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Linking Antarctic krill larval supply and recruitment along the Antarctic Peninsula

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Abstract

Antarctic krill (*Euphausia superba*) larval production and overwinter survival drive recruitment variability, which in turn determines abundance trends. The Antarctic Peninsula has been described as a recruitment hot spot and as a potentially important source region for larval and juvenile krill dispersal. However, there has been no analysis to spatially resolve regional-scale krill population dynamics across life stages. We assessed spatiotemporal patterns in krill demography using two decades of austral summer data collected along the North and West Antarctic Peninsula since 1993. We identified persistent spatial segregation in the summer distribution of euphausiid larvae (*E. superba* plus other species), which were concentrated in oceanic waters along the continental slope, and *E. superba* recruits, which were concentrated in shelf and coastal waters. Mature female *E. superba* were more abundant over the continental shelf than the slope or coast. Euphausiid larval abundance was relatively localized and weakly correlated between the North and West Antarctic Peninsula, while *E. superba* recruitment was generally synchronized throughout the entire region. Euphausiid larval abundance along the West Antarctic Peninsula slope explained *E. superba* recruitment in shelf and coastal waters the next year. Given the localized nature of krill productivity, it is critical to evaluate the connectivity between upstream and downstream areas of the Antarctic Peninsula and beyond. Krill fishery catch distributions and population projections in the context of a changing climate should account for ontogenetic habitat partitioning, regional population connectivity, and highly variable recruitment.

Introduction

The Antarctic Peninsula (AP) is a key region for understanding population dynamics of the Antarctic krill (*Euphausia superba*), a dominant species in the Southern Ocean food web and in biogeochemical cycles (Trathan and Hill 2016; Cavan et al. 2019). A recent study indicates that Antarctic krill distribution in the Southwest Atlantic sector shifted southward from the Scotia Sea to the AP shelf from 1976 to 2016 (Atkinson et al. 2019). This range contraction coincided with regional warming and reduced seasonal sea ice coverage during the second half of the 20th century (Meredith and King 2005; Stammerjohn et al. 2008b; Henley et al. 2019). Further twenty-first century ocean warming, acidification, and sea ice decline will likely impair recruitment by reducing larval survival over winter (Flores et al. 2012; but see Melbourne-Thomas et al. 2016). Although previously distributed throughout the Southern Ocean, commercial krill fishing effort has focused on the North Antarctic Peninsula (NAP) in the last two decades (Nicol and Foster 2016). Understanding krill demographic patterns will improve population dynamic studies in the context of AP climate change and fishing pressure.

It is well-established that *E. superba* recruitment is episodic throughout the Southwest Atlantic sector. From 1991 to 2013, 4- to 6-year cycles in *E. superba* post-larval abundance were apparent along the West Antarctic Peninsula (WAP) (Ross et al. 2014; Steinberg et al. 2015), NAP (Reiss 2016; Kinzey et al., 2019), and at South Georgia (Fielding et al. 2014). Larval abundance is relatively less studied despite its key role in mechanistic hypotheses explaining *E. superba* recruitment patterns (Siegel and Loeb 1995; Saba et al. 2014). Larvae spawned during summer develop to late stages and then overwinter before recruiting to the post-larval population the following summer.

While feeding larvae are most abundant in oceanic waters during summer, recruits are instead concentrated on the continental shelf (Siegel and Watkins 2016; Perry et al. 2019). Therefore, linking larval supply with recruitment must account for spatial segregation between these life stages.

Uncertainties in regional-scale connectivity further complicate Antarctic krill population dynamics. Physical model simulations suggest larvae spawned at the WAP and NAP can both be retained locally or advected northeast towards the Scotia Sea (Fach and Klinck 2006; Thorpe et al. 2007; Piñones et al. 2013). A mechanistic population model reproduced observed Antarctic krill biomass cycles at the WAP, NAP, and South Georgia only after allowing for transport among study areas (Wiedenmann et al. 2009). Available data suggest recruitment was positively correlated across these sites between 1983 and 2011 (Siegel et al. 2003; Reiss 2016), but larval abundance time series have not been compared across the region.

In this study we analyzed spatiotemporal patterns in larval euphausiid abundance as well as *E. superba* recruit and mature female abundance along the AP since 1993. Austral summer net sampling surveys were conducted along the WAP by the Palmer Antarctica Long-Term Ecological Research (PAL LTER) program and at the NAP by the United States Antarctic Marine Living Resources (U.S. AMLR) program. While *E. superba* recruitment was generally synchronized across the NAP and WAP, larval euphausiid abundance correlations were weaker between the two areas. The WAP continental slope was identified as a key larval supply region supporting *E. superba* recruitment the following summer on the continental shelf. Population connectivity must be considered to understand how krill will respond to climate change and to effectively distribute fishing effort.

Materials and Methods

Sample collection

U.S. AMLR – NAP

The U.S. AMLR Program conducted shipboard oceanographic and biological surveys in the NAP ecosystem during austral summer from 1993-2011, sampling an area of more than 124,000 km_2. The oceanographic survey usually consisted of two repeat legs. Leg-1 was typically conducted in mid-January and Leg-2 started several weeks later in February. The survey area extends from the southern end of Bransfield Strait to the tip of the AP at Joinville Island, and offshore into the Antarctic Circumpolar Current (ACC) on the north side of the South Shetland and Elephant Islands (Fig. 1). The number and location of sampling stations varied as the grid expanded throughout the time series. In general, 40–60 stations either 20 or 40 km apart along predefined transects were sampled during each leg.

For this analysis, the U.S. AMLR sampling grid was divided into Slope, Shelