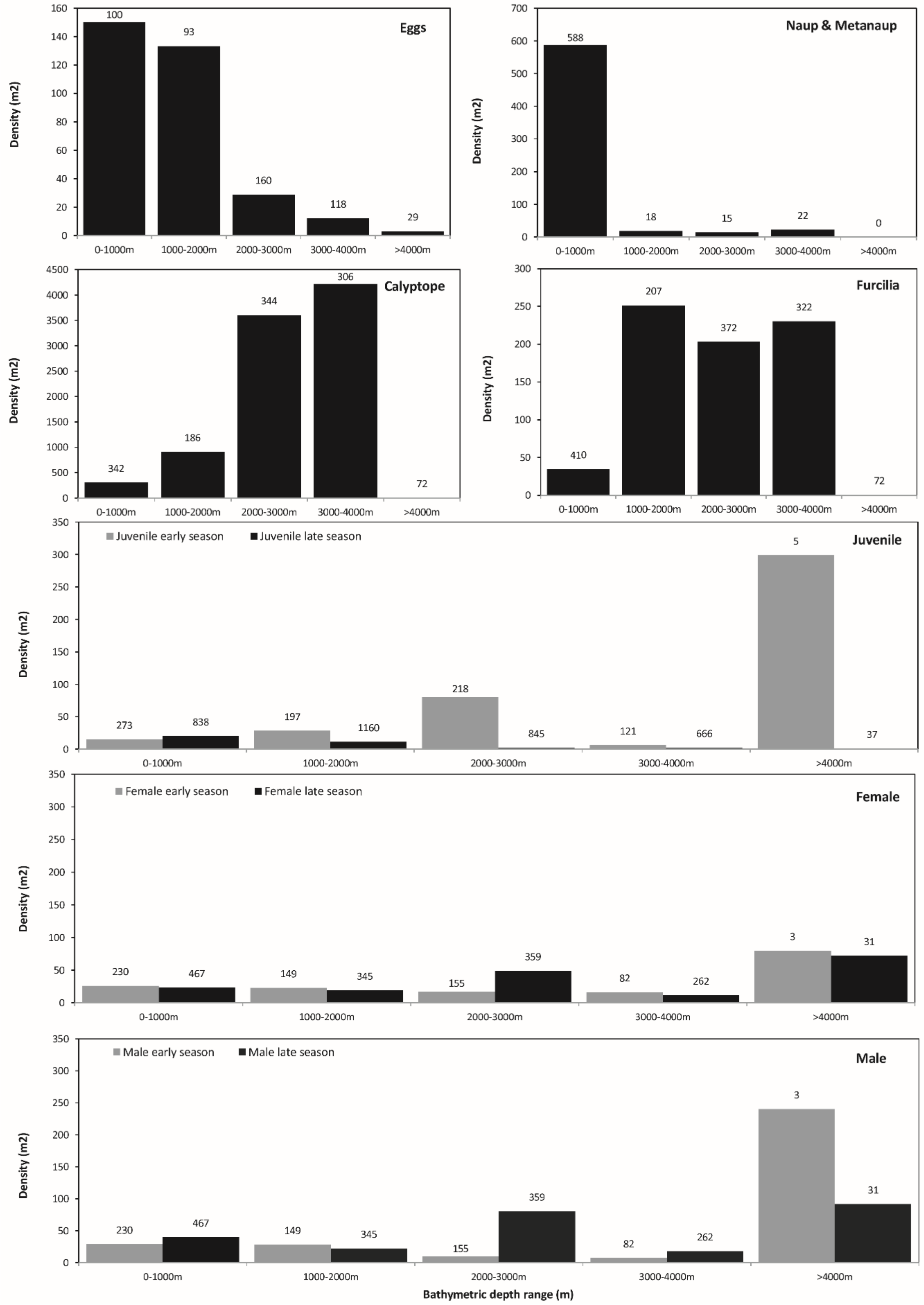
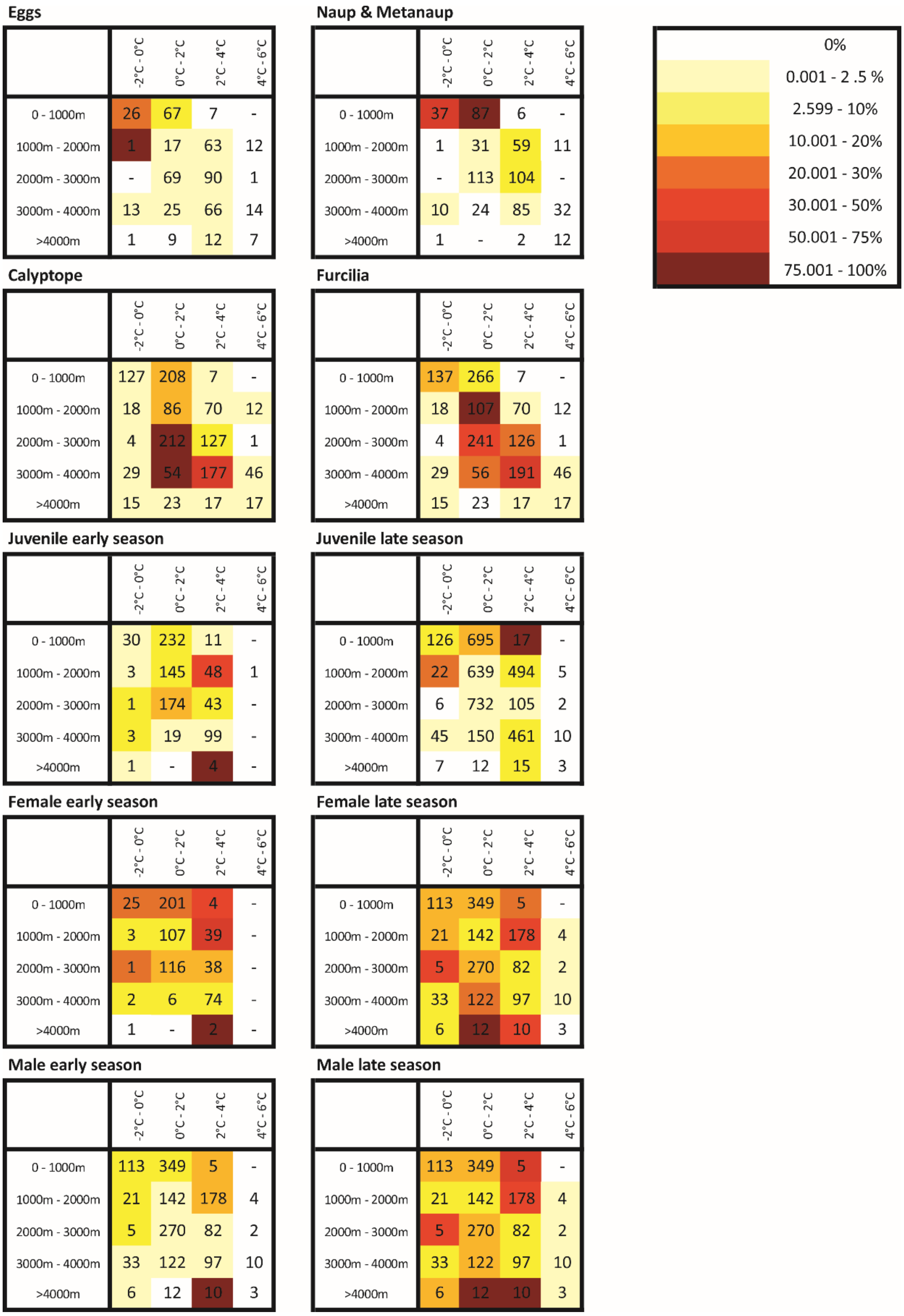


Figure 6. Mean densities of each life stage in relation to water depth of their sampling location. Note variation in scale of y-axis. These values were based on arithmetic mean density of all krill stations located within each water depth category. Number of stations contributing to each depth range is provided above the bars, to emphasise the low sampling density in the deepest environments – the narrow ocean trenches which lie adjacent to the Scotia Arc.



Eggs

	-2°C - 0°C	0°C - 2°C	2°C - 4°C	4°C - 6°C
0 - 1000m	26	67	7	-
1000m - 2000m	1	17	63	12
2000m - 3000m	-	69	90	1
3000m - 4000m	13	25	66	14
>4000m	1	9	12	7

Naup & Metanaup

	-2°C - 0°C	0°C - 2°C	2°C - 4°C	4°C - 6°C
0 - 1000m	37	87	6	-
1000m - 2000m	1	31	59	11
2000m - 3000m	-	113	104	-
3000m - 4000m	10	24	85	32
>4000m	1	-	2	12

0%
0.001 - 2 .5 %
2.599 - 10%
10.001 - 20%
20.001 - 30%
30.001 - 50%
50.001 - 75%
75.001 - 100%

Calyptope

	-2°C - 0°C	0°C - 2°C	2°C - 4°C	4°C - 6°C
0 - 1000m	127	208	7	-
1000m - 2000m	18	86	70	12
2000m - 3000m	4	212	127	1
3000m - 4000m	29	54	177	46
>4000m	15	23	17	17

Furcilia

	-2°C - 0°C	0°C - 2°C	2°C - 4°C	4°C - 6°C
0 - 1000m	137	266	7	-
1000m - 2000m	18	107	70	12
2000m - 3000m	4	241	126	1
3000m - 4000m	29	56	191	46
>4000m	15	23	17	17

Juvenile early season

	-2°C - 0°C	0°C - 2°C	2°C - 4°C	4°C - 6°C
0 - 1000m	30	232	11	-
1000m - 2000m	3	145	48	1
2000m - 3000m	1	174	43	-
3000m - 4000m	3	19	99	-
>4000m	1	-	4	-

Juvenile late season

	-2°C - 0°C	0°C - 2°C	2°C - 4°C	4°C - 6°C
0 - 1000m	126	695	17	-
1000m - 2000m	22	639	494	5
2000m - 3000m	6	732	105	2
3000m - 4000m	45	150	461	10
>4000m	7	12	15	3

Female early season

	-2°C - 0°C	0°C - 2°C	2°C - 4°C	4°C - 6°C
0 - 1000m	25	201	4	-
1000m - 2000m	3	107	39	-
2000m - 3000m	1	116	38	-
3000m - 4000m	2	6	74	-
>4000m	1	-	2	-

Female late season

	-2°C - 0°C	0°C - 2°C	2°C - 4°C	4°C - 6°C
0 - 1000m	113	349	5	-
1000m - 2000m	21	142	178	4
2000m - 3000m	5	270	82	2
3000m - 4000m	33	122	97	10
>4000m	6	12	10	3

Male early season

	-2°C - 0°C	0°C - 2°C	2°C - 4°C	4°C - 6°C
0 - 1000m	113	349	5	-
1000m - 2000m	21	142	178	4
2000m - 3000m	5	270	82	2
3000m - 4000m	33	122	97	10
>4000m	6	12	10	3

Male late season

	-2°C - 0°C	0°C - 2°C	2°C - 4°C	4°C - 6°C
0 - 1000m	113	349	5	-
1000m - 2000m	21	142	178	4
2000m - 3000m	5	270	82	2
3000m - 4000m	33	122	97	10
>4000m	6	12	10	3

Figure 7. Relative densities of krill life stages in relation to water depth and temperature. To help comparison across the multiple life stages, the colour coded values within each combination of water depth and temperature are normalised by calculating them as percentages of the maximum value (i.e. the water depth-temperature combination with the highest mean krill density). "Early" denotes the period October to December inclusive. "Late" is January to May. Number of stations contributing to each density estimate is provided for each cell.

2.4.3 Adults

The adult females and males appear to have very similar spatial distributions (Figures 4 and 5) and display the widest range of suitable physical habitat combinations. Highest densities of adult krill, for both sexes and in both the early and late parts of the season, tend to be in the vicinity of the Scotia Arc. These elevated densities occur both over the shelf and over the deep trench environments that lie frequently adjacent to the Scotia Arc. (Figures 4 and 5). When considering the effect of our other methods of depicting these data (Figures 6 and 7) the overall abundances and distributions of adult males and females are similar, being found across a broad range of water depth and temperature combinations. However, there is some evidence for a seasonal change with respect to depth distribution, this being congruent across both sexes. In the early part of the season before January, males and females are most abundant near shelf and slope waters, whereas in the late season the highest densities of both sexes are seen off-shelf (Figure 6).

2.4.4 Eggs and nauplii

In contrast to the wide distribution of adults, the greatest densities of eggs and nauplii appear over or near the shelves near the tip of the Antarctic Peninsula and the South Orkneys, with isolated occurrences in the Scotia Sea and south of South Georgia (Figure 3). Figures 6 and 7 show a strong association of both of these stages with cold shelf and shelf-slope waters.

2.4.5 Calyptopes and furcilia

Calyptopes and furcilia had similar distributions, but these were very different to those of all other life stages. Their highest densities were in oceanic waters of the Scotia Sea, stretching from the tip of the Antarctic Peninsula eastwards across the southern Scotia Sea. High densities were recorded during a 2011 survey in the Marguerite Bay area (Supplementary Table 1) and these are reflected in a secondary high density area in this area in the composite maps of Figure 4. Overall, both the calyptopes and the furcilia were found most commonly in habitats with deeper and warmer water than found for the eggs. This is well illustrated in both of our habitat depictions (Figures 6 and 7); highest densities in 2000 - 400 m water depth and 0 - 2 °C temperatures that are characteristic of the central/southern Scotia Sea.

2.4.6 Juveniles

To provide a comparison with the eggs and larvae data presented for the late season of January-May, we start by describing the late season distribution of juveniles. There are clear population centres evident in Figure 4, both at the Antarctic Peninsula shelf and around the South Georgia shelf. Exceptionally high juvenile densities have been associated with several notable spawning successes, for example in 1981 and 1996. Summaries of the habitat (Figures 6 and 7) support a strongly shelf-centred late season distribution.

By contrast, interpreting the early season distribution of these 15 - 30 mm juvenile krill is not so straightforward, as these krill may represent a mixture of year classes. In October to December the smallest in this size range may be nearing 1- year old (i.e. 0+ age class) whereas the largest may be 1-year older (1+ age class). Whatever their age, they have a clearly more oceanic distribution (Figures 6 and 7), albeit with the same broad range of habitat temperatures as late season juveniles. This movement of the juvenile distribution onto the shelf through the season is thus opposite in direction to the off-shelf movement of adult males and females.

2.5 Discussion

Our analysis based on composite data collected over multiple surveys spanning 41 years provides overview maps similar in style to the large scale distribution maps from >80 years ago (Marr, 1962; Mackintosh, 1973), an era when most of the large baleen whales had already been killed and when temperatures were cooler (Whitehouse et al., 2008). We believe that a synthesis of these krill life stage distribution data from the modern era into a series of quantitative maps is useful for a series of reasons. First it brings the wealth of larval krill data collected over the last 41 years into one place, to allow comparison with existing compilations of post-larval krill data within KRILLBASE (Atkinson et al., 2017). Second, it allows the identification of specific habitats that may be particularly sensitive for krill, for spawning, nursery of larvae or for recruitment, allowing improved spatial planning for fisheries management or conservation. Thirdly, given the ongoing rapid climate change within this region, we hope that the data and maps can be used for ongoing efforts to model past, present and future krill distributions and how these may respond to environmental change (Hofmann and Hüsrevoğlu, 2003; Le Quéré et al., 2016; Piñones and Fedorov, 2016).

We will first discuss how we addressed the caveats associated with the data, after which we will focus on our key findings: the distribution of spawning, the evidence for partitioning of the habitat and finally the implications of our findings in relation to fisheries management and climate change.

2.5.1 How well do composite maps represent krill life stage distributions?

While net sampling has contributed much to our knowledge of krill, there are several factors that might affect the quality of data collected. Avoidance (Marr, 1962; Everson and Bone, 1986; Everson, 2000; Wiebe et al., 2004, 2013), escapement and damage (Watkins, 2000), net feeding (Hirota, 1984; Nicol, 1984) and bias towards certain life stages (Skjoldal et al., 2013) all affect net sample data. Previous studies (Atkinson et al., 2009; Kawaguchi et al., 2010b) have argued that there is significant under sampling of the juvenile stage of krill, potentially because of avoidance (Everson, 2000) and the mesh size used for nets (Siegel, 1986b). For the younger stages, the early developmental descent and re-ascent cycle (Siegel and Watkins, 2016a), will mean that only a portion of the standing stocks of eggs, nauplii, metanauplii and even calyptopes will be retained by net sampling, which is typically only to 200 m depth (Supplementary Figure 1). Even the post-larval stage make extensive vertical migrations, leading to underestimates of density based on net sampling in the upper layers (Clarke and Tyler, 2008; Schmidt et al., 2011). For all of these reasons, the emphasis of this study is on horizontal patterns of abundance of each stage within the surface layers rather than comparisons of densities across life stages.

Our maps are generated from composite data collected over many seasons and should not be interpreted as single-season snapshots. They are thus akin both to the *Discovery* maps and more recent coarser-scale composite maps of the circumpolar distribution for calyptopes, furcilia and post-larval krill (Siegel, 1986b). A number of large-scale, short-term synoptic surveys have been used to determine the distributions of krill (FIBEX 1981, SIBEX 1984-85, CCAMLR 2000, Southern Ocean GLOBEC 2001-2005, US AMLR 2011). These examples form part of the composite database analysed here (Supplementary Figure 1). Larval distributions, in particular, vary between surveys such that some of these surveys provided similar distributions to ours and others did not.

A potential issue for all distribution maps is the uneven distribution of sampling effort. To address this, all of the data have been averaged by grid cell to provide estimates of mean no m^{-2}. However, given the patchiness of krill, the precision of these mean values will inevitably be much lower in the less intensively sampled oceanic areas. This leads to juxtaposed grid cells with high and low calculated mean density in the distribution plots of Figures 4 and 5. Notwithstanding these various issues of sampling, our maps are based on thousands of sampling stations over multiple years (Table 2) and thereby provide the best available overview of relative distribution of krill life stages from observational data over the last 41 years. In addition, we have also used multiple data visualisations (Figures 4 to 7) to portray the distribution patterns.

2.5.2 Are there spawning hotspots and larval nursery areas?

The calyptope and furcilia stages appear to occur in two main regions of the south-west Atlantic sector. These are off the tip of the Antarctic Peninsula in the south Scotia Sea and with a secondary area in Marguerite Bay off the WAP. These two areas almost create a band of later larval stages from the base of the WAP through to 36 °W, with a gap between the top of Adelaide Island and the southern point of the South Shetlands. Importantly, these areas of elevated densities of calyptopes and furcilia are much more restricted than those of adult krill or eggs.

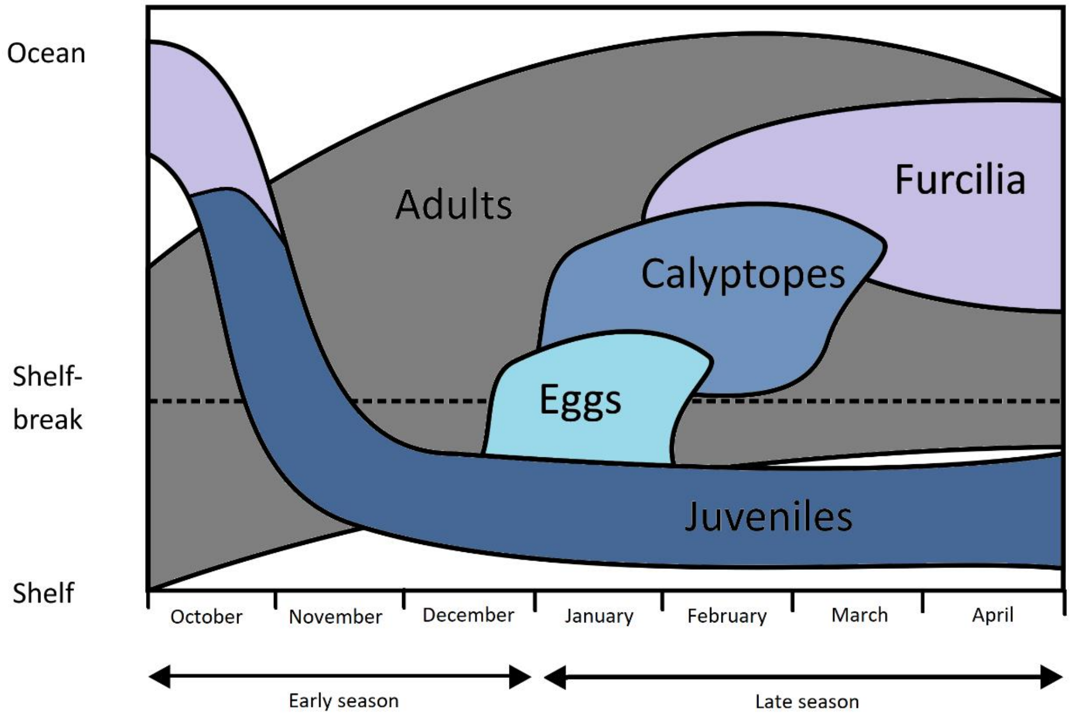


Figure 8. Schematic of seasonal change in on-shelf off-shelf distributions of krill life stages. This illustration is based mainly on our Figure 6. The schematic portrays the main areas of the distribution relative to the shelf throughout the austral spring to autumn period. It builds on a schematic published in Figure 2.6 of Siegel and Watkins (2016), but includes the observed redistribution of juvenile krill from oceanic waters back to shelf waters throughout the austral spring. This schematic simply reports the changing distributions seen in our study and does not propose candidate mechanisms such as advection, migration or differential mortality.

The reasons why calyptopes and furcilia are located only in parts of the adult distributional range are unclear. It has been suggested (Hofmann et al., 1992) that the presence of warmer Antarctic Circumpolar Current (ACC) water along the Antarctic Peninsula speeds the development time of eggs, allowing the hatched nauplii to return to the surface waters with greater energy reserves, giving them more time to find food. This interpretation suggests that the chance of an egg reaching the calyptope stage is dependent on the correct environmental conditions. Temperature has already been shown to have an impact on the developmental capacity on the early larval stages (Ross et al., 1988; Yoshida et al., 2004). The metanauplii stage is the last non-feeding stage; once they have metamorphosed into calyptopes they must be able to feed. So one explanation for the relatively localised larval krill distribution is that they exhibit both the correct environmental conditions for rapid egg development (Ross et al., 1988; Hofmann et al., 1992), coupled to high levels of the correct food sources both for spawning females (Schmidt et al., 2012) and for the calyptope and furcilia stages.

The next conundrum is where the eggs that successfully reach the furcilia stage were spawned. Our density maps (Figure 4) and analyses (Figures 6 and 7) show that the greatest densities of eggs, nauplii and metanauplii are found are found on the shelf or shelf-slope around the tip of the Antarctic Peninsula and the South Orkneys. Importantly, we found very few eggs present in the areas where there were high densities of calyptopes and furcilia. One explanation for this is a disproportionately high mortality of eggs laid over shelf habitats, either through sinking to the seafloor and unable to undertake the developmental cycle or due to elevated predation (Tarling et al., 2007).

An alternative (and non-mutually exclusive) explanation for the disconnect between the distributions of feeding and non-feeding larval stages is that eggs laid near the shelf edge were being advected offshore, in a general northerly and easterly direction (Marr, 1962; Brinton, 1985). Modelling of particles released along the continental shelf break to the west of the Antarctic Peninsula shows that they are carried north-northeast by Ekman drift into the path of the fast flowing ACC (Hofmann et al., 1998; Murphy et al., 1998; Thorpe et al., 2007). Modelled trajectories of larval krill across the Scotia Sea yielded maps of distribution (Fach et al., 2006) that are similar to those presented here. Importantly some models have also shown that the speed of particle advection allows enough time for larval development. It has been suggested (Hofmann et al., 1998) that krill from the Antarctic Peninsula could potentially reach South Georgia within 140-160 days. Therefore, we suggest that the presence of calyptopes and furcilia in the middle of the Scotia Sea is the result of spawning on the continental shelf break region off the tip of the Antarctic Peninsula. As these life stages develop, they are advected further off-shore by the regional hydrographic regimes.

Calyptopes and furcilia have also been found around Marguerite Bay at the base of the WAP. The importance of Marguerite Bay for krill populations has been noted in the past (Lascara et al., 1999; Ashjian et al., 2004; Piñones et al., 2013). Interestingly the hydrographic systems along the WAP mean that Marguerite Bay is a retention point for krill (Hofmann et al., 1996; Smith et al., 1999). Further modelling work has shown that particles released as far north as ~65 °S along the Antarctic Peninsula will be moved southwards in the coastal current (Thorpe et al., 2007). This evidence suggests that eggs spawned along the WAP (as far north as ~65 °S) could end up within Marguerite Bay. It is also possible that these larvae originate from local spawning, but there are no data to corroborate this.

Notwithstanding our uncertainties over spawning migrations, the evidence from the overall distributions of adults, eggs, nauplii and metanauplii suggests that laying of eggs occurs over wide areas including both shelf and adjacent deep water habitats, and from the Antarctic Peninsula up to South Georgia. However, the much more restricted distribution of calyptopes and furcilia suggests that many of these advected early stages fail to reach the feeding larval stages.

2.5.3 Partitioning of habitat by different life stages

We found strong evidence for habitat partitioning, visible both on the distribution maps themselves and through the use of water depth and mean temperature as simple habitat descriptors (Figures 6 and 7). While these are not complete descriptions of the krill habitat (which would include sea ice, food levels and other factors) they are sufficient to illustrate clearly that differing spatial distributions of the life stages exist. We have attempted to trace the strong differences in distribution between the life stages and between the early and late halves of the austral summer season in Figure 8. This illustrates the spatially-separated distributions of the larvae and juveniles, as well as the opposing on-shelf – off-shelf shifts in distributions of adults and juveniles throughout the season.

The strong on-shelf – off-shelf divide between larvae and juveniles is clear in all our depictions of distribution. Eggs were found in greatest densities in cooler, (-2 °C – 0 °C) shallower waters (1000 m - 2000 m) than furcilia, which were found in warmer (0 °C - 4 °C), deeper water (2000 m - 4000 m). This partitioning could be driven partially by the hydrological processes described above, that advect developing larvae from regions of egg production into downstream oceanic waters of the Scotia Sea. The survival of the calyptope and furcilia in the offshore region will likely also depend on food availability. This was highlighted by previous research that modelled the transport of larval stages across the Scotia Sea and found that it could only be successful under certain food conditions (Fach et al., 2006). Food availability is thought not only to determine the success of larval stages but, through intraspecific competition for food, large scale population fluctuations in adults (Ryabov et al., 2017). Across this whole sector, the density of post-larval krill can vary both coherently and greatly between years (Atkinson et al., 2014) reflecting high recruitment success only once or twice per decade (Quetin et al., 2003). This episodic recruitment leads to episodic one or two-year periods with enormous numbers of small krill (e.g. 1981/1982, 1996/1997). For schooling species, local grazing impact may be intense in years of high abundance, and only partially alleviated by dietary diversity (Atkinson et al., 2014) and by their nutrient excretion and fertilisation effects (Schmidt et al., 2016). During years of exceptionally high abundance of larval and juvenile krill, the partitioning of the main habitat between the life stages would reduce this competition for food.

The mechanisms behind the differing distributions of furcilia and juveniles are difficult to explain based on our current understanding of krill. The furcilia show a very clearly defined distribution over waters between 1000 m - 4000 m deep and 0 °C - 4 °C; these are characteristic of the Scotia Sea. In contrast, the juveniles have a strong affinity for shelf and shelf-slope habitats (0 m - 2000 m) which are both upstream and to the south. As our main distribution patterns are compared for the late season period (i.e. January to May), this means that these late-season juveniles will be one year older than the corresponding calyptopes and furcilia. This suggests that, during this intervening year, the developing juveniles have travelled south-west onto shelf habitats of the Scotia arc (Figure 8). The Antarctic Peninsula experiences annual sea ice cover, and the association of krill furcilia and juveniles to sea ice has been well documented (Daly and Macaulay, 1988; Marschall, 1988; Stretch et al., 1988; Daly, 1990a; Melnikov and Spiridonov, 1996; Frazer et al., 1997). The roles of sea ice for krill is an issue of active study (Ikeda, 1981; Ligowski, 2000) but the prevailing drift, both with ice and currents, transports larvae in a general north-easterly direction towards the Scotia Sea (Meyer et al., 2017). To counter this, it could be that the juveniles migrate back to the southern Scotia Arc where they concentrate during the summer. This possibility is in line with previous suggestions of horizontal migrations of krill throughout the season, for example, the concept of an offshore spawning migration (Siegel, 1988) and inshore migrations to overwinter (Cleary et al., 2016; Reiss et al., 2017). Contrasting early and late season bathymetric distributions of juveniles and adult male and female krill (Figure 7) provide further support for the concept of an active migration.

In contrast to all of the other life stages, the adult krill (males and females in both the early and later season) are much more ubiquitous throughout the study area. The very highest densities are found in habitats with very deep water (>4000 m) and relatively warm temperatures (2 °C - 4 °C) characterising north-eastern Scotia Sea. Adult krill can maintain swimming speeds of 10-15cms^{-1} (Kils, 1981) and advection must clearly play a strong role in governing their distribution (Murphy, 2004; Murphy et al., 2004). However, the ability of krill to swim may allow them to move perpendicularly to the dominant flows (Kanda et al., 1982; Atkinson et al., 2008; Tarling and Thorpe, 2014). This ability to influence their destination, in combination with a multi-year adult lifespan that allows time for dispersal, could explain such a broad distribution of the adult stages of krill.

2.5.4 Wider implications

Notwithstanding our uncertainty over the driving mechanisms, our study shows that life stages of krill are partitioned between a range of habitats within their population centre in the south-west Atlantic sector. For a krill to reach adulthood, these different habitats must be utilised sequentially over the course of their development. One area that is particularly important to krill appears to be the tip of the Antarctic Peninsula, being the only location where we find high densities of eggs, adults and juveniles, and where the high densities of calyptopes and furcilia could originate from.

This localised nature of successful spawning is important in the context of the krill fishing industry. Since the mid-1990s almost all krill fishing in the Southern Ocean has taken place in the south-west Atlantic, particularly around South Georgia, the South Orkneys and the South Shetland Islands and, more recently, in the Bransfield Strait (Grant et al., 2013b; Nicol and Foster, 2016; Santa Cruz et al., 2018). The overlap of areas targeted by the fishery and the location of high adult densities is not surprising. However the presence of eggs in fished locations and the short time between spawning and hatch (~7 days at 0.5 °C (Yoshida et al., 2004)), suggests that the fishery also overlaps with spawning sites. An objective of krill fishery management is to maintain stable recruitment of the target stock (Hinke et al., 2017). This objective might be harder to achieve if fishing intensity at spawning sites increases due either to an overall increase in fishing effort or a concentration of effort in these sites. CCAMLR aims to develop a finer scale management approach than the large subarea catch limits shown in Figure 2 (Nicol and Foster, 2016). Information on the location of spawning, such as that provided here, should be considered in the development of this approach to help minimise fishery impacts on recruitment.

Our study contributes to the evidence that spatial heterogeneity in the south-west Atlantic sector results in the concentration of many activities, including critical krill life cycle processes, foraging of land-based predators, fishing, tourism and scientific research (Griffiths, 2010; Powell et al., 2012; Hinke et al., 2017; Santa Cruz et al., 2018). Indeed, many of these activities occur in the same shelf areas, increasing the potential for human activities to impact the ecosystem. The region is also undergoing long-term climatic warming and krill distribution and abundance appear to be changing in response (Atkinson et al., 2019). Given the need to understand how krill will respond to future change, we hope that our data and maps describing the key areas for life-cycle completion form a baseline for future modelling initiatives

Chapter 3 Temperature-induced hatch failure and nauplii malformation in Antarctic krill

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Keywords: Antarctic krill, hatching success, nauplii, malformation, temperature

FAP helped to lead the conceptualisation of the experimental design, carried out all of the field experiments, analysed all of the field experiment samples, analysed the data created the figures and wrote the original paper. Experimental conceptualisation was undertaken with help from SK, RK, AA, SFS, and GAT. AC and RK conducted the laboratory experiments and analysis. All authors contributed significantly to the supervision, review and editing of this manuscript.

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3.1 Abstract

Antarctic krill inhabit areas of the Southern Ocean that can exceed 4.0 °C, yet they preferentially inhabit regions with temperatures of -1.5 to ≤1.5 °C. Successful embryonic development and hatching are key to their life cycle, but despite the rapid climatic warming seen across their main spawning areas, the effects of elevated temperatures on embryogenesis, hatching success and nauplii malformations are unknown. We incubated 24,483 krill embryos in two independent experiments to investigate the hypothesis that temperatures exceeding 1.5 °C have a negative impact on hatching success and increase the numbers of malformed nauplii. Field experiments were on krill collected from near the northern, warm limit of their range and embryos incubated soon after capture, while laboratory experiments were on embryos from krill acclimated to laboratory conditions. The hatching success of embryo batches varied enormously from 0 - 98% (mean 27%).

Both field and laboratory experiments showed that hatching success decreased markedly above 3.0 °C. Our field experiments also showed an approximate doubling of the percentage of malformed nauplii at elevated temperatures, reaching 50 % at 5.0 °C. At 3.0 °C or below however, temperature was not the main factor driving the large variation in embryo hatching success. Our observations of highly variable and often low success of hatching to healthy nauplii suggest that indices of reproductive potential of female krill relate poorly to the subsequent production of viable krill larvae and may help to explain spatial discrepancies between the distribution of the spawning stock and larval distribution.

3.2 Introduction

The success or failure of the early life stages is a key part of species' life cycles. For broadcast spawners, embryonic success is reliant upon internal reserves, parasitism, predation and the physical environment. In marine crustacean species, some embryonic stages are very sensitive to environmental conditions, specifically temperature (García-Guerrero et al., 2003). High temperatures have been found to cause higher metabolic rates, lower growth and survival rates, and greater numbers of larval malformations in crustacean embryos (Rhodes, 1981; Jones, 1995; Naylor et al., 1999; Kumlu et al., 2000; Paula et al., 2001; Manush et al., 2006). All of these responses to temperatures can lead to reduced embryonic success, higher levels of nauplii failure, and lower recruitment to the larval population. Identifying the relative importance of temperature on embryonic development, success, and nauplii malformations will lead to development of more accurate population dynamic models on both spatial and temporal scales.

Antarctic krill, (*Euphausia superba)* hereafter "krill", are an ecologically and commercially valuable stenothermal crustacean species in the Southern Ocean where they inhabit a temperature range of -2.0 °C to 4.0 °C (Tarling et al., 2006; Cuzin-Roudy et al., 2014). Within this 6.0 °C temperature envelope, krill are considered to preferentially inhabit regions with temperatures between -1.5 °C and ≤1.5 °C (Cuzin-Roudy et al., 2014; Perry et al., 2019). Experimental results by Atkinson et al. (2006) show that adult krill growth rates peak at 0.5 °C and decrease rapidly to zero above 3.0 °C. Yet, the upper temperature tolerance of krill embryos has never been defined. Anecdotal evidence published by George & Stromberg (1985) stated that an incubation temperature of 4.0 °C caused complete embryonic failure but their finding requires further investigation. The lower temperature tolerance of krill embryos was more exhaustively tested by Yoshida et al., (2004) who recorded successful hatching down to -2.1 °C. Krill embryos are negatively buoyant and, once spawned, they sink until they hatch as nauplii (Fraser, 1936; Marr, 1962). Throughout their roughly six-day descent, embryos experience a range of temperature conditions that affect water density and hence sinking rate (Ross et al., 1988). The variation in temperature during this descent also affects the speed at which they develop (Marschall, 1983; George, 1984; Ross et al., 1988; Yoshida et al., 2004).

The south-west Atlantic sector of the Southern Ocean is key for krill, being the region with the highest krill densities, where the fishery operates and where the population extends to its warmest thermal limit around the island of South Georgia (Atkinson et al., 2008). Surface water temperatures around South Georgia can reach over 4.0 °C, yet its waters contain high densities of sexually mature adult krill that support the fishery (Marr, 1962; Perry et al., 2019). This adult population does not, however, translate to high larval recruitment as expected (Ward et al., 1990; Tarling et al., 2007; Siegel and Watkins, 2016a). Suggested reasons for this lack of larval recruitment include the area being unsuitable for spawning, predation on larvae, and larval export during the winter (Ruud, 1932; Tarling et al., 2007). However, the effect of temperature on embryonic development and larval recruitment around South Georgia has not been examined. A wider understanding of the factors that modulate krill embryogenesis and hatching success will allow us to better understand, model and predict their population distribution and dynamics (Kawaguchi, 2016).

We tested the hypothesis that temperatures approaching the warm distributional limit have a negative impact on egg hatching success and naupliar development. To investigate this, we ran two independent incubation experiments. In one, we incubated embryos from gravid females collected and immediately incubated from around South Georgia and the South Sandwich Islands. In the other, we incubated embryos from females that had been collected and then laboratory-acclimated at the aquarium of the Australian Antarctic Division in Tasmania.

3.3 Methods

3.3.1 Overview

For this study, we incubated 24,483 embryos from twenty females across six temperature treatments. These twenty females were collected from two sources. Fourteen gravid females were collected from a field expedition and incubated for short periods at sea to harvest their eggs; experiments carried out on these embryos will hereafter be referred to as field experiments. Embryos from field females were incubated at 0.5, 3.0 and 5.0 °C. The remaining six females had been originally collected from the field and were subsequently maintained in controlled conditions for a minimum of ten months, and re-matured in captivity. These are hereafter referred to as laboratory experiments. Embryos from laboratory females were incubated at 0.0, 1.0, 3.0, 5.0 °C, and 7.0 °C. Differences in the range of set temperature between our field and laboratory experiments were a result of the different amounts of space and resources available in each context.

3.3.2 Embryos from our field experiments

3.3.2.1 Sampling method and collection of embryos

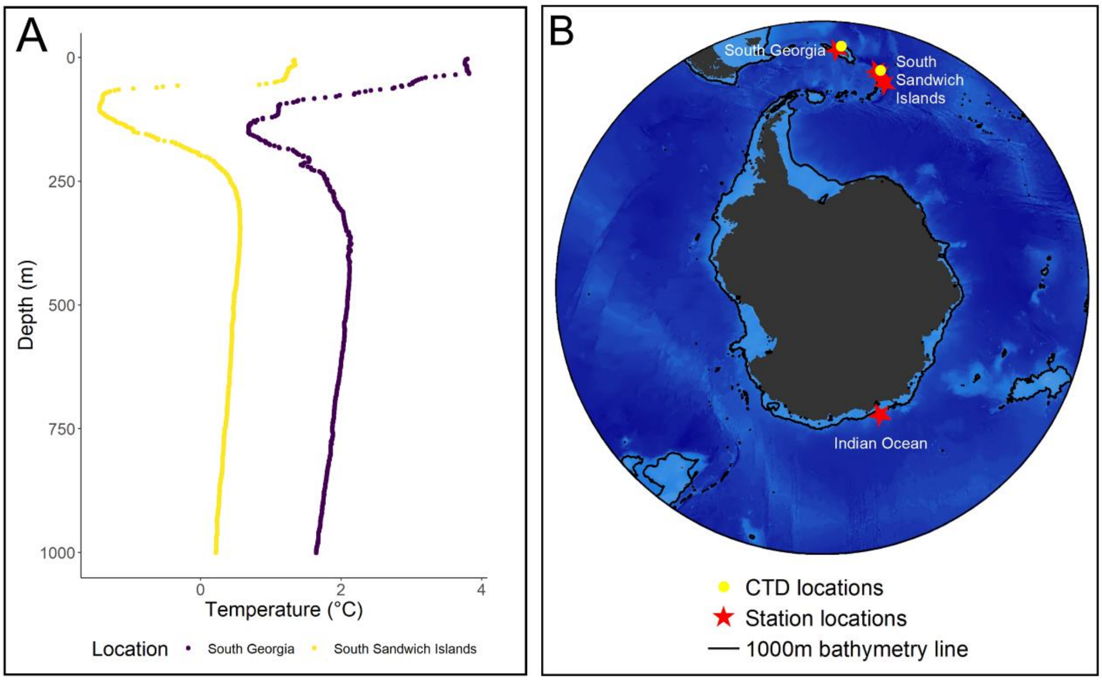

Figure 9. Sample locations for field and laboratory experiments as well as temperature details from the field experiments. A) The station locations at which gravid females were captured for our field and laboratory experiments. Field samples were collected from the Atlantic sector. Laboratory samples were collected from the Indian Ocean sector of the Southern Ocean B) Temperature profiles collected from CTD casts at South Georgia and the South Sandwich Islands during the cruise on which the field experiments were undertaken.

Krill were collected from the Scotia Sea using a Rectangular Midwater Trawl with an effective mouth area of 8m^2 net (RMT8), or an RMT 1 + 8 (Baker et al., 1973) on board the RRV *Discovery* during January and February 2019 (Figure 9). Within 30 minutes of net recovery, undamaged gravid females were relocated to stable environmental conditions similar to those described in Tarling et al. (2006). Gravid females were transferred individually into perforated 500 ml lidded containers with a 1 mm mesh placed 25 mm from the bottom to allow spawned embryos to sink to the bottom to avoid cannibalism (Ross and Quetin, 1983). These containers were then stacked up to six high inside 9 cm diameter perforated pipes within a 320 L aquarium. Unfiltered ambient temperature seawater, at a flow of 20 L per minute from the ship's non-toxic intake at 5 m depth, was passed through the aquarium to provide the females with a constant turnover of fresh oxygenated seawater and any available plankton. We did not provide any supplementary food to the females. Water temperature of the aquarium was monitored frequently to ensure it aligned with ambient ocean conditions. Temperature profiles from both South Georgia and the South Sandwich Islands are shown in Figure 9. A cover was placed over the top of the aquarium so that krill were kept in subdued light conditions except for routine maintenance checks.

Krill were checked every twelve hours (12:00 and 00:00 local time) for embryos, until they had spawned. All females spawned within seven days of being placed in the aquarium. An embryo batch refers to a complete spawn from a single female that was consequently used for experimentation. No more than a single batch was used per female. All egg batches were checked for fertilisation which was determined by looking for the formation of fertilization jelly (Jia et al., 2014). All egg batches checked were fertile and were progressed to the next stage of the experiment. Each of the females, from which embryo batches were taken, was weighed and measured (AT = from anterior edge of eye to tip of telson) (Morris et al., 1988), then frozen at -80 °C with any remaining embryos from the batch.

From fertilised embryo batches (of >1000), ~ 30 embryos were immediately fixed in 4 % formalin as an initial (T0) sample and the remaining embryos were progressed to the experimental stage. Embryo batches from fourteen different females were collected from five different stations split between two main locations (South Georgia and the South Sandwich Islands). Of these fourteen females, four originated from South Georgia and ten were from the South Sandwich Islands (Table 3).

3.3.2.2 Experimental method

For each of our fourteen embryo batches, we investigated embryonic development at three different temperature treatments (Supplementary Figure 1). This allowed hatching success between females to be examined in addition to change caused by temperature. Individual embryo batches (i.e. embryos from a single female) were immediately randomly divided into nine 250 ml bottles, each containing ~60 embryos. The 250 ml bottles were prepared with 0.45 µm filtered seawater. All seawater was pH-tested at this stage of the experiment, but a malfunction resulted in the readings being inaccurate, so pH levels are not reported for these experiments. Three bottles from each batch were placed in scientific fridges at each of our treatment temperatures. Fridges maintained temperatures within ±0.5 °C of set temperatures. We used three temperature treatments for our field experiments. Our lowest temperature was 0.5 °C, representing the temperature optimum for post-larval growth (Atkinson et al., 2006). The other treatment temperatures were 3.0 °C and 5.0 °C chosen to be either side of 4.0 °C that George & Stromberg (1985) suggested to be the point of embryonic failure.

Table 3. Field station details. Gravid females incubated in our field experiments were captured from five stations within the south-west Atlantic sector of the Southern Ocean. Blank cells refer to unknown depth of krill schools.

Station code	**General location**	**No. of females to successfully spawn**	**Depth of krill school (m)**	**Latitude (°S)**	**Longitude (°W)**	**Time**	**Surface water temperature (°C)**	**Water depth (m)**	**Female weights**	**Female lengths**
SG	South Georgia	4	20	53.837	39.179	03:04	4.1	276	1.8, 2.1, 1.85, 1.55	58, 60, 57, 55
SSI1	South Sandwich Islands	5	-	55.652	27.706	15:31	1.1	1376	1.45, 1.7, 1.65, 1.25, 1.85	55, 58, 56, 52, 58
SSI3	South Sandwich Islands	1	-	57.265	24.370	00:34	1.4	6522	1.5	54
SSI2	South Sandwich Islands	3	48	56.110	26.601	21:09	1.6	2770	1.85, 1.35, 1.65	60, 52, 57
SSI4	South Sandwich Islands	1	30	56.146	26.588	22:35	1.5	2876	1.6	56

Every 24 hours, ~30 embryos were removed from each experimental temperature and fixed using 4 % formaldehyde solution. Each bottle started with ~60 embryos such that each bottle contained two days' worth of embryos. Experiments lasted for six days (Ross et al., 1988; Yoshida et al., 2004). Oxygen consumption of sixty krill embryos for six days is predicted to be 15 - 30 µl (Ikeda, 1984; Yoshida et al., 2011). Considering that the oxygen saturation level in seawater would be 2.5 ml of oxygen per 250 ml, a reduction in oxygen of 30 µl would be minimal even at the elevated temperature treatments. Taking this into consideration, we did not measure oxygen levels in the experimental bottles during our field experiments. Our experiments resulted in nineteen samples from each egg batch: six from each of the three temperature treatments and one T0 sample. From the fourteen embryo batches, three out of the total 266 samples were damaged and impossible to analyse.

3.3.2.3 Laboratory analysis

Preserved embryos and larvae were observed using an Olympus SZX16 microscope with Olympus SDF PLAPO 1 x PF lens and photographed with a Canon EOS550D camera and captured with EOS utility software. Each sample was photographed and analysed for different life stages (Supplementary Figure 2). Three embryonic stages were identified prior to hatching: two cell, multiple cell and limb bud. We used photographs from Jia et al. (2014) to help identify these stages. Hatched nauplii were categorised as either healthy or malformed, with total hatching success being the sum of these two categories. Three additional stages were also identified; entrapped embryos were nauplii that either died whilst hatching, or were fixed in formalin at the time they were hatching, unclassified embryos were those that were damaged and therefore unclassifiable, and all embryos that could not be categorised were recorded simply as embryos.

3.3.3 Embryos from the laboratory experiments

3.3.3.1 Sampling method and collection of embryos

The krill population used in the laboratory experiments originated from the Indian Ocean sector of the Southern Ocean between 64.67 to 64.71 °S and 109.44 to 109.69 °E during the 2017/2018 field season (Figure 9). Male and female krill were returned to the Australian Antarctic Division's marine research aquarium and maintained at 0.5 °C, where they matured and spawned naturally (Kawaguchi et al., 2010a). Embryos were obtained in November 2018. While these krill were caught from different swarms the locations caught were in close proximity, and they all experienced an identical environment for the ten months prior to spawning, so we have referred to them as a single entity “Laboratory krill”. Individual gravid females were isolated and floated in 2 L spawning bottles with mesh set 1 cm from the bottom of the bottle to ensure embryos were not cannibalised by the female after spawning. Spawning was checked for twice a day. When spawning was observed, the eggs were gently transferred to 5 L containers and checked under the microscope for fertilisation by looking for the formation of fertilization jelly (Jia et al., 2014). Six batches of >1000 embryos originating from six different females were used.

3.3.3.2 Experimental method

Each egg batch was randomly divided into 30 experimental bottles (250 ml) with ~30 embryos per bottle. Each experimental bottle had a window with 400 µm mesh to allow exchange of temperature-controlled seawater in the bottle. Experimental bottles were then randomly placed in five different incubation tanks with recirculating temperature-controlled water at five different temperature settings (six experimental bottles each in 0.0, 1.0, 3.0, 5.0, and 7.0 °C respectively). One bottle from each batch and temperature treatment was sampled every 24 hours. The temperature-controlled recirculating seawater was measured for temperature, salinity and pH prior to pipetting out the embryos and larvae into glass vials and fixing with 4 % formaldehyde solution.

3.3.3.3 Laboratory analysis

Embryos and larvae were observed with Leica M205C dissecting stereomicroscope with a Leica DFC 450 camera and Leica LAS V4.0 software. Data regarding embryonic developmental stages and nauplii malformations were not collected from the laboratory data.

3.3.4 Statistical analysis

All statistical analyses were conducted in the R 3.4.1 programming environment (R Core Team, 2017). The relationship between the number of hatched and unhatched eggs was examined using a generalized linear model (GLM) using a quasibinomial distribution following the method used by Mayor et al. (2012). Field and laboratory results were tested independently of each other. The effects of the following variables were also investigated using this model: temperature (field levels = 0.5, 3.0 and 5.0 °C, laboratory levels = 1.0, 3.0, 5.0 °C) and individual female (field levels = females 1-14, laboratory levels = females 1-6). An optimal model was backwards selected from a full model containing all variables.

We examined the relationship between the number of healthy and malformed nauplii at different temperature treatments using a non-parametric Kruskal-Wallis test. We only performed this analysis on embryos from our field experiments where the data were available. The same method of analysis was used to test the difference between weight and length of field females on hatching success and number of nauplii malformations. For all analyses $\alpha = 0.05$.

We acknowledge that our sample size of 20 females will affect the statistical power of our analyses. However, we emphasise the difficulty in obtaining field samples of healthy gravid females, which subsequently spawn within an experimental setting that has limited sample sizes in all previous attempts of this sort (Table 5). Furthermore, the numbers obtained in the present study still allow robust statistical analyses to be performed. The design of our field experiments means that repeat sampling could bias our analysis. To account for this, we ran a sensitivity analysis using (1) all days between 1 and 6, (2) odd days only and (3) even days only. We found that the repeat sampling did not produce false trends and consequently we have reported on the analysis that used all six days of sampling.

Table 4. Effect of temperature on hatching success from both field and lab experiments. At each of the temperature treatments three values are given: (1) mean percentage of hatching success, (2) +/- standard deviation (SD) and (3) a range of hatch percentages in brackets. Mean values have been used (rather than medians) to allow direct comparison with other experimental results (Table 5).

Location	**0.0**°C	**0.5**°C	**1.0**°C	**3.0**°C	**5.0**°C	**7.0**°C
Laboratory	73 ± 35 (13 - 98)	-	77 ± 28 (36 - 98)	67 ± 29 (28 - 96)	31 ± 30 (0 - 72)	5.0 ± 6.5 (0 - 16)
South Georgia	-	5.7 ± 2 (3 - 8)	-	18 ± 14 (7 - 39)	6.5 ± 4.4 (0 - 10)	-
South Sandwich Islands	-	21 ± 22 (0 - 54)	-	23 ± 21 (0 - 52)	5.8 ± 6.3 (0 - 16)	-

3.4 Results

Firstly, we present the results of our quasibinomial GLM which examined how hatching success was affected by female and temperature in both our field and laboratory experiments. Secondly, we describe the effects of temperature on the number of nauplii malformations and egg death.

3.4.1 Variation in hatching success

3.4.1.1 Variation in hatching success between females

Hatching success was significantly affected by female in both our field (Quasibinomial GLM, F = 4.204, df = 38, p = <0.001) and laboratory results (Quasibinomial GLM, F = 8.6008, df = 38, p = <0.01) (Figure 10). The wet weights and lengths of females from the field experiments ranged from 1.25 - 2.1 g and 52 - 60 mm (Table 3). We found that neither the weight nor length of the field females had a significant effect on the hatching success or the occurrence of nauplii malformation. Weight and length data are not available for the laboratory data.

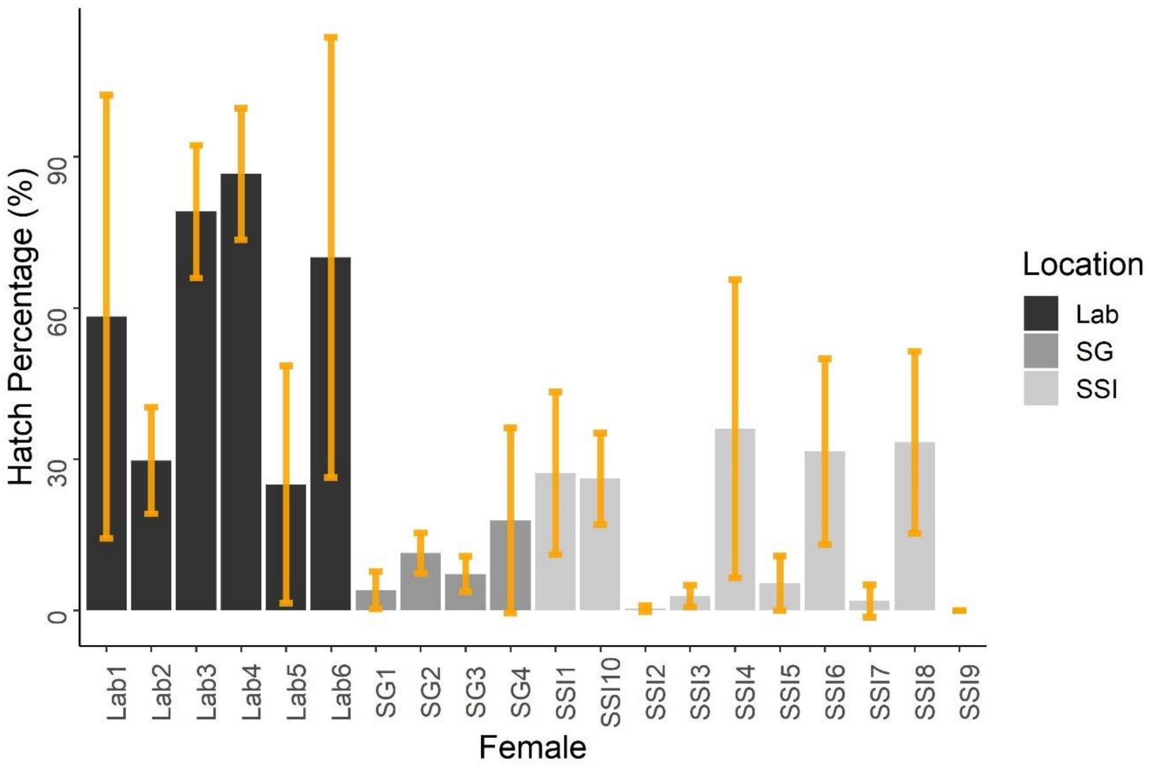

Figure 10. Mean hatch percentages of females from both the field and laboratory experiments. Egg batches from all twenty females were categorised into the two experiments from the laboratory (black bars) or the field. Field experiments are subdivided further into either South Georgia or the South Sandwich Islands. Average hatching success values and the standard deviation (shown by orange bar) were calculated for each female. The laboratory average hatching success was created using results from 1.0, 3.0 and 5.0 °C treatments. These temperature treatments were chosen as they were the closest match to the three temperature treatments averaged here in the field experiments (0.5, 3.0, 5.0 °C).

3.4.1.2 Variation in hatching success between temperature

Temperatures had a highly significant effect on hatching success in both the field- (Quasibinomial GLM, $F = 10.435$, df = 13, $p = <0.001$) and the laboratory experiments (Quasibinomial GLM, $F = 11.1707$, df = 15, $p = <0.01$).

Embryos from our field experiments had greatest hatching success at 3.0 °C, whereas laboratory embryos had greatest hatching success at 1.0 °C (Figure 11). The lowest recorded mean hatching success from our field experiments occurred at 0.5 °C from embryos collected from South Georgia (mean = 5.7 ± SD 2 %). At all temperatures in the field experiments, some embryo batches had no nauplii hatching. The highest mean hatching success in our field experiments occurred at 3.0 °C from embryos collected from the South Sandwich Islands (mean = 23 ± SD 21 %).

The minimum mean hatching success between 1.0-5.0 °C from the laboratory experiments was recorded at 5.0 °C (mean = 31 ± SD 30 %). The highest recorded mean hatching success occurred at 1.0 °C (mean = 77 ± SD 28 %) (Table 5).

Embryos from both the field and laboratory experiments showed very similar trends in embryonic development, peaks and development times at both 3.0 °C and 5.0 °C, even though the hatching successes were different (Figure 12). Day six of both experiments showed that the percentage of larvae hatched at temperatures up to and including 3.0 °C were more than double that at 5.0 °C. Although hatching success was minimal, hatching did occur at the 7.0 °C treatment in the laboratory experiments.

3.4.2 Effect of temperature on nauplii malformation and egg death

Differentiation of embryos stages and nauplii into healthy or malformed was only done for the field experiments. We found a significant difference in the number of healthy nauplii hatching at different temperature treatments (Kruskal-Wallis, chi-squared = 6.97, df = 2, $p = 0.03$). Nauplii that hatched at 5.0 °C were twice as likely to be malformed than at the two lower temperature treatments (Figure 13). A negative correlation was identified between the total hatch percent and the percentage of hatched malformed nauplii ($R^2 = 0.11$, $p = 0.0589$, $n = 33$).

Field experiments showed an average of 53 % of embryos developing on day one, and 34 % by day six (Figure 14). Across the six days of the experiment the average number of embryos developing differed at each treatment; 40 % (0.5 °C), 41 % (3.0 °C) and 34 % (5.0 °C). The percentage of embryos reaching the multiple cell stage on day one decreased with increasing temperature, from 56 % to 49 %. The average percentage of embryos failing to develop from the multiple cell stage to limb bud ranged from 30-32 % across treatments. The average percentage of entrapped nauplii was 2 % at 0.5 °C and 3.0 °C but increased to 5 % at 5.0 °C.

Table 5. Prior hatching success results. Results of all known experiments on egg hatching success rates in Antarctic krill give context to our results.

Reference	Mean (range) of egg hatching success (%)	Source of females	Egg incubation temperature (°C)	Experiment details	Number of females used
Kikuno, 1981	20 (0 – 63)	Southern Indian Ocean	0.4	Females incubated immediately for egg production. Females not fed.	6
Harrington and Ikeda, 1986	70 (45 – 89)	Prydz Bay	0 ± 0.5	Females incubated immediately for egg production. Females not fed.	43
Hirano et al., 2003	19 (0-71)	West Atlantic Sector/Australian Antarctic Division Stocks	0.4	Females maintained for up to three months before eggs collected. Females fed.	28
Yoshida et al., 2004	44 (7-58)	Unknown	-2.1 – 2.4	Females maintained for up to four months before eggs collected. Females fed.	4
Yoshida et al., 2011	24 (0-48)	Western Indian Ocean	0.5	Females incubated immediately for egg production. Females not fed.	5

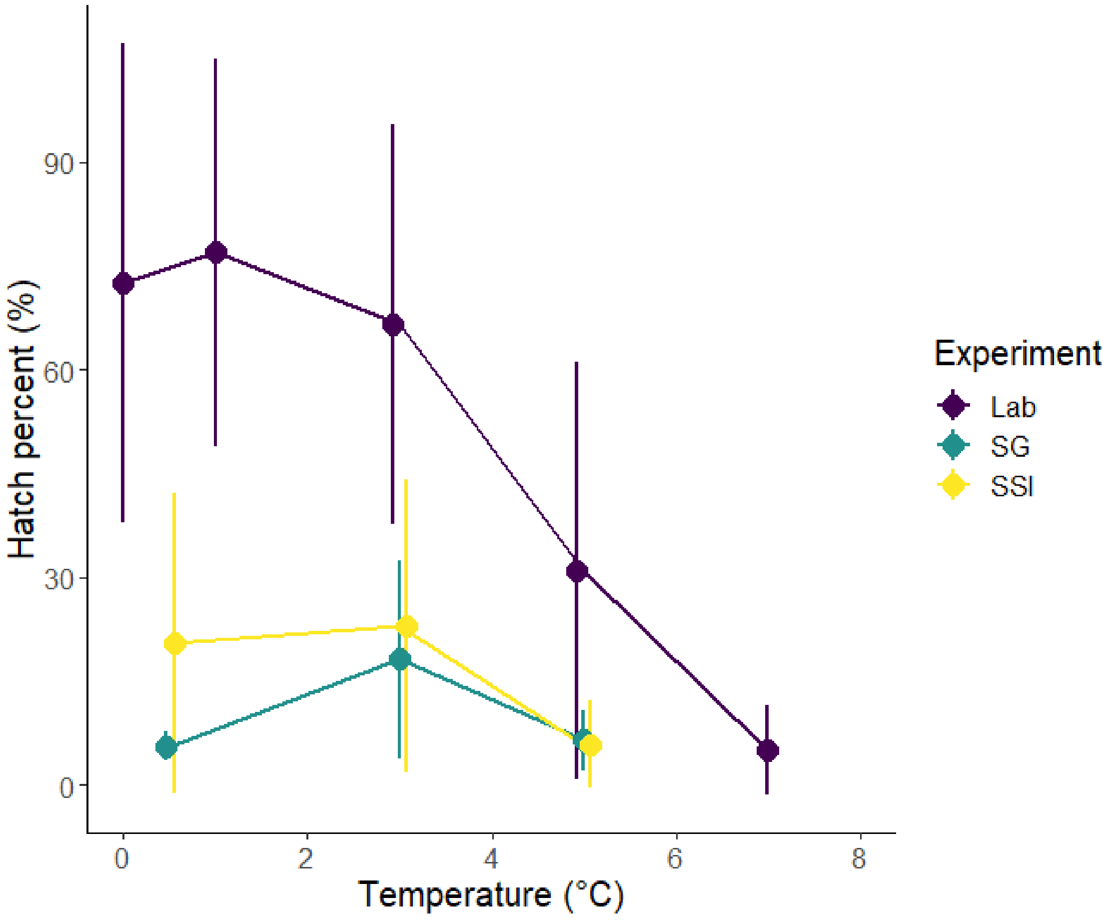

Figure 11. Variation in hatching success with temperature in field and laboratory experiments. Field experiments are divided into South Georgia and the South Sandwich Islands. Mean hatching success values presented here highlight the variation between the two experiments. Each data point has been slightly offset to ensure the bar showing standard error is visible.

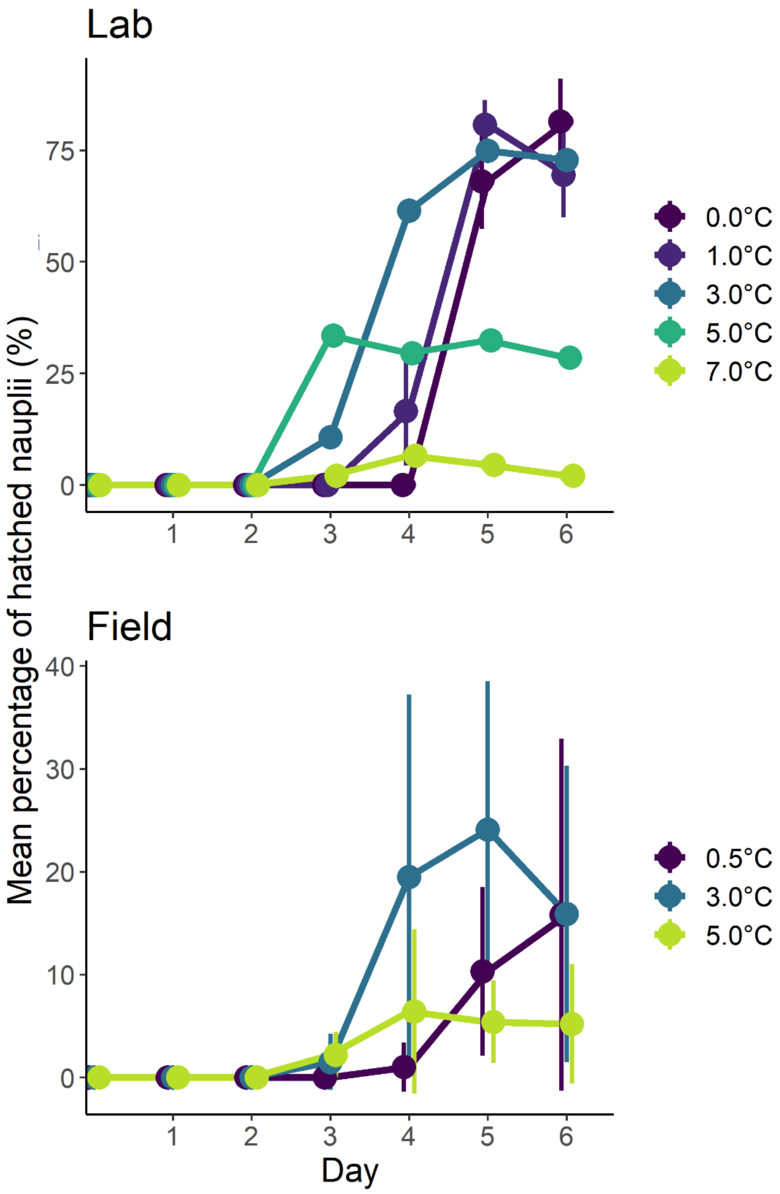

Figure 12. Effect of temperature on rate of embryonic development. The mean percentage of nauplii hatched for each of the temperature replicates for each day of the incubation experiments. Each data point has been slightly offset to ensure the bar showing standard error is visible.

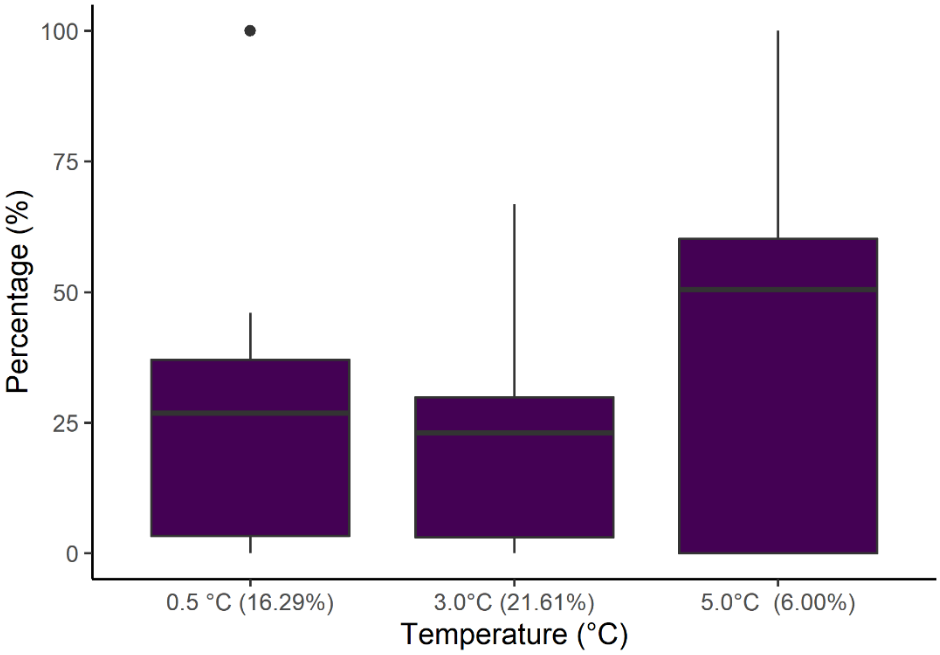

Figure 13. Percentages of malformed nauplii. All hatched nauplii in our field experiments were categorised as either healthy or malformed. This table presents the percentage of malformed nauplii for each of the three temperature treatments. On the x-axis the number in brackets is the mean total hatch percent at the corresponding temperature. The error bars show standard deviation, and the horizontal bar shows the mean percentage values.

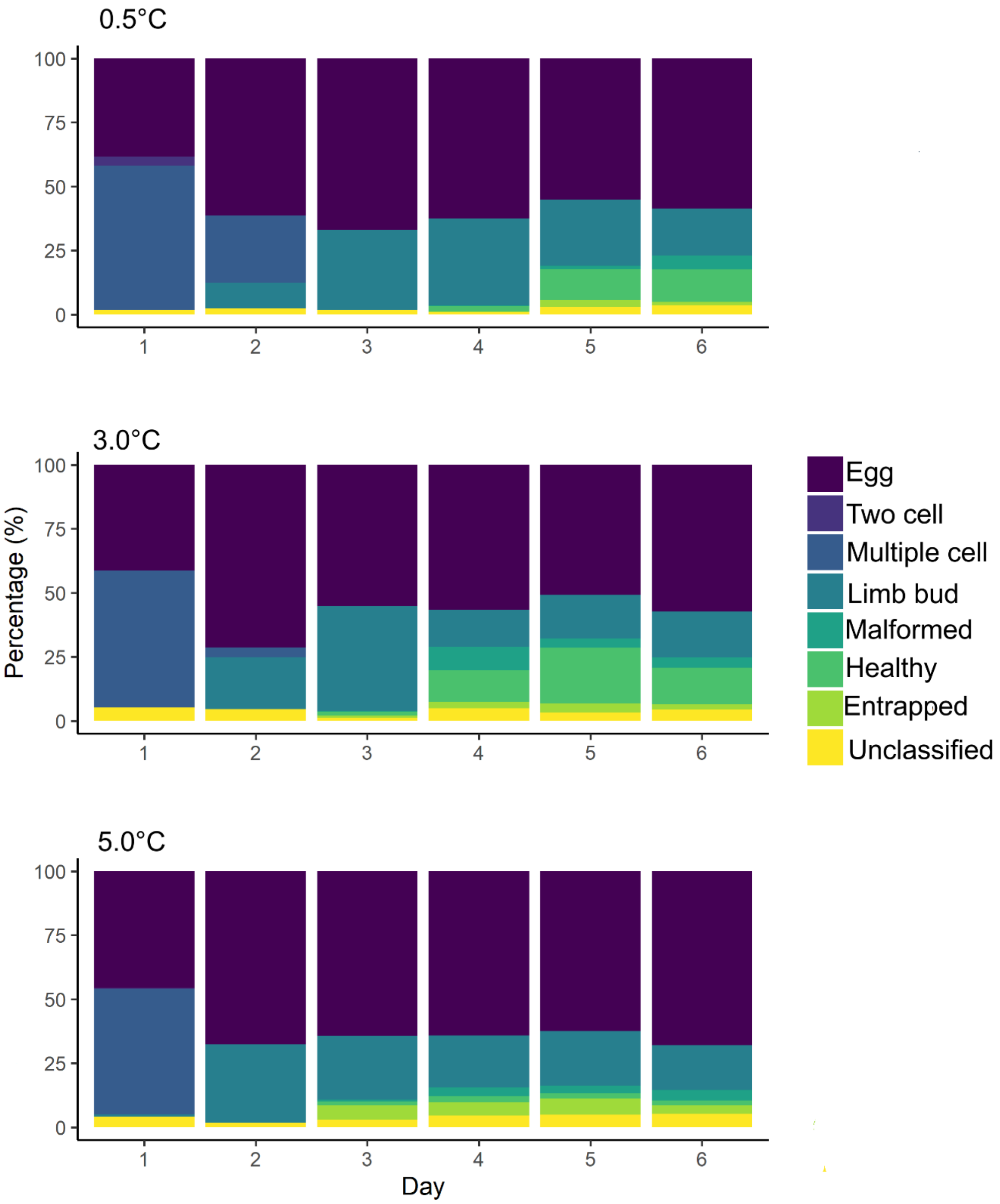

Figure 14. Rate of embryonic development. The rate of embryonic development from each of the temperature treatments in our field experiments. Each of the recorded embryonic development stages is shown in a different colour. For each day of the experiments the mean percentage of each developmental stage is given.

3.5 Discussion

Total hatching success in our field experiments was low and variable and the percentage of nauplii hatching with malformations increased significantly above 3.0 °C. Total hatching success in our laboratory experiments was higher, but also highly variable. In regard to our hypothesis we found that both field and laboratory experiments showed the inhibitory effect of temperature above 3.0 °C regardless of the reported mean hatching success. From our field experiments we also found a doubling of the percentage of malformed nauplii between 3.0 and 5.0 °C. Below, we describe the influence of temperature on embryonic success in both the field and the laboratory experiments, the implications of our findings for understanding krill recruitment at a regional scale, and how krill reproduction may be affected in a warming climate.

3.5.1 Effect of temperature on hatching success

Krill embryos did not hatch well above 3.0 °C, either in the laboratory or the field. However, contrary to previous suggestions (George and Stromberg, 1985), we did not find complete inhibition of embryonic development above 4.0 °C in either of our experiments. Embryos hatched at 5.0 °C in both our field and laboratory experiments and in very low numbers at 7.0 °C in the laboratory experiments, a finding that shows krill embryos are more resilient to temperature than suggested by George and Stromberg (1985). Field experiments also showed other responses to high temperatures, namely a lower percentage of embryos reaching the multiple cell stage, an increase in the percentage of embryos becoming entrapped during hatching and a significant increase in the percentage of nauplii hatching with visible malformations.

These results suggest that temperatures above 3.0 °C have a strong effect on hatching success and the prevalence of nauplii malformations in krill. Antarctic marine species are known for their stenothermy (Peck et al., 2004) reflecting their long evolutionary isolation (Hempel, 1985). Their physiology, such as enzyme reactions, diffusion and membrane transport are adapted for polar temperatures, and warmer temperatures inhibit these processes. This variation of biological function in response to changing temperatures could be the reason for the variation in embryonic development speeds described in Ross et al. (1988) and Yoshida et al. (2004) and similarly reported from our own experiments. Adult krill growth rates are also highly sensitive to small temperature changes; growth rates peak at ~0.5 °C and decrease rapidly towards zero above 3.0 °C (Atkinson et al., 2006). We suggest that future work should investigate exactly why the physiology of krill is so negatively affected by seemingly small changes in temperature.

Low hatching success recorded from prior incubation experiments have been attributed to handling effects, as shown in *Euphausia pacifica* (Ross, 1981). We handled the embryos carefully, just once, and in a consistent manner across all experiments. Such methods have been shown to yield high embryo hatching success in several experiments (Harrington and Ikeda, 1986; Yoshida et al., 2004, 2011) as well as in our own laboratory experiments. We found consistent trends in either low or high hatching success of fertilized embryos across multiple krill sampled from different schools which, given our consistent methods, would be hard to explain in terms of handling-based artefacts. Furthermore, studies on copepods have shown that, when embryo success is low, more of the hatching nauplii are malformed (Mayor et al., 2012; Maud et al., 2015), which aligns with our results. Taken together, the evidence suggests that our results are not an artefact of experimental procedures.

3.5.2 Causes of high variability in hatching success

Evidence from our results and from other published studies (Table 5), show that krill embryos exhibit a high variability in the hatching success of their embryos and, on occasion, have extremely high or low success. This phenomenon also holds true for other euphausiid species (Gómez-Gutiérrez, 2006). Hatching success of *Euphausia pacifica* have been reported to range from 50 to 94 % (Feinberg et al., 2006), <5 to >95 % (Ross, 1981) and <10 to <40 % (Gómez-Gutiérrez, 2002). In accordance with results from prior studies, we also found high levels of variability in mean hatching success between females in both our field (15 %, 0-54 % ± SD 17 %) and laboratory (58 %, 0-98 % ± SD 34%) studies. Our field results showed that neither the weight nor the length of the female krill had a significant effect on the hatching success or the number of malformed nauplii. The well-defined relationship between female length and brood size in euphausiid species suggests that brood size does not have an effect hatching success and malformed nauplii (Ross and Quetin, 1983; Harrington and Ikeda, 1986; Feinberg et al., 2007). Results from our field experiments also showed a high incidence of malformed nauplii, a factor poorly reported on in the literature.

The reasons behind this high level of variation are unclear; however, we suggest that one, or a number of other environmental factors drive hatching success below 3.0 °C. The extremely high energetic cost of egg production in krill (Nicol et al., 1995) makes it likely that food quality and availability has a significant effect on quality of embryos. A modelling study by Rumsey and Franks (1999) suggested that variability of hatching success reported in *E. pacifica* could be due to female nutrition and the oceanic environment at the time and location of embryo release. Hatching success in krill has also been associated with quantity and composition of fatty acids in the embryos, which in turn is influenced by the maternal diet (Yoshida et al., 2011). Our findings show that future studies should prioritise assessing numbers of healthy nauplii and not just hatching success, as well as investigating the reasons for nauplii malformation. This level of variation is important to consider when estimating larval recruitment using spawning estimates.

3.5.3 Implications for understanding spatial variability in krill recruitment

Because krill are a key species in the food web and exploited commercially, there is much interest in identifying areas of successful spawning and recruitment (Hofmann and Hüsrevoğlu, 2003; Murphy et al., 2004; Perry et al., 2019; Thorpe et al., 2019). Our results highlight the extremely variable and often low krill hatching success in the field, suggesting that we need to refine our models to account for maternal factors as well as temperature.

As one important example, krill are abundant at South Georgia, where the females are the largest anywhere in the Southern Ocean (Schmidt et al., 2014) and clearly benefit from the high food concentrations (Pond et al., 2005). Yet, larval abundances are typically low here (Ward et al., 2006; Tarling et al., 2007; Perry et al., 2019). A variety of explanations have been proposed, including high predation and mass advection (Tarling et al. 2007). We found the mean hatching success of embryos from South Georgia to be 10 % in surface waters (~150 m) where temperatures can exceed 3.0 °C during summer (Whitehouse et al., 1996). While temperatures exceeding 3.0 °C will have increasingly negative impacts on hatching success, embryos spawned in the top 100m of the water column will sink out of these sub-optimal temperature conditions within 24 hours (Quetin and Ross, 1984; Hempel and Hempel, 1986) (Figure 9). It is also possible that embryos will be spawned below the surface warm layer and avoid interacting with warmer temperatures until they ascend as nauplii (Kawaguchi et al., 2011). To fully understand the interaction between embryonic development and temperature, we must understand how high initial temperatures within 24 hours of spawning may affect subsequent hatching success. Nevertheless, the degree of variation exhibited in our experiments strongly suggests that temperature conditions at South Georgia are not the only reason for embryonic failure, reduced nauplii survival and consequent poor recruitment to larvae.

Recruitment of juvenile krill to the adult population is highly variable from year to year (Quetin et al., 2003; Saba et al., 2014; Atkinson et al., 2019), and the causal factors vary regionally and possibly temporally (Loeb and Santora, 2015), with sea ice extent, ENSO and the Southern Annular Mode all being invoked. However there does not appear to be a clear stock-recruit relationship; moderate or high recruitment can follow years with exceptionally low biomass of the spawning stock (Siegel and Watkins, 2016). Fecundity of krill is known to vary with their age (Cuzin-Roudy, 2000; Tarling et al., 2016), but this study shows that, in addition to consideration of the overall output of eggs, we need to incorporate the large and unexplained variability of egg hatching success into our understanding of krill population dynamics.

3.5.4 Krill reproduction in a changing climate

Irrespective of any maternal effect, temperatures of 5.0 °C reduce hatching success by half compared to 3.0 °C. Concurrently, nauplii are more likely to be entrapped during hatching and are twice as likely to be malformed. Yet, neither current nor predicted Southern Ocean temperatures for 2100 create conditions whereby the full descent of an embryo will exceed temperatures of 3.0 °C (Meredith and King, 2005; Clarke et al., 2007; Barnes and Peck, 2008; Sallée et al., 2013). For the next century, it is unlikely that larval recruitment of krill will be driven directly by temperature, especially due to the smaller predicted changes below the surface waters of the Southern Ocean. However, this statement comes with a caveat, as we did not test temperature in tandem with any other future climate change stressors. Pressure from multiple climate change stressors, including pH and food availability (Atkinson et al., 2004; Quetin et al., 2007; Kawaguchi et al., 2011, 2013) may cumulatively make embryos more sensitive to temperature as they will ultimately have to expend more energy maintaining homeostasis.

Overall, our results show that krill embryos are negatively impacted by incubation temperatures that exceed 3.0 °C. Below this temperature, other environmental factors and individual female variability dictate hatching success. Further understanding of these controls may help to explain the discrepancy in the spatial distributions of spawning females and larvae (Perry et al., 2019). To model the distribution of krill in a changing climate to the level required for effective fishing management to operate (Hill et al., 2006), we need to take account of the factors that dictate embryo hatching success.

Chapter 4 Re-assessing the paradigm of an off-shelf spawning migration of Antarctic krill at the western Antarctic Peninsula

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FAP worked with SFS and GAT to conceptualise this study. FAP, collated and analysed the data, created the figures and wrote the original paper. Advice on the visualisation of data was provided by AA, SFS and GAT. GAT and SFS provided expertise on the use of generalised additive models. All authors contributed significantly to the supervision, review and editing of this manuscript.

Keywords: Antarctic krill, spawning, off-shelf, migration, CCAMLR

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4.1 Abstract

Only limited portions of the Antarctic shelf are thought to support successful spawning of Antarctic krill, since deep water is needed for early life stage development. Consequently, the current paradigm at the WAP is that larger krill migrate offshore to spawn in summer. This has major implications for seasonal overlap with shelf-based predators including fisheries. We examined this paradigm by analysing distributions of three length categories of krill (30-39 mm, 40-49 mm and 50-69 mm) using 41 years of data from the Antarctic Peninsula. Contrary to the current paradigm, we found no evidence for an off-shelf spawning migration. Instead, all adult size fractions were strongly concentrated over the shelf throughout the spawning season. This region is characterised by strong on-shelf-off-shelf gradients in chlorophyll-a (chl-a) and sea surface temperature. Using generalised additive models (GAMs) we found that the largest individuals (50-69 mm) are the most environmentally constrained. We suggest that the high food requirement of large spawning females, coupled with an oligotrophic off-shelf environment, means that they do not migrate

offshore to spawn, but remain in the richer feeding grounds on the WAP shelf. The presence of large, nutritious krill over the shelf throughout the season may be advantageous to land-based predators but raises concern for the management of fisheries that are also strongly shelf based at the WAP.

4.2 Introduction

The south-west Atlantic sector of the Southern Ocean contains key Antarctic krill spawning grounds, the highest population densities of the species and supports the entire commercial krill fishery (Grant et al., 2013b; Perry et al., 2019). Within this sector, krill densities vary at a range of scales. Spatially, there is habitat partitioning of krill life stages, with localised hotspots of spawning and reproduction in the Southern Scotia Arc (Perry et al., 2019). Considerable variation in densities has been noted between seasons (Siegel, 1988; Lascara et al., 1999; Cleary et al., 2016; Reiss et al., 2017) and years (Quetin and Ross, 2003; Fielding et al., 2014; Ross et al., 2014). However, the spatial distributions of these varying densities have been less well characterised, precluding any mechanistic understanding of the processes involved (Meyer et al., 2020).

Seasonal differences in krill distributions are attributed both to horizontal and to vertical migration patterns (Siegel, 1988; Sprong and Schalk, 1992; Lascara et al., 1999; Atkinson et al., 2008; Krafft et al., 2012). At the WAP, two major, and possibly inter-linked, horizontal krill migrations have been proposed. The first is a seasonal northward expansion of krill in summer and southward contraction towards inner shelf waters in winter (Kanda et al., 1982; Atkinson et al., 2008; Cleary et al., 2016; Reiss et al., 2017). The second is an off-shelf movement of adults in summer to spawn, as evidenced by a spatial segregation of length categories of mature adults over the shelf, shelf break and oceanic regions during the summer spawning season (Siegel, 1988; Lascara et al., 1999). This suggested spawning migration is thought to be a crucial component of the life cycle as it would allow spawned eggs to undertake their developmental descent to ~850 m without encountering the benthos before they hatch (Quetin and Ross, 1984; Hofmann et al., 1992; Hofmann and Hüsrevoğlu, 2003; Nicol, 2006). However, both Siegel (1988) and Lascara et al. (1999) used data collected from different seasons during different years, so seasonal and inter-annual variability may be conflated. To date, the migration theory has not been revisited using the multi-decadal composite databases now available.

The off-shelf migration of spawning adults reduces the availability of energy-rich prey for large populations of land-based predators and their young along the WAP (Ruck et al., 2014; Trathan and Hill, 2016).Krill experience greatly reduced food availability in the oligotrophic off-shelf WAP waters, however, predation pressure in this region is greatly reduced indicating that there is a potential risk-benefit trade-off in the habitat they occupy (Atkinson et al. 2008). Post-larval krill are estimated to require 17 – 28 % of their body carbon per day (Clarke et al., 1988; Quetin et al., 1994), and thus need access to a high quantity of suitable food to sustain their reproductive potential (Yoshida et al., 2011). Adult krill undergo profound changes in their metabolic demands as they grow, given the comparatively high weight exponent (>0.9) in respiration rate (Tarling, 2020). Consequently, different length categories of adult krill may have different relationships with key environmental variables, such as food availability. This may be especially true in the case of adult females that must also provide for the accumulation of large egg masses. However, distribution studies often treat adult krill (≥30 mm) as a single group (Marr, 1962; Perry et al., 2019) which loses resolution in how different life-stages may segregate spatially.

Using average krill densities created from 41 years of krill abundance and length-frequency data, as well as sea surface temperature (SST), chlorophyll-a (chl-a), distance from the shelf (1000 m) and bathymetry data, we investigated seasonal adult krill distributions along the WAP and their relationship to these environmental variables. In so doing, we address the null hypothesis that adult krill make a spawning migration offshore during the austral summer and that the largest krill move off-shelf.

4.3 Methods

4.3.1 Spatiotemporal domain of analysis

Our selected study domain was the CCAMLR subarea 48.1, located within the Atlantic sector of the Southern Ocean (and including the WAP) (Figure 15). This area was selected because it contains a major spawning area for krill (Perry et al., 2019), a strong focus of fishing activity (Grant et al., 2013b), and is where the current paradigm of an off-shelf spawning migration originated (Siegel, 1988; Lascara et al., 1999; Meyer et al., 2020). The region also contains the greatest amount of scientific net catch data.

For the fisheries management subarea 48.1, we generated numerical mean krill density (no. m^{-2}) values for three different length categories of adult krill (30-39mm, 40-49mm and, 50-69mm). We selected data from three seasonal periods: (1) October to December, (2) January, (3) February to April, excluding the austral winter period (May to September) owing to the paucity of data. This process required combining information from two different krill databases, KRILLBASE-abundance (Atkinson et al., 2017) and KRILLBASE-length-frequency (Atkinson et al., 2020). The composite nature of these krill databases means the data they contain are not evenly distributed in space or time. As a result, we applied several methods to select data. Only krill data from the “modern era” 1976 – 2016 were used for the present study. This modern era covers 41 years of data and represents the most comprehensive period of uninterrupted krill net catch data that overlaps with satellite-derived environmental data. Subarea 48.1 is a highly dynamic region that has undergone rapid climate change, including significant ocean warming (Meredith and King 2005). However, since the late 1990s, it has experienced a warming hiatus, when the recorded change in mean atmospheric temperature was <0.05 °C (Turner et al., 2016).

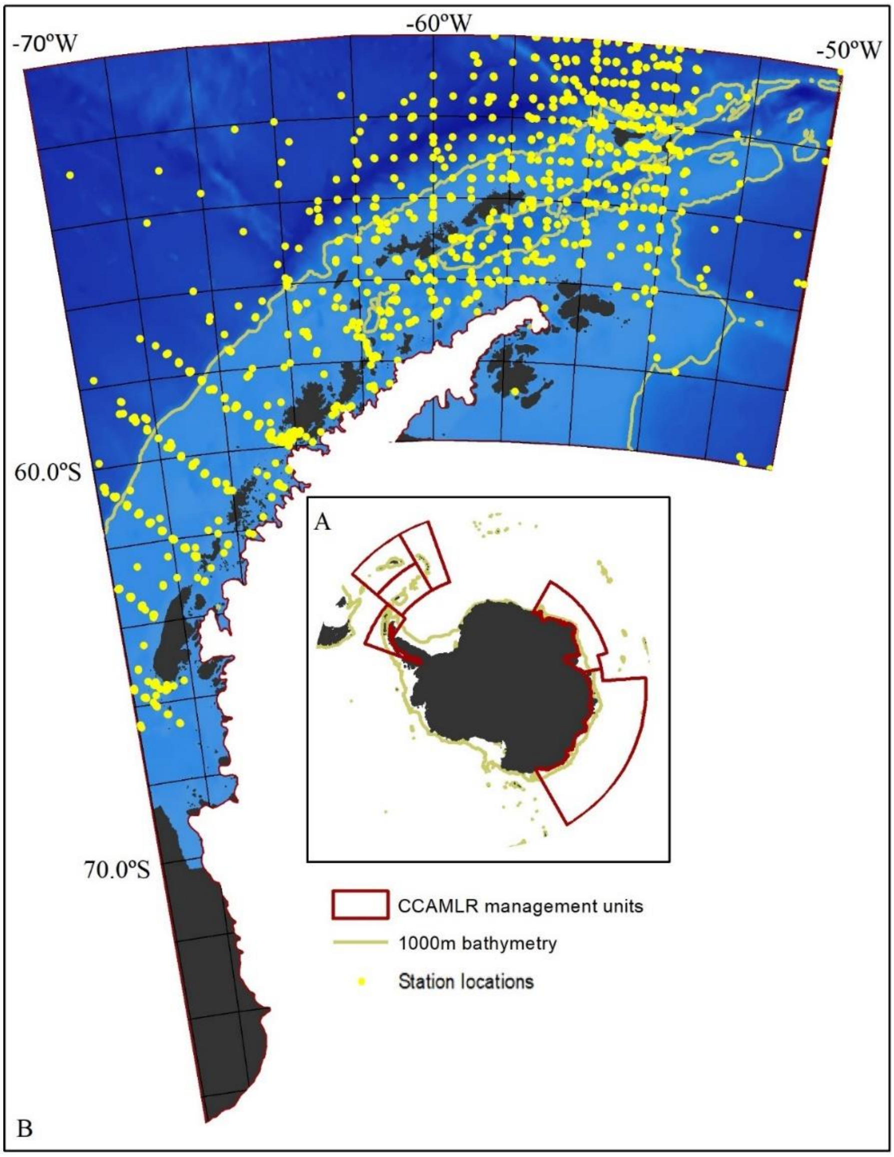


Figure 15. A map of our study area and its position in relation to the Antarctic continent. A) The location of the CCAMLR management units within the Southern Ocean are shown in red. B) CCAMLR subarea 48.1 within the south-west Atlantic sector of the Southern Ocean. The 1° latitude × 2° longitude grid cells that we have used for some of our analysis is shown in black. The 1000m shelf break is shown in yellow. Yellow circles identify the locations of KRILLBASE-abundance station points used as the key sampling unit within this study.

Krill density data were related to four environmental variables which fell into two categories: static and dynamic, of which the former were bathymetry and distance from the shelf and the latter, sea surface temperature (SST) and surface chlorophyll-a (chl-a) concentration (Table 6). Because of the lack of concurrently measured variables, it was necessary to utilise climatologies for SST and chl-a, which generally moderates regional levels of variability.

Table 6. Description of the environmental variables included in our generalised additive models.

Classification	Variable name	Units	Spatial resolution	Temporal resolution	Source
Static					
Bathymetry	Depth	m	$10km^2$	-	GEBCO 1-min grid
Distance from shelf break	Shelf distance	km	m	-	GEBCO 1-min grid
Latitude	Lat	Decimal degrees	1km	-	KRILLBASE-abundance
Longitude	Long	Decimal degrees	1km	-	KRILLBASE-abundance
Dynamic					
Chlorophyll a	Chl	mg m^3	$60km^2$	Monthly	SeaWiFS
Sea surface temperature	SST	°C	$10km^2$	Monthly	KRILLBASE-abundance

4.3.1.1 Abundance database

KRILLBASE-abundance is an open access database that contains net-catch derived juvenile and adult krill, and salp densities (doi: 10.5285/8b00a915-94e3-4a04-a903-dd4956346439) (Atkinson et al., 2017). The database contains data from >200 independent surveys using different sampling techniques with varying sampling efficiencies. This necessitated all krill densities (nos. m^2) to be standardised to those from a common sampling method in order to reduce the effect of this imbalance. Further details of the standardisation methods are available in Atkinson et al. (2017).

From the KRILLBASE-abundance database, we extracted all standardised krill density data from stations within subarea 48.1. We further filtered the data to ensure that the upper sampling depth was at least 20 m below the surface and the bottom sampling depth was at least 50 m below the surface, as described in Atkinson et al. (2008). This left 6644 stations.

4.3.1.2 Length-frequency database

The KRILLBASE-length-frequency database contains length measurements for 612888 individual krill collected from both scientific net hauls and commercial fisheries throughout the Southern Ocean (doi: 10.5285/dfbcbbf9-8673-4fef-913f-64ea7942d97a) (Atkinson et al., 2020). Sex and maturity data are also available for a portion of the database. In contrast with the KRILLBASE-abundance database, horizontal hauls were included in this study to maximise sample sizes. We filtered the KRILLBASE-length-frequency database using the same spatiotemporal criteria as for the KRILLBASE-abundance database. In addition, records sampled with a >6 mm mesh were excluded due to the possibility of net mesh selection and under-representation of smaller krill. This removed both commercial trawl data and some of the scientific trawls. Data from some scientific nets were further excluded where mesh size was not stipulated, including nets described as trawls. This left 134,953 krill, measured from 2422 stations.

From these filtered length-frequency data, we constructed ratios of different length categories of adult krill (here defined as ≥ 30mm following Saba et al. (2014) for each 1° latitude × 2° longitude grid cell within our study area; Figure 15). Subsequently, we subdivided these records into three further categories: 30-39 mm (small), 40-49 mm (medium), and 50-69 mm (large)

4.3.1.3 Creating densities of adult krill length categories

For our GAM analyses, the key sampling unit was each KRILLBASE-abundance station, and the final screening provided 5211 of these stations within area 48.1. Using ArcGIS version 10.2.2, we first overlaid a 1° latitude × 2° longitude grid onto our baseline map in the WGS 1984 stereographic co-ordinate system. By joining the KRILLBASE-length-frequency stations to the grid, we obtained the mean fraction of different size classes of adult krill within each grid cell. The abundance of each size fraction was thus obtained for each individual station as a product of its value for total post-larval abundance (from KRILLBASE-abundance) and the relevant grid mean value for the fraction of the size class (from KRILLBASE-length-frequency). Calculations were only made if values from both KRILLBASE databases existed for a respective grid cell.

4.3.2 Environmental variables

Although there are a number of environmental variables that can affect adult krill distributions, we focussed on four principal variables: SST, chl-a, bathymetry and distance from shelf, identified as being influential by a number of previous studies (Hofmann and Hüsrevoğlu, 2003; Atkinson et al., 2008; Piñones and Fedorov, 2016; Silk et al., 2016) (Table 6). The key sampling unit we used for each of the environmental variables was KRILLBASE-abundance station location (Figure 15).

4.3.2.1 SST climatology

The SST values were extracted from the KRILLBASE-abundance data set (Atkinson et al., 2017). These SST values were not taken at the time of sampling but were based on long-term averages of climatological mean sea-surface values for the month of February in years 1979 – 2014. Atkinson et al. (2017) generated the SST values by extracting a mean value using a 10 km radius point around a station location. Further information on how the SST data were treated is available in Atkinson et al. (2017). Climatology values are shown in Figure 16.

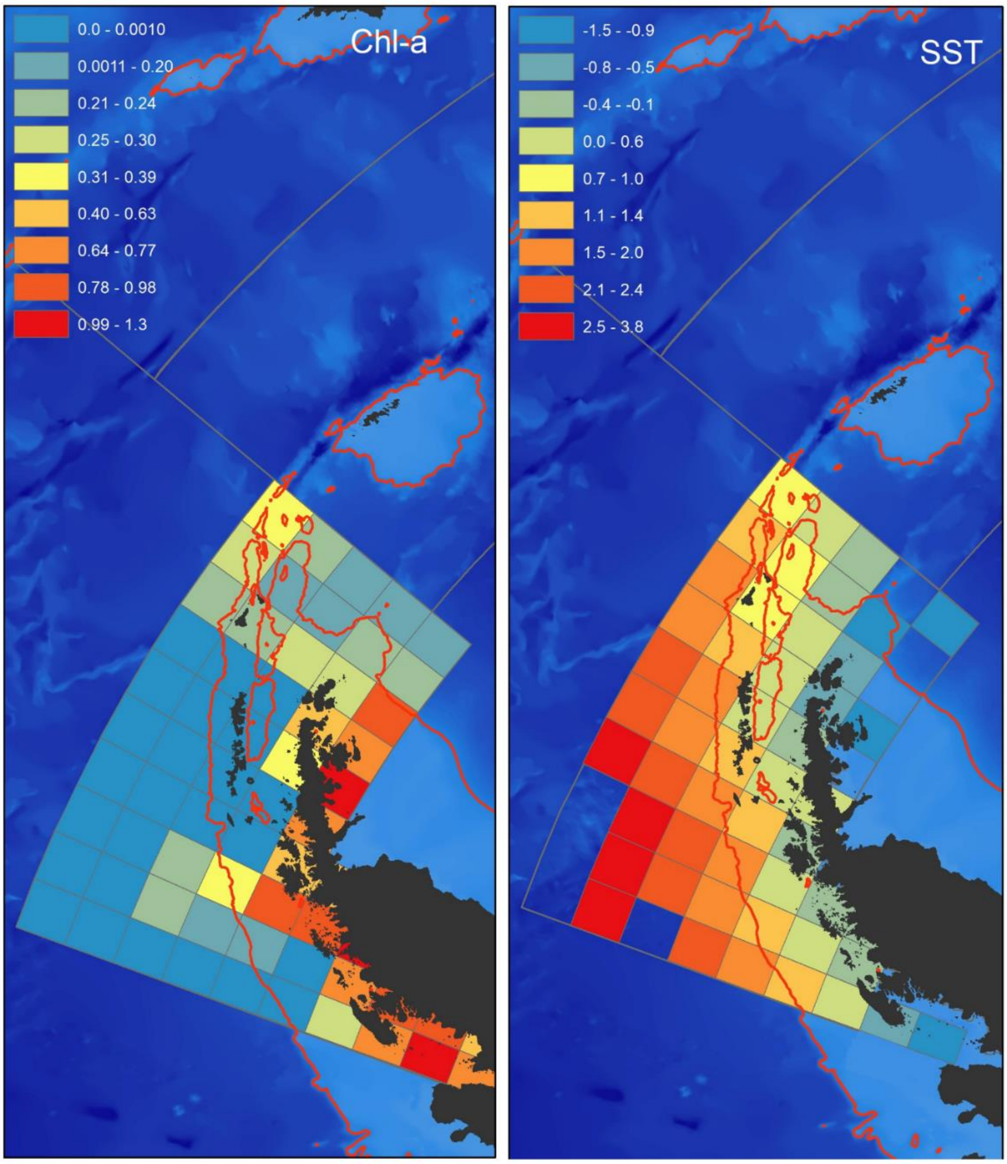


Figure 16. February climatologies of chlorophyll-a (chl-a) (mg chl-a m^3) and sea surface temperature (SST) (°C). Chl-a climatologies created from 19 years of Ocean colour – Climate Change Initiative data from the European Space Agency. Monthly means from each year of data were generated using a minimum of 30 % data coverage from each month for the grid cell to be included in the climatology. Mean SST, based on long-term averages of mean SST values of the month of February between 1979 - 2014. Further information on SST data treatment available in (Atkinson et al., 2017). Data are displayed for February, when sea ice is at its lowest extent, thus creating the fewest issues with averaging data.

4.3.2.2 Chl-a climatology

Chl-a data were extracted from the European Space Agency's Ocean Colour –Climate Change Initiative (OC-CCI) data portal, where satellite-derived ocean colour data are available from 1997 through to the present day, meaning that it covers only the latter 19 years of our 41-year study era.

Further information on the structure of this database is available in Jackson et al. (2019). Data were downloaded at a 4 km^2 resolution and plotted onto our 1° latitude × 2° longitude cell to create monthly average chl-a values for each of these grid cells for each of the years of available data. We set a requirement that each respective 1° latitude × 2° longitude grid cell contained at least 30 % data coverage for each month for a mean chl-a value to be valid. This severely limited the number of grid cells with monthly chl-a averages due to the cloudy nature of the Southern Ocean. Consequently, we decided to generate a monthly climatology of chl-a values, i.e. a monthly average was created across all 19 years of data for each of the 1° latitude × 2° longitude grid cells in our study area (Figure 16). This gave us chl-a values for 3127 out of 5211 data points within our study area.

4.3.2.3 Bathymetry

We applied the bathymetry values generated previously by Atkinson et al. (2017) for the KRILLBASE-abundance stations using the 2014 GEBCO bathymetry (http://www.gebco.net). Atkinson et al. (2017) applied a 10 km radius around each station location and averaged each of the GEBCO bathymetry values from within this radius. We removed any data points on the land before averaging the values.

4.3.2.4 Distance from shelf

GEBCO 2014 Grid bathymetry (http://www.gebco.net) was also used to determine the distance of each station from the shelf break, defined as the 1000 m isobath, following Hofmann & Hüsrevoğlu (2003). ArcGIS version 10.2.2 was used to calculate the minimum distance between each KRILLBASE-abundance station and the 1000m isobath. Values were negative if the station was on-shelf (< 1000 m) and positive if it was off-shelf (>1000 m).

4.3.3 Data analysis

We explored all our data for collinearity before determining functional relationships between krill distribution and environmental variables. We found significant collinearity between both latitude and longitude, and latitude and SST. For this reason, we removed both latitude and longitude from our analysis.

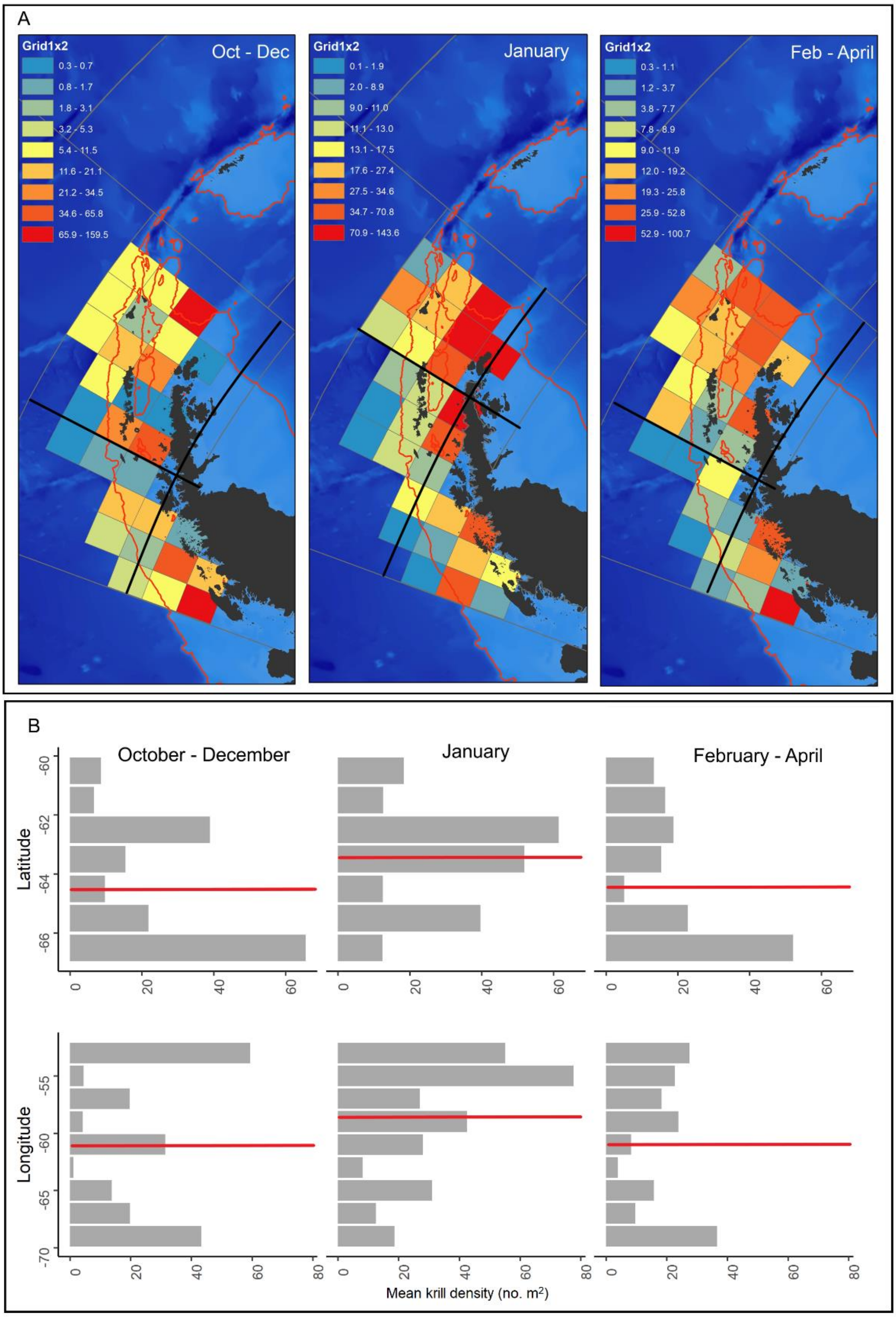


Figure 17. Mean adult krill distributions and population centre of gravity in subarea 48.1 for three seasonal periods: October to December, January and February to April. A) Mean densities (no. m^2) for all adult krill (≥30 mm). The red line shows the location of the shelf break (1000 m), and the grey boxes show the limits of the CCAMLR fisheries management units. The black crosshairs reflect the centre of the population for each of the seasons. Note the difference scales between panels. Grid panels are 1° latitude

× 2° longitude. B) The mean density of krill within each band of latitude and longitude for each seasonal period. The red lines show the centre of gravity for each of the seasons and translate to the location of the crosshairs on panel A.

4.3.3.1 Generalised Additive Models - GAMs

We identified outliers using Cleveland dot plots; collinearity using multi-panel scatterplots, Pearson correlation coefficients and variance inflation factors (VIF) (Zuur et al., 2010). The resulting data exclusions left 2203 stations, which divided into 376, 980, 847 in October-December, January, and February-April respectively. Our environmental variables exhibited non-linear trends and were therefore analysed using GAMs. Krill density data were not transformed prior to analysis. The optimal GAM structure for each krill length category was forward selected using Akaike Information Criterion (AIC) (Akaike, 1974). Using AIC values rather than p-values meant that we reduced the inflation of false positive results and model overfitting. We applied model validation to our optimal GAMs to verify our underlying assumptions. Having tested several GAM families, we found that a negative binomial GAM was best for our database due to slight over dispersion of our data. All of our calculations were done using R (R Core Team, 2017) using the package mgcv (Wood, 2006).

4.3.3.2 Calculating the population centre by bands of latitude and longitude

To calculate the central latitude and longitude of the adult krill population for each seasonal period, we divided subarea 48.1 into seven bands of latitude one degree wide, and nine bands of longitude two degrees wides (Figure 15). We then applied the same “centre of gravity” (COG) calculations as given in Atkinson et al. (2019), where the centre of the population given by latitude and longitude positions is calculated as the sum of the products of stratum mean density and stratum mid-latitude/longitude divided by the sum of stratum mean densities. The krill density values used for these calculations were generated by averaging all krill values within each 1° latitude × 2° longitude grid cell.

4.4 Results

4.4.1 Seasonal location of adult krill population

Our seasonal density distribution maps of adult krill highlight the importance of the tip of the Antarctic Peninsula (east of the South Shetland Islands) for consistently supporting high krill densities (Figure 17). Further investigation into krill density distributions using COG calculations show that the position of the population centre differs only during January, when it shifts ~250 km to the north-east along the Antarctic Peninsula. This relatively small shift does not show the COG of the population moving off-shelf or into deeper water during the spawning season (principally in January).

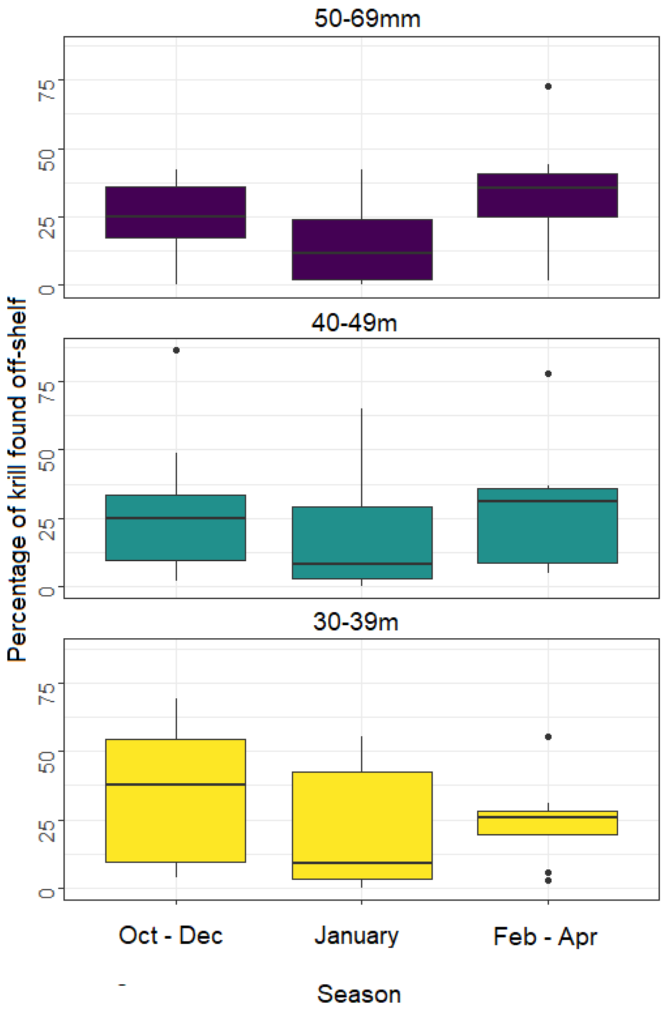


Figure 18. Seasonal mean ratios of three length categories of post-larval krill off-shelf (>1000 m) in subarea 48.1. Using the metadata associated with the 2203 KRILLBASE-abundance stations we identified the seasonal period during which the sample had been collected (i.e. October to December, January, and February to April). Then we selected abundance stations from any 1° latitude × 2° longitude grid cell that contained data from at all three seasonal periods. All the filtered abundance station data were associated with one of nine bands of longitude, two degrees wide, and were categorised as either on-shelf or off-shelf. Consequently, we created mean densities for each 1° latitude × 2° longitude grid cell from the sorted abundance station data. This resulted in us comparing 371 mean krill densities on-shelf and 339 data points off-shelf. For each band of longitude, we then compared the mean densities of krill on/off-shelf for each seasonal period.

The mean percentage of the adult krill found off-shelf is lowest in January and highest in the period between October to December (Figure 18). However, the mean percentage values of krill densities found off-shelf between seasons (October to December, January and February to April) were not significantly different for any length category of krill (30-39 mm: ANOVA, $F = 0.647$, $p = 0.533$; 40-49 mm: ANOVA, $F = 0.537$, $p = 0.592$; Figure 18). The 50-69 mm krill have a p value that is close to significant (50-69 mm: ANOVA, $F = 3.005$, $p = 0.069$), specifically between the January and February to April seasonal periods when it appears a larger percentage of these animals are found off-shelf later in the season. We repeated the analysis by subdividing krill density data into other spatial and temporal categories (e.g. by decade, by latitude) but none of these variants were statistically significant, supporting our original finding that there is a lack of seasonal change in spatial distribution.

Further investigation into the relationship between different length categories of adult krill densities and our static environmental variables (bathymetry and distance from shelf) revealed certain trends. For instance, there was a tendency for the two smaller length categories of krill to be found in shallower waters, particularly in October to December (Figure 19a). There is also evidence to suggest a temporal increase in the highest densities of small, medium and large krill in deeper waters during January, and to some extent February to April (Figure 19a). However, although the highest densities of adult krill (no. m^{-2}) may be found off-shelf during January (Figure 19a), when multiplied by area, the absolute number of animals (N) appears to be higher on shelf (Figure 18).

Nevertheless, in January, all three length categories showed peaks and troughs in density with increasing habitat depth. In relation to the shelf, adult krill were found with the greatest certainty ≤25 km before the shelf break. Although krill densities often appeared greatest ~75 km inshore of the shelf break. This was most notable in the 50-69 mm size class where this pattern was apparent across all three seasons (Figure 19b). It was also apparent in October to December and January in the 40-49 mm size class and in January in the 30-39 mm size class. As indicated by the bathymetric analysis, smaller krill also tended to be inshore, particularly during the periods October to December and January. Confidence intervals widen towards the spatial limits of the dataset, making it difficult to broaden the spatial context of these findings beyond ±150 km from the shelf edge and into bathymetric depths greater than 2500 m.

4.4.2 Adult krill and their relationship with environmental variables

Chl-a and SST climatology data for February are visualised in Figure 16, showing clear on-shelf off-shelf gradients for both dynamic variables. SST is cooler on-shelf and in the Weddell Sea, whereas the more northerly off-shelf waters are consistently warmer. Chl-a concentrations tend to be greater on-shelf and are greatest in near shore regions.

Table 7. Generalised additive model equations for all three length categories of adult krill. Each of the environmental variables used within the model is given with the smoothing coefficient applied.

Length category	**Model**
30-39mm	$\rho = s(SST, 4.46) + s(shelf\ dist., 4.01) + s(chl - a, 6.69)$
40-49mm	$\rho = s(shelf\ dist., 5.61) + s(chl - a, 7.99) + s(depth, 4.47) + s(SST, 3.66)$
50-69mm	$\rho = s(chl - a, 5.93) + s(temp, 8.3) + s(depth, 7.85) + s(shelf\ dist., 4.77)$

The percentage deviance explained by the four environmental variables was 5 %, 9 %, and 17 % for 30-39 mm, 40-49 mm and 50-69 mm krill respectively. The deviance explained is low for all three krill length categories but increases with the krill length. The environmental variable that explained the most deviance changed between length categories of krill. SST, shelf distance, and chl-a described most of the variation in the density of small, medium and large krill respectively (Figure 20). Chl-a abundance is the only environmental variable that increases in importance as krill length increases. In the 50-69 mm length category, chl-a exhibits a clear inverse relationship with krill density (Figure 20). The models and the smoothing coefficients for each length category of krill are provided in Table 7.

The above analyses demonstrate a lack of strong seasonal differences in horizontal distribution. Therefore, in Figure 21 we have maximised data volume to provide a composite distribution pattern of size classes from October to April for each krill size class. Krill densities averaged from October to April (Figure 21) highlight the importance of the tip of the Antarctic Peninsula for all three length categories of adult krill. Calculations of the COG for each of the length categories show that there is no clear difference in the COG between the different length categories (Figure 21& Table 7).

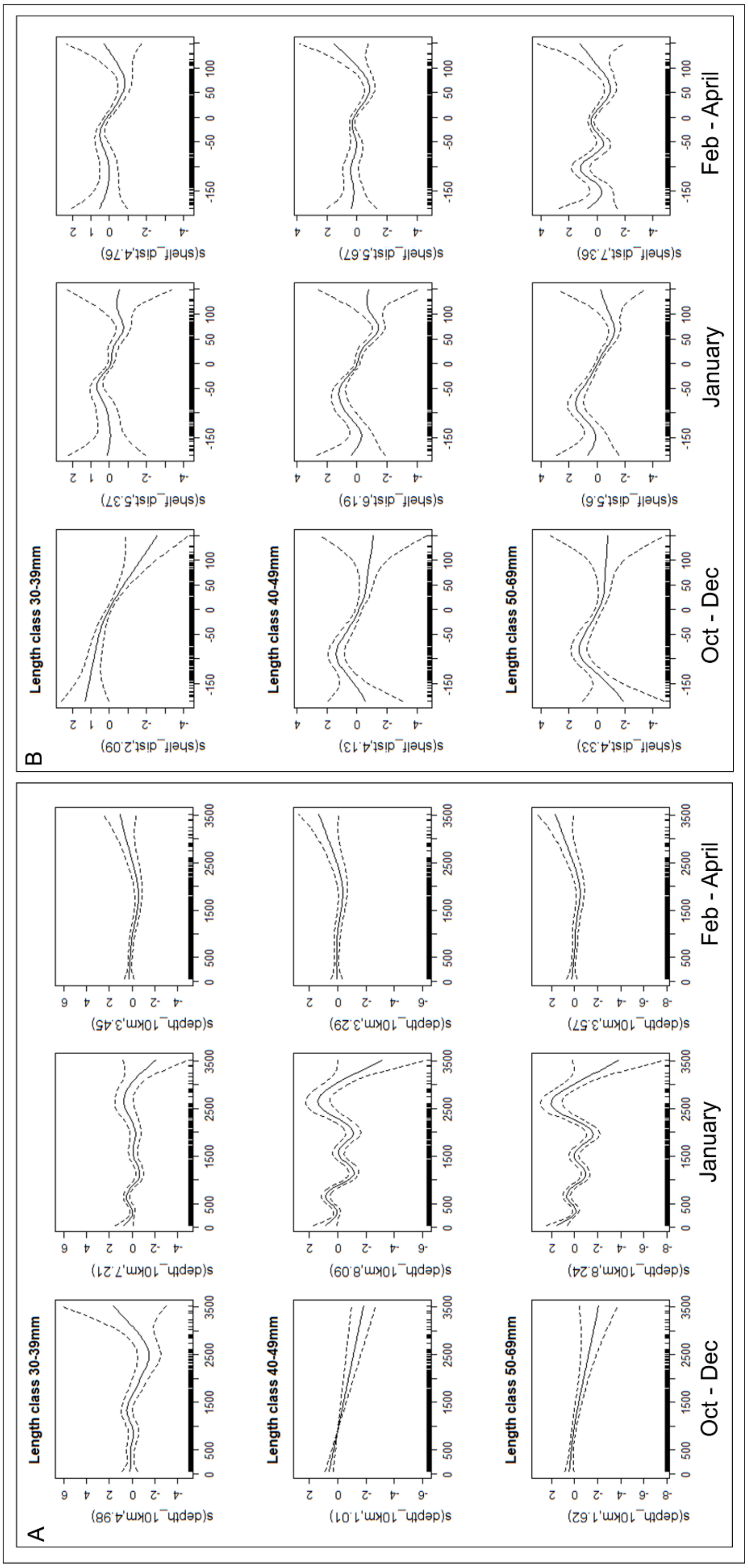


Figure 19. Seasonal relationships between 30-39 mm, 40-49 mm, and 50-69 mm adult krill densities and (A) bathymetry (m) and (B) distance from shelf (km) using generalised additive models. The dashed lines indicate the 95 % confidence interval.

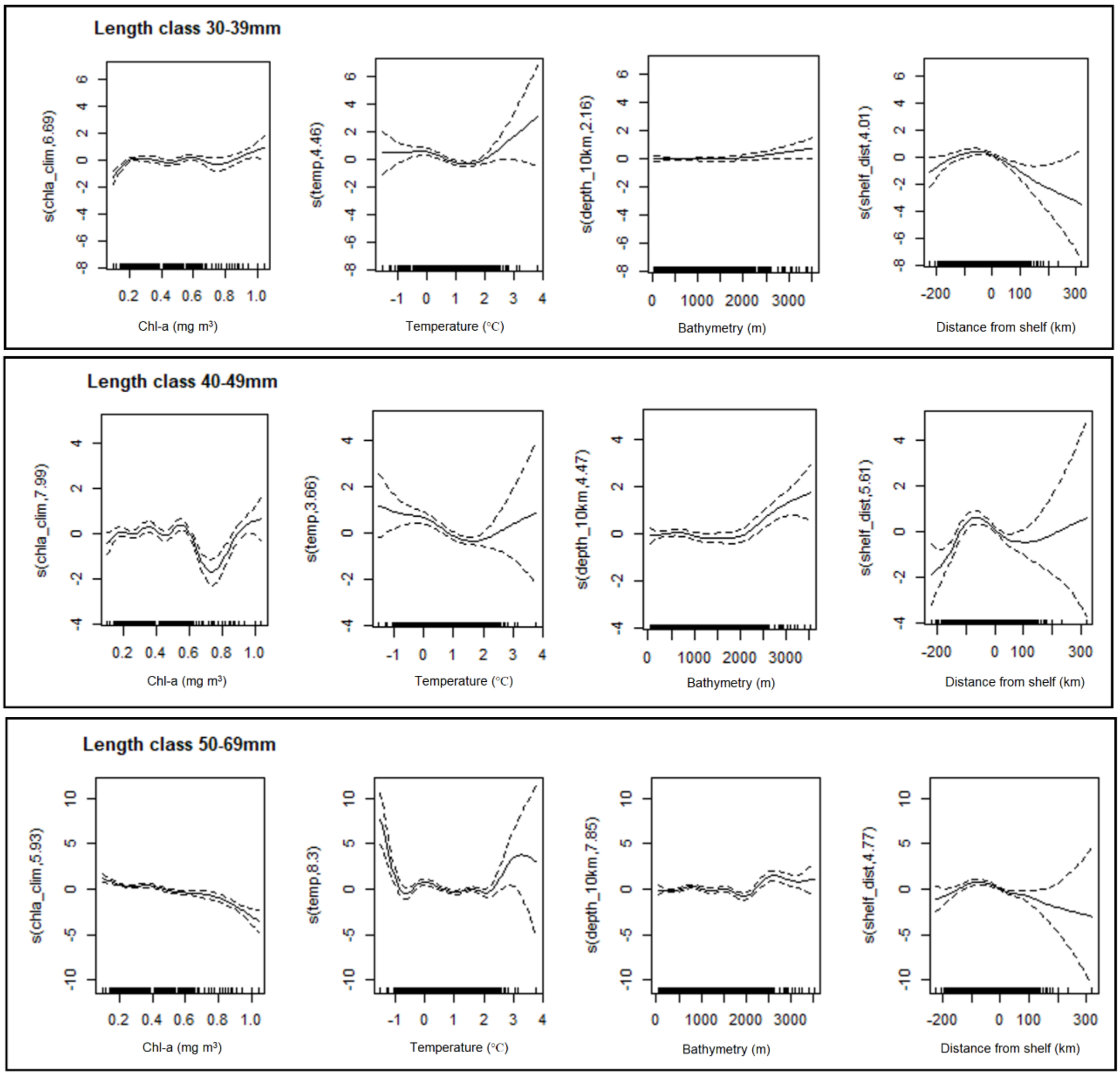


Figure 20. CCAMLR subarea 48.1 generalized additive models. Relationships between three length categories of post-larval krill (30-39 mm, 40-49 mm, 50-59 mm) and environmental variables. Each of our environmental variables are in respective columns to allow comparison between the length categories. We give the degrees of freedom for each smoother in brackets on the y-axis. Note that the scales on the y-axis vary between the environmental variables. The dashed lines indicate the 95 % confidence intervals.

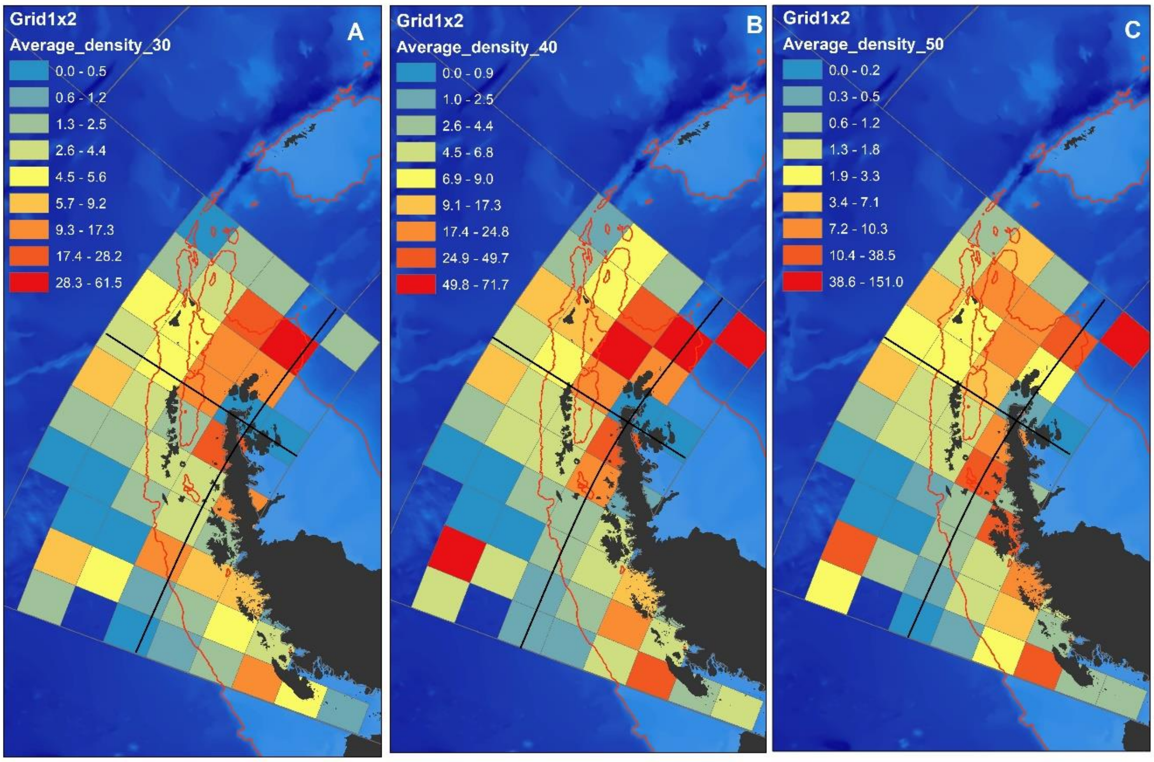


Figure 21. Distributions of post-larval krill in three length categories. The mean densities (no. m^2) of three length categories of post-larval krill (A) 30-39 mm, (B) 40-49 mm, (C) 50-69 mm within the CCAMLR management unit 48.1. Grid panels are 1° latitude × 2° longitude. Note that the scales are different between the panels.

4.5 Discussion

Our results show evidence of an on-shelf length separation of krill size classes with smaller krill found further in-shore, especially from October up to the peak spawning time in January. However, our evidence does not suggest the largest adult krill (50-69 mm) migrate off-shelf during the summer. These large krill appear to be the most environmentally constrained of the three length categories of adult krill. Furthermore, the inverse relationship between large krill and chl-a concentration is consistent with some level of top-down control on phytoplankton biomass.

4.5.1 Evidence for an off-shelf spawning migration

An off-shore seasonal spawning migration of adult krill at the WAP was first suggested by Siegel (1988), who used data from six surveys carried out between October and June between 1977 and 1986 to describe a pattern of spatial succession of krill life stages along the WAP. Data collection occurred during a period of variable and exceptionally high krill recruitment, specifically 1980/81 and 1985/86 (Siegel and Loeb, 1995). In summer, juveniles were found on the inner shelf and the largest adults found in off-shelf oceanic waters, a trend that reversed after the spawning season. Siegel (1988) reported densities of krill being far greater in offshore waters during the summer season compared to autumn, a feature of the krill population that has also been described by (Reiss et al., 2017). An interaction between krill migratory behaviour and current regimes was suggested as the cause for the staggered distribution of krill life stages (Siegel, 1988). This idea that a horizontal migration of krill may contribute to seasonal variations in krill biomass at the WAP were furthered by Lascara et al. (1999), who reported an across-shelf pattern of length-frequency distribution of krill in all seasons except winter at the WAP. They described a trend for large adults (45-60 mm) to predominate offshore beyond the shelf break, and that larger (>40 mm) krill were often found further offshore than smaller individuals during the summer spawning period. The thorough multiyear databases used in both studies and the clear separation between length categories of krill have helped to fix the seasonal spawning migration of adults at the WAP as a key paradigm in krill research (Meyer et al., 2020).

Surprisingly, our results contrast with some of the findings regarding seasonal horizontal krill migrations. The composite nature of both the KRILLBASE databases means that our analyses include the original krill density data from both the Siegel (1988) and Lascara et al. (1999) studies, and length-frequency data from the Siegel (1988) study, alongside a wealth of other data from this region. Our analyses do not show any temporally and spatially consistent evidence of an off-shelf spawning migration. We found the mean percentage of adult krill found off-shelf did not differ significantly between seasons. In fact, the lowest mean values for adult krill off-shelf were observed in January, which is the peak month of spawning (Spiridonov, 1995). Although the densities of adult krill (no. m^{-2}) may be higher off-shelf, the absolute number of animals is no greater than those on-shelf. This lack of evidence is unexpected as the off-shelf spawning migration of larger adult krill is considered a crucial component of the natural history of the WAP (Siegel, 1988, 2005; Trathan et al., 1993; Lascara et al., 1999; Meyer et al., 2020). The requirement for eggs to be spawned over deep water to allow them to complete their developmental ascent without encountering the benthos is the driving concept to the summer off-shelf spawning migration (Nicol, 2006). However, during much of the spawning season at the WAP, the additional depth needed for embryos to hatch before encountering the benthos is <100 m (Hofmann and Hüsrevoğlu, 2003) and sinking rates may be reduced through local upwelling features (Thorpe et al., 2019). Additionally, egg densities at the WAP are more uniformly distributed on or near the shelf boundary than off-shelf (Perry et al., 2019). Crucially the highest densities of nauplii and metanauplii are also in these shelf waters (Perry et al., 2019). These factors further support the idea that off-shelf migration of 50-69 mm adults during summer may not be key to successful adult spawning at the WAP.

We also identified a mismatch between the densities of krill inshore during the autumn according to our analyses and those expected from the prevailing hypothesis. During the autumn, when krill are hypothesized to migrate further inshore in high numbers (Siegel 1988), we found there was no resultant increase in coastal densities of krill. A seasonal change in habitat use of adult krill, who have the capacity to feed in cryopelagic and benthopelagic habitats, could explain this discrepancy (Kawaguchi et al., 1986; Schmidt et al., 2014). Such in situ vertical movements could provide an incorrect impression of horizontal migrations or changes in on/off-shelf ratios.

A further important point to consider is that we averaged data over 41 years, so any consistent seasonal trends should be highlighted in our results. However, if offshore migrations only occurred in some years, our analyses would not resolve such inter-annual variability. Prior studies have also identified the importance of small scale bathymetric features in the structuring of krill distributions (Hofmann et al., 1998; Piñones et al., 2013). However, the resolution of the data used within this study, especially in the southern part of our study area off Marguerite Bay do not allow analysis to occur at a scale of these bathymetric features. Consequently, although we can be certain about the lack of a consistent off-shelf migration in our data, there remains the possibility that offshore migration does take place in some years, with a high degree of inter-annual variability, and that further work is required to identify migratory behaviours at finer geographic scales.Previous studies have suggested a southward contraction of the krill population in autumn (Kanda et al., 1982; Atkinson et al., 2008), and that the krill population spends the winter in more southerly locations. Further evidence of a north-south seasonal migration of krill has been found in other regions of the Southern Ocean, including the Weddell Sea and the Pacific sector of the Southern Ocean off Enderby Land (Kanda et al., 1982; Sprong and Schalk, 1992). Our Centre of Gravity (COG) calculations indicate that, in January, the adult krill population is neither further off-shore nor in deeper waters, but instead, appears to move ~250 km to the north-east along the Antarctic Peninsula (Figure 21 & Table 7). This summer expansion of adult krill is a distinctly different concept to the off-shelf spawning migration defined by Siegel (1988) and Lascara et al. (1999). This life history strategy keeps adult krill separate from developing larvae at a time of low food availability which may provide a selective advantage. Further understanding of this seasonal expansion and contraction of the krill population requires greater quantities of krill density data, specifically between May and September.

4.5.2 Environmental drivers of krill distribution

Our GAMs reveal that SST, chl-a, bathymetry and distance from shelf explain only a part of the variance that we see in the distribution of 30-39 mm, 40-49 mm and 50-69 mm adult krill, and consequently are not reliable predictors of krill density. Clear relationships between single environmental factors and krill are difficult to find and vary considerably between region and individual study (Weber and El-Sayed, 1985; Siegel, 2005; Nicol, 2006; Silk et al., 2016). The low explanatory power of these studies is likely attributable to the intense swarming behaviour of krill, a factor which makes their distribution inherently difficult to understand and predict. Prior studies at the Antarctic Peninsula demonstrate that krill are associated with on-shelf waters (Siegel, 2005; Atkinson et al., 2008) and with moderate chl-a concentrations (Silk et al., 2016). A domed relationship between krill and chl-a has also been reported from other regions of the Southern Ocean (Atkinson et al., 2008; Whitehouse et al., 2009). The deviance explained by the results of our GAMs is highest for the largest length category of krill (50-69 mm; 17 %) and lowest for the smallest length category (30-39 mm; 5 %).

Two noticeable trends did appear from our GAM analysis (Figure 20). Firstly, adult krill of all length categories are most abundant on-shelf in subarea 48.1. This trend has previously been described using both fisheries data (Murphy et al., 1997; Trathan et al., 1998) and scientific haul data (Siegel, 2005; Atkinson et al., 2008; Silk et al., 2016). More specifically, we found all length categories in highest densities ~75 km inside the shelf break. Slightly lower densities of krill of all length categories were found with the greatest certainty ≤25 km before the shelf break. These high densities of krill may be due to the deep canyons that bisect the shelf-break at the Antarctic Peninsula through which circumpolar deep water (CDW) currents transport krill onto the shelf (Ashjian et al., 2004; Lawson et al., 2004). These canyons also create episodically higher plankton biomass as they act as conduits for upper CDW which delivers micronutrients to the region (Kavanaugh et al., 2015).

Secondly, we found that the relationship with chl-a differs between different length categories. The highest densities of the largest length category of krill appear to be associated with low chl-a concentrations (Figures 16, 20, 21). Our chl-a climatologies also displayed a strong on-offshore gradient (Figure 16), a trend that concurs with prior chl-a measurements at the WAP, where values can be four times greater inshore than offshore (Smith et al., 1998; Garibotti et al., 2003). In general, the Southern Ocean is a high nutrient, low chl-a region (Holm-Hansen et al., 1977), and is considered to be limited by iron availability (Takeda, 1998; Garibotti et al., 2003). Yet, the shelf at the tip of the Antarctic Peninsula is one of the most biologically productive regions in the Southern Ocean, where the krill based ecosystem supports numerous apex predators (Fraser and Trivelpiece, 1996; Arrigo et al., 1998; Marrari et al., 2008). Adult krill require a food rich environment prior to and during the spawning period, as both the quantity and quality of food available to female krill affects the viability of their embryos (Yoshida et al., 2011). A prior study by Whitehouse et al. (2009) in the waters around South Georgia also found that, in areas of high krill density, krill can drive down their food supply. The negative relationship between the abundance of large krill and chl-a potentially suggests that this size class exerts top-down control on their food owing to their increased metabolic demands. We estimate that a 50-69 mm krill could graze a maximum of 74 % of available phytoplankton per day, compared to 15 % by 40-49 mm krill, and just 5 % by 30-39 mm krill (Supplementary Information 1). This may be a result of a combination of the high energy demands for maturation and reproduction (Clarke and Morris, 1983) and how body size increases the costs of remaining pelagic exponentially (Kils, 1981).

4.6 Implications

Our results suggest that, contrary to prior multi-year studies, adult krill at the WAP do not consistently migrate off-shelf to spawn. Rather, high densities of adult krill within subarea 48.1 are most predictably found on-shelf throughout much of the year, including the largest adult krill that are the most fecund and likely to contribute to the spawning stock. If the descent-ascent model of early development is necessary for successful recruitment, the population in subarea 48.1 may be reliant on the relatively small proportion adult krill found off-shelf during the spawning season. Consequently, it is vital to understand the sensitivity of this off-shelf environment particularly to projected climatic changes.

The on-shelf location of large, lipid-dense krill during the summer reproductive period means that they could be within the foraging range of shelf-based predators. This may be especially beneficial as many krill predators are size-selective foragers that preferentially target larger krill (Osman et al., 2004; Miller and Trivelpiece, 2008). The recent increase in both the spatial and temporal concentration of fisheries catches (Santa Cruz et al., 2018) has coincided with a greater occurrence of poor krill predator performance (Watters et al., 2020). This has questioned the suitability of the current fisheries management as it highlights the spatio-temporal scales of current krill catch limits are more coarse than those of predator-prey interactions (Watters et al., 2020).

A marine protected area (MPA) is currently being developed at the WAP and Southern Scotia Arc to protect the krill centric food web (CCAMLR, 2017). Increasing the resilience of the krill population, and the ecosystems they support, by creating no-take zones in regions pivotal to their life cycle will help by mitigating the detrimental effects of climate change (Dahood et al., 2020). Considering the seasonal distributions of krill and the impact of migratory behaviours is key to effectively protecting krill centric habitats.

Chapter 5 Discussion

5.1 Introduction

Krill recruitment has been repeatedly highlighted as a key knowledge area that requires further research (Flores et al., 2012; Meyer et al., 2020). In the introduction, I identified three specific gaps in understanding of Antarctic krill recruitment to be addressed through my thesis research:

- The distribution of all life stages of krill in the south-west Atlantic sector, with emphasis on identifying hotspots and nursery areas.
- The effect of temperature on krill embryo hatching failure and nauplii malformation and its role in controlling spawning area distribution.
- Patterns of off-shelf spawning migrations and the consequent distribution of adult krill along the WAP to identify spawning population distribution during the summer spawning season.

The following discussion summarises how each of the data chapters in my thesis have contributed to these knowledge gaps and suggests future research directions considering the expanding krill fishery, ongoing climate change and spatial management.

5.2 New findings and implications

Using 41 years of krill data extracted from three composite KRILLBASE databases, chapter 2 demonstrates that between January and March, adult krill are widely distributed within the south-west Atlantic sector of the Southern Ocean. This contrasts sharply with the distribution of eggs, nauplii and metanauplii, which show that spawning is most successful and intense over the shelf and shelf-slope. Furthermore, calyptopes and furcilia are concentrated in the deeper waters in the Southern Scotia Sea, and juvenile krill are found over the shelf regions of the Scotia Arc. My findings suggest that there is habitat partitioning between the different key life stages of krill, a feature of krill behaviour that may reduce intraspecific competition for food. Chapter 2 identifies the tip of the Antarctic Peninsula as an area of particular importance to the krill population within the south-west Atlantic sector as it is the only location where high densities of adult krill and eggs are found and where calyptopes and furcilia most likely originate from. Modelling studies suggest that there may be other regions along the WAP that contain high densities of larval krill (Piñones et al., 2013).

However these results created from net-catch data identify the spatially restricted nature of krill spawning, which has important implications for krill fishery management practises. My results emphasise that the vast scale of the current CCAMLR fisheries subareas is too large to allow for the effective management of the comparatively small regions where key aspects of the krill life cycle occur.

The management of the fishery within the Atlantic sector of the Southern Ocean is considered precautionary as the regional catch limit is equivalent to ~1% of the regional biomass (SC-CAMLR, 2010). However, the combined pressures of the increasingly intense spatial and temporal concentration of the fishery (Santa Cruz et al., 2018), and rapid climate change (Meredith and King, 2005) have the potential to cause lasting damage to the krill-based ecosystem (Brooks et al., 2020). Information on the krill population structure and reproduction are vital to understanding how the fishery affects krill and their predators (Hill et al., 2016). Future management decisions must consider both the pressure of the fishery removing valuable spawning stock simultaneously with the likelihood of a krill recruitment failure caused by changing environmental conditions. The reliable location of much of the spawning population in subarea 48.1 raises the issue of fishery-krill-predator interactions. The recent increase in the spatio-temporal concentration of fisheries catches (Santa Cruz et al., 2018) has coincided with a greater occurrence of poor krill predator performance at the Antarctic Peninsula (Watters et al., 2020). The reproductive success of krill predators is indirectly linked to the abundance of krill (Croxall et al., 1999; Fraser and Hofmann, 2003). The suitability of the current fisheries management has consequently been questioned as the scales of current krill catch limits are more coarse than those of predator-prey interactions (Watters et al., 2020). My research identifies key regions that are critical for krill to complete certain parts of their life cycle before broadcasting themselves over much wider scales. These regions must be part of a new consideration of how the krill stock is best managed.

A Marine Protected Area (MPA) is being proposed for the WAP and Southern Scotia Arc to protect the krill-centric food web (CCAMLR, 2017; Brooks et al., 2020). Increasing the resilience of the krill population by creating no-take zones in regions vital to their life cycle has been suggested as a means of mitigating the detrimental effects of climate change (Dahood et al., 2020). However, planning for this MPA is being based around the needs of land-based krill predators and not the krill population itself. As a result the current MPA proposal is limited to inshore regions of the shelf at the Antarctic Peninsula. This protects the krill population within proximity to the krill predator breeding colony sites, so allowing the predators to thrive, at least in the short term. However, the proposal does not allow for the equal representation of all habitats required by krill throughout their complex life cycles, as identified in chapter 2. My results suggest that at the Antarctic Peninsula key krill spawning areas occur either in the 75 km proceeding the shelf-break or in off-shelf waters. Currently neither of these areas are incorporated within the present MPA proposal. This oversight may ultimately be detrimental to krill predators in the long term if krill recruitment regions are not equally protected and stocks decline.

Chapter 4 investigates the long-standing paradigm that adult krill undertake an off-shelf spawning migration during the austral summer season at the Antarctic Peninsula. My results demonstrate that there is no temporally or spatially consistent off-shelf spawning migration of adult krill within CCAMLR subarea 48.1 (Figure 18). Furthermore, it appears that, from October to April, high densities of adult krill of all length sizes are reliably found on-shelf, mainly within ~75 km inshore of the shelf break. Identifying the summer location of the adult krill within subarea 48.1 thus challenges the major paradigm that there is an offshore spawning migration. Results from Chapter 2 identify that eggs at the Antarctic Peninsula are more consistently found in shelf waters, as are the highest densities of nauplii and metanauplii. Whereas the highest densities of both calyptopes and furcilia are found in the southern Scotia Sea.

There are two potential explanations for the observaion of most spawning females on the shelf and most larvae in the ocean. First, successful recruitment may be possible from embryos spawned in the higher chlorophyll waters onshelf, where the majority of the population are located. Alternativley, if embryos have to encounter upper CDW during their descent-ascent cycle without encountering the benthos then recruitment may rely on the small proportion of the spawning population found off-shelf (Ross et al., 1988; Hofmann et al., 1992; Hofmann and Hüsrevoğlu, 2003). Identifying hotspots of successful spawning is vital to understanding the sensitivity of krill to climate change and fishing as certain spatially restricted areas of successful spawning may supply the whole Scotia Sea stock (Hofmann and Hüsrevoğlu, 2003; Thorpe et al., 2019).

Within the south-west Atlantic the krill population extends to its warmest thermal limit around South Georgia where high densities of sexually mature krill fail to translate to high larval recruitment. Within chapter 3, I investigated the effect of warmer temperatures associated with northerly regions on egg hatch success and viability using laboratory-based experimental studies of temperature effects on krill embryo hatching success and viability. Hatching success of krill embryos is significantly reduced above 3.0 ˚C and concurrent nauplii malformations exceed ~50% at 5.0 ˚C,. Below 3.0 ˚C, the large variation in embryo hatching success is not the result of temperature. Variation in hatching succes ranges between 0 – 98 % (mean 27 %). This range of hatching success identifies that prior indices of female fecundity relate poorly to the consequent production of viable larvae. Larval models predicting embryonic success (Tarling et al., 2007) and models of habitat suitability for spawning (Hofmann and Hüsrevoğlu, 2003) could be further refined by considering the highly variable and often low embryo hatching success. The results presented in chapter 3 indicate that embryonic success will not be limited by warming ocean temperatures predicted for the end of this century. However, my work only considered temperature and did not investigate other climate change pressures, such as ocean acidificatin, deoxygenation, and greater surface stratification, that would be affecting embryos in tandem.

5.3 Prognosis for the future

The proportion of the krill population within the south-west Atlantic sector of the Southern Ocean has been considered to be as much as 71 % (Atkinson et al., 2008b). Between the 1920's and 1930's the average krill densities within the Atlantic sector were eight times those in other sectors of the Southern Ocean (Yang et al., 2020). Since the 1950s, there have been increasing occurences of positive Southern Annular Mode (SAM) phases (Stammerjohn et al., 2008; Swart and Fyfe, 2012; Dätwyler et al., 2018) which produce warmer, windier and cloudier weather and reduce sea ice, water column stability and phytoplankton biomass (Saba et al., 2014). These positive phases are also associated with lower krill egg production and larval survival (Steinberg et al., 2015). In more recent years, the concentration of krill within the Atlantic sector has declined from eight times to double that of other sectors (Yang et al., 2020) in line with increased frequency of positive SAM phases. Debate continues, however, about the trends in krill abundance within this sector. Studies investigating both regional trends in krill and indices from their predators suggest that there has been a decline in the abundance of krill, (Loeb et al., 1997; Huang et al., 2011; Loeb and Santora, 2015; Atkinson et al., 2019) a southward contraction of their range, and an increase in mean body length (Atkinson et al., 2019). However, alternative analytical approaches have concluded that the numerical or biomass density of krill within the Atlantic sector has remained stable (Fielding et al., 2014; Kinzey et al., 2015; Cox et al., 2018). The lack of consensus on krill population trends may be due to the large inter-annual variability in krill abundances and the complex non-linear relationship between the indices and scales of analysis (Atkinson et al., 2019; Hill et al., 2019). Resolving this issue is key to providing a clear message to stake holders (Meyer et al., 2020). To aid this debate the results presented in this thesis identify behavioural patterns that help establish the vulnerabilities in the life-cycle that, when combined with our knowledge of water mass circulation and distribution, can assist in predicting how future environmental change may affect krill stocks.

The rapid and sometimes contrasting effects of climate change in the Southern Ocean make it vital to gain better understanding of past and present trends in the krill population at both regional and circumpolar scales to clarify varying scientific opinions and facilitate projections of future population trends and responses to management framework. These demands require a step change in approaches for collection of krill-related data and concurrent environmental data. Chapters 2 and 4 utilised multi-decadal composite databases of net-catch derived data, and the temperature experiments reported in chapter 3relied upon net-caught krill from field studies. Net catch data are extremely valuable and can provide historical information on the krill population and remain the most accurate sampling method for identifying larval krill stages. However, data collection methods are evolving, and net-catch data are becoming sparse, as ship time is becoming increasingly difficult to obtain. We must, therefore, look to new methods of data collection that can complement historical net-catch data to help improve our understanding of the krill population in the future.

Promisingly, the increasing use of moorings, gliders, and sail buoys to gather acoustic data (WBAT, ADCP) means that year-round data collection is becoming more viable (Brierley et al., 2006; van Haren, 2007; Cisewski et al., 2010; Wallace et al., 2010; Guihen et al., 2014; La et al., 2015; Meinig et al., 2019). These methods provide new data that will enable investigation of seasonal krill population dynamics in a previously unobtainable way. There is also increasing interest in the scientific community of using fisheries data to aid our understanding of krill (Trathan et al., 1998; Kawaguchi et al., 2005; Taki et al., 2005). The number of hours of fishing effort accrued by commercial fishing vessels far exceeds those during scientific cruises each season. Therefore, fisheries data could provide considerable information to the scientific community on krill feeding, length-frequency, growth, behaviour, seasonal distributions and abundance (Kawaguchi and Nicol, 2007). Improved sampling of early larval stages could be achieved through the augmentation of the Continuous Plankton Recorder (CPR) by fishing vessels in key fisheries areas. Additionally, small net samples could be collected from vessels of convenience, such as those used for the increasing tourist traffic in the Southern Ocean. These additional data collected through citizen science programmes could complement scientific datasets when designed with an appropriate statistical-based sampling protocol.

A recent synthesis of krill research identified a number of key questions that must be resolved in order to gain a better understanding of future changes in the krill stock. This study identifies three questions that parallel the outcomes of this thesis. Specifically, we must; understand the mechanisms that control krill recruitment, identify hotspots of successful krill spawning, understand where the fishery overlaps with areas where key krill life cycle events occur (Meyer et al., 2020). In order to answer some of these unresolved questions we must utilise modern technologies as well as historical data. Using both observations and experiments to better understand biological and ecological mechanisms we can then develop conceptual models that can be implemented using numerical models such as those by Murphy et al. (2017) and Veytia et al. (2020) that consider how future change will affect how and where krill can grow and reproduce. Future models can be further refined by the data provided by my research. By incorporating habitat partitioning between krill life stages (chapter 2) and seasonal trends in adult krill distribution (chapter 4) into future krill life cycle models will add nuance to our understanding of krill population dynamics. Pinpointing the location of krill during key life cycle events (chapter 4), will begin to unravel the question of when and where these processes overlap with fishery activity. Finally, understanding the highly variable and often low hatch success of krill embryos (chapter 3) will create more refined indices of female reproduction.

5.4 Recommendations for future research

5.4.1 Krill population and recruitment modelling

Within the south-west Atlantic sector it is thought that only a small proportion of the adult krill population spawns successfully, in a relatively small area of habitat (Meyer et al., 2020). Lagrangian particle tracking experiments have shown that there is connectivity between krill populations in both the Bellingshausen and Weddell Seas and the WAP (Renner et al., 2012; Piñones et al., 2013). To date, there are limited data available that would help us determine whether such a small proportion of the total krill biomass could sustain the Scotia Sea krill population or if there are source populations from other regions of the Southern Ocean.

Pinpointing the source locations of successful krill recruits could identify the area of successful adult spawning. Both calyptopes and furcilia are found in relatively high densities at both the tip of the Antarctic Peninsula and at Marguerite Bay on the WAP (Siegel et al., 2013; Chapter 2). Modelling suggests that successful krill spawning can occur at the northern tip of the Antarctic Peninsula but may be limited elsewhere at the peninsula due to shallow bathymetry and seasonal sea ice advance which cause larval mortality (Hofmann and Hüsrevoğlu, 2003; Piñones and Fedorov, 2016; Thorpe et al., 2019). Regardless of the spawning location, there remains a mismatch between the numbers of both calyptopes and furcilia reported from the south-west Atlantic and the numbers required to sustain the adult population (Meyer et al., 2020). Identifying where calyptopes and furcilia originate from within the Southern Ocean, i.e. where the key krill spawning grounds are, remains a major, outstanding question. Near-surface ocean drifters suggest the source locations of these larval stages are at a wide variety of locations along the Antarctic Peninsula (Meyer et al., 2020), and from both the Bellingshausen and Weddell Sea (Renner et al., 2012; Piñones et al., 2013). Further use of modelling to track the trajectories of krill larvae could prove valuable for identifying further krill spawning grounds, especially when incorporated into the larval recruitment model produced by Thorpe et al. (2019). Specifically, I propose that larval distributions produced from my chapter 2 results could be embedded into high resolution circulation models to create backward projections of larval locations and identify where the larval points of origin are. These points of origin should then be compared to modelled maps of successful spawning areas within the south-west Atlantic

(Hofmann and Hüsrevoğlu, 2003; Thorpe et al., 2019) to identify the connectivity between regions. This exercise would emphasise key spawning sites and as such areas of heightened conservation concern. Once these areas of successful spawning have been identified, the sensitivity of these habitats to projected climate change can also be identified, to help predict future changes in krill recruitment. Areas that require protection from the fishery during spawning can also be identified at a higher spatial resolution.

My chapter 4 results did not identify any consistent seasonal trends of an off-shelf spawning migration, but my method of analysis would not have been able to reconcile any inter-annual variability in seasonal distribution of krill. Consequently, there is the possibility that offshore migration does take place in certain years with a high level of inter-annual variability, or at a spatial resolution not resolvable with the data from the net-catch databases. Understanding these horizontal movements will provide insight into how to represent the seasonal distribution of krill in future advection models. Examining the mechanics behind seasonal adult migrations is also vital. For example, are they a reaction to predation or are they are an intrinsic characteristic of the krill life cycle? Year-round data must be used in order to understand fully the seasonal distribution of krill. A combination of data collected from fixed acoustic equipment and from the fishery would provide both estimates of the biomass of krill migrations between seasons and regions and demographics of krill being removed from the population by the fishery.

5.4.2 Laboratory experimentation

Krill recruitment term is a pivotal term in the generalised yield model used for krill fisheries management (Constable and De La Mare, 1996). As one component of recruitment, creating more accurate indices of potential female reproductive output and how this translates to a density value of viable larvae requires an understanding of embryonic variability. My observations demonstrate the highly variable and often low success of hatching to healthy nauplii. This suggests that indices of reproductive potential of female krill relate poorly to the subsequent production of viable krill larvae and may help to explain spatial discrepancies between the distribution of the spawning stock and larval distribution. In order to understand what causes the variability in hatching success, further research is required into both the environmental factors that contribute to hatch failure and causes of individual female variability, such as maternal diet. Improving our mechanistic understanding of these process through laboratory experimentation will vastly improve our understanding of recruitment drivers and will enable more realistic population models that are required for effective fishing management to operate (Hill et al., 2016).

The effect of maternal diet on embryonic success deserves further investigation. Hatching success in krill has been associated with the quantity and composition of fatty acids in the embryos, which in turn is influenced by the maternal diet (Yoshida et al., 2011). The maternal diet could also have a negative effect on embryo hatching success. Research into the inhibitory effect of diatoms on copepod reproduction has shown that compounds, such as oxylipins, can reduce hatch success rates and larval survival (reviewed in Paffenhöfer 2002, Russo et al. 2019). A number of species of diatoms from the genera *Chaetoceros* and *Thalassiosira* that have a negative effect on copepod hatch rates are common in krill habitat (Ban et al., 1997; Paffenhöfer, 2002). This theory is highly debated in the literature and some suggest that diatoms could be beneficial to copepod reproduction (Jonasdottir et al., 1998; Irigoien et al., 2002).

The large amount of study effort on diatoms and copepod egg hatch success has not been matched by reseach for euphausiids. Diatoms can dominate krill diet in both the spring and summer in certain locations in the south-west Atlantic sector (Schmidt et al. 2014). Specifically, at the WAP there are numerous regions of upwelling upper CDW that create diatom rich blooms with which krill are associated (Prézelin et al., 2000). These diatoms have been shown to contribute to produce rapid growth rates and increase the speed of ovary development (Cripps et al., 1999; Pond et al., 2005; Schmidt et al., 2012, 2014; Schmidt and Atkinson, 2016). The importance of diatoms to krill health (Pond et al., 2005) and the quantities in which krill consume them (Schmidt et al., 2014; Schmidt and Atkinson, 2016) justify further investigation into the possible effect of different species of diatoms and their effect on krill maternal health, hatch success and consequently larval recruitment.

The stenothermal nature of krill makes temperature a key climate variable to investigate, but individual climate variables do not act in isolation. Increasing atmospheric CO_2 concentrations are driving the global increase in temperatures, and these are also causing a reduction in the pH of surface waters, a factor that will act in tandem with changing ocean temperatures (Kawaguchi et al., 2013). Future work should investigate the effects of multiple stressors on hatching success of krill using a variety of approaches to gain a fuller appreciation of how climate change is affecting krill. Ideally, long-term studies that combine physiological, biochemical and molecular approaches provide the needed framework for addressing questions of climate effects on krill. When used in triplicate these methods will enable us to identify whether multiple climate change stressors decrease a krill's capacity to react to environmental change, whilst identifying any change in gene expression that may lead to new environmental tolerance though acclimation or potentially adaptation.

A key assumption in the modelling of krill embryonic development is that if krill embryos encounter the benthos they are no longer viable due to either mechanical damage or predation (Hofmann and Hüsrevoğlu, 2003; Thorpe et al., 2019). Using laboratory studies to identify the hatching success of krill embryos in contact with the benthos would identify conclusively whether any eggs encountering the benthos can contribute to successful recruitment. An experiment where krill embryos are incubated using three treatment conditions; 1) directly onto a benthic sample, 2) directly onto a sterile glass surface, 3) into a gentle upward flow of water to avoid contact with any surface, would identify the effect of benthic resting on hatch success in krill embryos.

5.5 Conclusion

The research presented in my thesis furthers our understanding of krill recruitment processes, an aspect of krill population dynamics that has been repeatedly highlighted as a key knowledge area that requires further research (Flores et al., 2012; Meyer et al., 2020). My observations have helped:

- Pinpoint spawning hotspots and larval nursery grounds (chapter 2),
- identified that indices of reproductive potential of female krill may relate poorly to the subsequent production of viable larvae (chapter 3),
- and provided further insight into the location of spawning adult krill within the south-west Atlantic sector of the Southern Ocean (chapter 4)

Future research into krill recruitment should utilise numerical modelling studies to identify pivotal trends in krill population dynamics that are parameterised by biological and physiological laboratory experiments. Data from this research must identify regions vital to krill recruitment, determine how these areas overlap with fishing activity, and resolve how both recruitment processes and areas key to recruitment may be sensitive to ongoing climate change within the Southern Ocean.

We are now at an important juncture in understanding how the krill life cycle interacts with its environment. In order for the sustainable management of expanding fishery it is vital to comprehend these processes even more fully if we are to understand the fate of krill.

Appendix A Chapter 2 Appendices

Supplementary Table 1. Source of larval krill data arranged with each row of data corresponding to a single research cruise. The complete larval database was larger than this, but the records listed here correspond to the screened subset of data that were used for plotting the distributions. References provided give more details on the specific research cruises. For a breakdown of the larval stages analysed on each cruise please see Supplementary Table 2.

Year	**Month**	**Net type**	**Net depth (m)**	**No. of Stns.**	**Survey (Reference)**	**Source of data**
1976	2,4	RMT1*, Bongo	0-200	128	German south-west Atlantic cruises (Hempel and Hempel, 1978)	Transcribed by one of us (AA) from figures and tables of this reference
1977	1	0.8 m Juday	0-200 (mainly)	13	Norwegian Bouvet/Weddell Survey (Fevolden, 1979)	Data were used in Fig. 2.5 in Siegel and Watkins (2016) and were provided by Siegel
1979	2	1 m Nansen	0-300	17	Norwegian Weddell Sea Survey (Fevolden, 1980)	Data were used in Fig. 2.5 in Siegel and Watkins (2016) and were provided by Siegel
1980	1,2	Bongo	0-150 (variable)	57	German *Polarsirke*l cruise (Hempel and Hempel, 1982)	Data were used in Fig. 2.5 in Siegel and Watkins (2016) and were provided by Siegel
1981	1-3	RMT1* 100 µm Juday 200 µm Nansen	0-200 0-200 0-500/ 1000	307	International FIBEX surveys (Russia, Argentina, Poland, Germany, Chile) across south-west Atlantic	Data were used in Fig. 2.5 in Siegel and Watkins (2016) and were provided by Siegel Russian data transcribed by AA from Makarov and Menshenina (1992).
1982	2-3	RMT1* 200 µm Nansen	0-1000** (variable)	118	German leg of *John Biscoe* Cruise (Marschall and Mizdalski, 1985)	Transcribed by one of us (AA) from figures and tables of this reference
1985	1-3?	RMT 1?	0-200	136	German *Walter Herwig* cruise	Data were used in Fig. 2.5 in Siegel and Watkins (2016) and were provided by Siegel

1987	1-3	330 µm 1m ring net	0-200** 0-1000**	10	US *Polar Duke* Cruise (Marin et al., 1991)	Transcribed by one of us (AA) from figures and tables of this reference
1989	1-2	RMT1*	0-250**	1	German Survey (reported in Ber. zur Polarforsch. 68 Ant-VII/4)	Data were used in Fig. 2.5 in Siegel and Watkins (2016) and were provided by Siegel
1996	1	200 µm Bongo	0-200	21	British Antarctic Survey *James Clark Ross* Cruise (Ward et al., 2003)	Obtained from BAS Polar Data Centre https://data.bas.ac.uk/
1997	1	200 µm Bongo	0-200	1	British Antarctic Survey *James Clark Ross* Cruise (Ward et al., 2003)	Obtained from BAS Polar Data Centre https://data.bas.ac.uk/
1998	1	200 µm Bongo	0-200	8	British Antarctic Survey *James Clark Ross* Cruise (Ward et al., 2003)	Obtained from BAS Polar Data Centre https://data.bas.ac.uk/
2000	1-2	RMT1*	0-200	157	CCAMLR 2000 Synoptic Survey (Japan, Russia, USA and UK vessels) (Siegel et al., 2004)	Data were used in Fig. 2.5 in Siegel and Watkins (2016) and were provided by Siegel
2001	4-5	300 µm Bongo	0-300	13	German *Polarstern* Cruise to Maguerite Bay (Pakhomov et al., 2004)	Original data provided by Pakhmov
2001	1	200 µm Bongo	0-200	8	British Antarctic Survey *James Clark Ross Cruise*	Obtained from BAS Polar Data Centre https://data.bas.ac.uk/

					(Tarling et al., 2007)	
2001	5	335 µm MOCNESS	0-500** (variable)	20	USA (Southern Ocean GLOBEC cruises) (Wiebe et al., 2011)	Obtained from GLOBEC database www.globec.org
2002	4-5	335 µm MOCNESS	0-500** (variable)	20	USA (Southern Ocean GLOBEC cruises) (Wiebe et al., 2011)	Obtained from GLOBEC database www.globec.org
2002	1,2	200 µm Bongo	0-200	58	British Antarctic Survey *James Clark Ross Cruise* (Tarling et al., 2007)	Obtained from BAS Polar Data Centre https://data.bas.ac.uk/
2003	1,2	200 µm Bongo	0-200	61	British Antarctic Survey *James Clark Ross* Cruise (Ward et al., 2008)	Obtained from BAS Polar Data Centre https://data.bas.ac.uk/
2004	4	RMT 1*	0-200	92	German *Polarstern* LAKRIS cruise (Siegel, 2012)	Data were used in Fig. 2.5 in Siegel and Watkins (2016) and were provided by Siegel
2004	3	200 µm Bongo	0-200		British Antarctic Survey *James Clark Ross* Cruise (Ward et al., 2008)	Obtained from BAS Polar Data Centre https://data.bas.ac.uk/
2005	1	200 µm Bongo	0-200		British Antarctic Survey *James Clark Ross* Cruise (Ward et al., 2008)	Obtained from BAS Polar Data Centre https://data.bas.ac.uk/
2008	1,2	Bongos 200 µm LHPR	0-400 0-1000**	67	British Antarctic Survey *James Clark Ross* Cruise	Obtained from BAS Polar Data Centre

					(Ward et al., 2012)	https://data.bas.ac.uk/
2009	3,4	Bongos 200 µm LHPR	0-400 0-1000**	70	British Antarctic Survey *James Clark Ross* Cruise (Ward et al., 2012)	Obtained from BAS Polar Data Centre https://data.bas.ac.uk/
2011	1	RMT1*	0-200	94	German *Polarstern* Cruise (Siegel et al., 2013)	Data were used in Fig. 2.5 in Siegel and Watkins (2016) and were provided by Siegel
2011	1	505 µm IKMT	0-170	81	US AMLR cruise (Siegel et al., 2013)	Data were used in Fig. 2.5 in Siegel and Watkins (2016) and were provided by Siegel

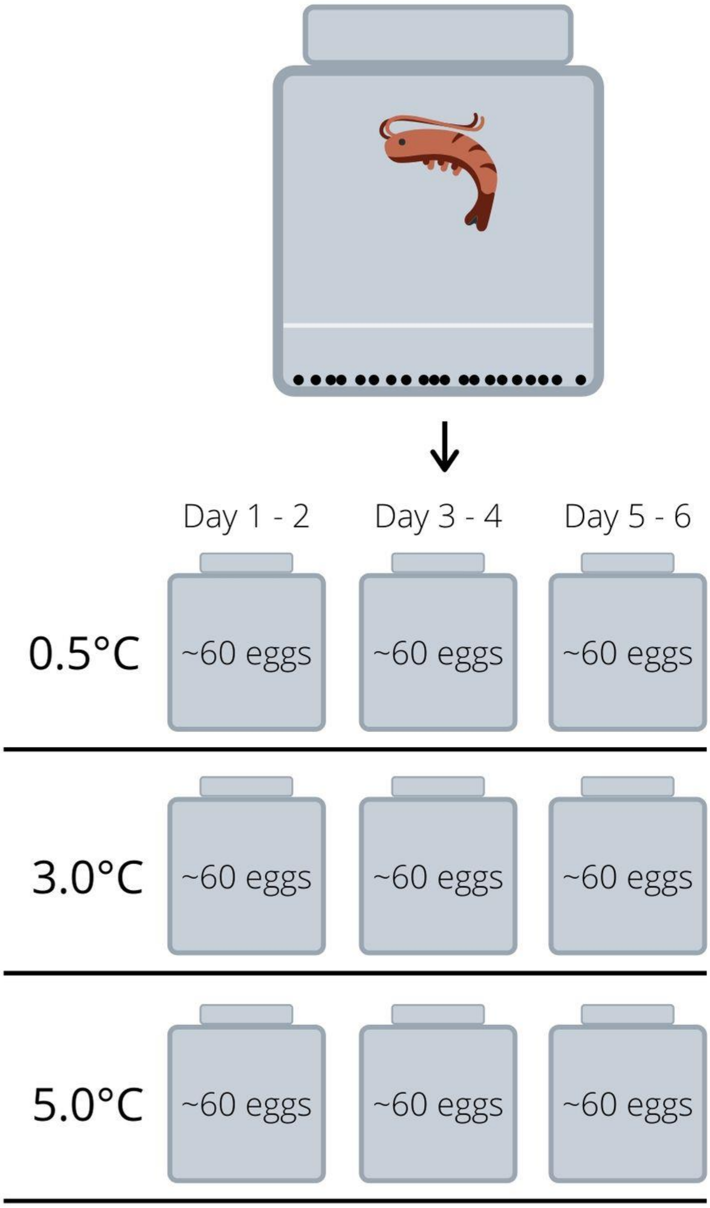
* Typical mesh size of RMT 1 net is 330 µm

** Stratified hauls, here combined to provide total densities under 1 m^2 in whole sampled water column

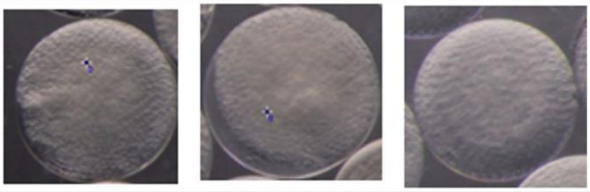
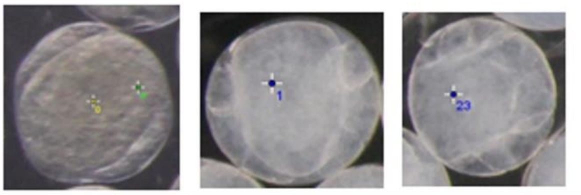
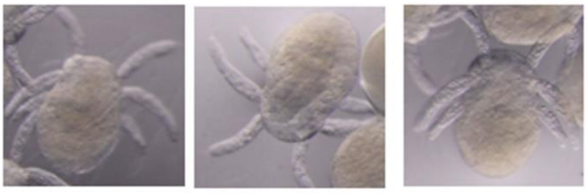
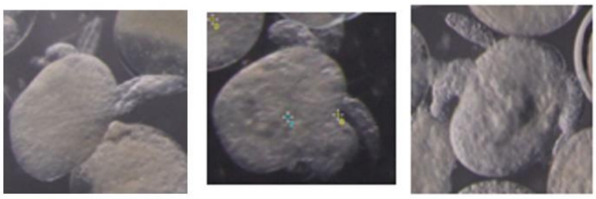
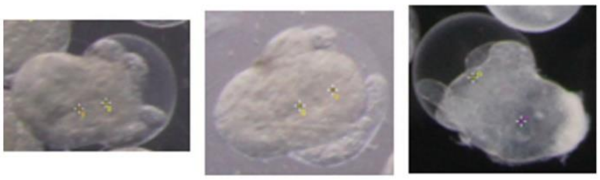
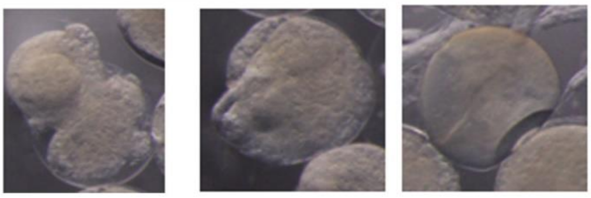
Supplementary Table 2. The number of stations for each of the life stages is shown for each of the 41 seasons within the study period. In brackets next to this number is the percentage of those stations at which Antarctic krill were present. This table provides a breakdown of the stations into early and late season.

Number of stations (percentage presence)										
	larval_data				length-frequency_data				abundance_data	
SEASON	Eggs	Nauplii	Calyptopes	Furcilia	15-30mm_early	>30mm_early	15-30mm_late	>30mm_late	early	late
1976			128(41)	127(21)			60(93)	60(100)	60(85)	133(78)
1977			13(0)	13(0)						
1978					39(85)	39(95)	107(68)	107(97)	51(86)	172(97)
1979			17(82)	17(0)			8(75)	8(100)		
1980			57(24)	57(2)	3(100)	3(100)	120(3)	120(100)		52(4)
1981		79(3)	307(68)	307(39)	24(96)	24(91)	179(59)	179(100)	23(100)	169(53)
1982	118(73)	118(33)	118(76)	118(23)	32(97)	32(97)	337(85)	337(91)	191(45)	59(86)
1983							30(93)	30(97)		3(100)
1984					162(98)	162(80)	195(46)	195(96)	150(85)	192(55)
1985				136(51)	175(45)	175(98)	274(15)	274(100)	197(67)	230(84)
1986							92(29)	92(92)		22(86)
1987	1(100)	10(30)	10(90)	10(60)	6(67)	6(83)				18(89)
1988					76(82)	76(96)	85(65)	85(100)	79(97)	131(75)
1989			1(100)	1(0)	20(95)	20(90)	2(100)	2(100)	21(95)	11(45)
1990					21(24)	21(100)	76(30)	76(100)	24(83)	139(55)
1991					14(86)	14(100)	107(36)	107(97)	19(0)	80(43)
1992							110(66)	110(98)		162(89)
1993							136(29)	136(99)		211(86)
1994							107(27)	107(94)	3(100)	272(75)
1995					74(53)	74(96)	114(17)	114(100)	75(99)	255(79)
1996	21(0)	21(0)	21(24)	21(0)			163(67)	163(98)	72(29)	322(81)
1997	10(0)	1(0)	1(0)	1(0)	100(88)	100(99)	81(32)	81(96)	130(82)	194(90)
1998					3(67)	3(100)	140(72)	140(97)		321(84)
1999	8(0)	8(38)	8(0)	8(0)			57(2)	57(100)	29(21)	241(70)
2000	157(14)	36(6)	157(48)	157(9)	1(100)	1(100)	265(33)	265(99)		261(75)
2001	12(0)	12(0)	41(41)	41(71)	21(90)	21(100)	181(45)	181(98)	14(64)	369(80)
2002	59(0)	59(5)	78(44)	77(21)			120(54)	120(91)		313(61)
2003	61(15)	61(18)	61(39)	61(2)			108(71)	108(95)		306(78)
2004	19(0)	19(0)	111(54)	111(42)			95(21)	95(99)		271(75)
2005	37(3)	37(3)	37(16)	37(3)	1(0)	1(100)	89(11)	89(99)	20(0)	290(74)
2006							39(18)	39(100)		159(89)
2007							46(87)	46(100)	28(21)	170(95)
2008		56(0)	67(28)	67(1)			22(36)	22(100)		307(79)
2009		61(0)	70(59)	70(29)			9(0)	9(100)		197(68)
2010					9(67)	9(100)				107(79)
2011		120(2)	175(54)	174(10)	6(17)	6(100)	10(80)	10(100)		120(100)
2012							9(33)	9(100)		41(95)
2013					8(0)	8(100)				42(100)
2014					10(90)	10(100)				33(100)
2015					7(71)	7(100)				37(92)
2016					9(67)	9(100)				29(100)

Appendix B Chapter 3 Appendices



Supplementary figure 1. A schematic showing our field experiment set up. For each batch of eggs (>1000) produced by a gravid female the following experimental set up was used. We placed ~60 eggs into each of nine treatment bottles. Three bottles were placed in each of the three temperature treatments. Each day ~30 eggs were removed from each of the bottles and fixed in 4% formalin.

Developmental stage	Example images
Two cell	
Multiple cell	
Limb bud	
Healthy nauplii	
Malformed nauplii	
Entrapped	
Unclassified	

Supplementary figure 2. Recorded stages of embryonic development from field experiments. Photographic documentation for the different embryonic development stages recorded when analysing the eggs from the field experiment in the laboratory

Appendix C Chapter 4 Appendices

Supplementary information 1. To calculate the mean maximum percentage of carbon content of krill consumed per day we took the maximum 1° latitude × 2° longitude cell value for each length category of adult krill. We then calculated the daily carbon ration of these length categories (using relationships in Lenz (1974) and Morris et al. (1988)), assuming a conservative daily carbon ration of 17 % (Schmidt and Atkinson, 2016). Across subarea 48.1, the maximum chl-a value is 1.038 mg m^3 which is the equivalent of 51.9 mg C m^3 (using a C:chl-a ratio of 50) (Whitehouse et al., 2009). This equals 3.9 g C m^2 over a typical 75 m surface mixed layer (Korb and Whitehouse, 2004).

Glossary of Terms

Term	Definition/Description of the term
Adult krill	Any krill ≥30 mm
Austral season	For example, the austral season of 1980 would spawn the period between October 1979 to May 1980
Early season	1 October to December 31
Ectotherm	An organism that derives its heat from the environment
Egg	A single female reproductive cell
Embryo	A fertilised egg
Gravid female	A female adult krill carrying eggs internally
Juvenile krill	All post-larval krill >30 mm
Modern Era	1976 - 2016
Off-shelf	Habitat where water depth exceeds 1000 m
Offshore	Towards the sea from the land
On-shelf	Habitat where water depth is no more than 1000 m
Late season	1 Jan to 31 May
Post-larval	All individuals in the final adult krill form
Recruitment	The year class strength defined as the result of survival during the first year of life
Stenotherm	An ectotherm that functions within a narrow temperature range
Year	A calendar year, January to December

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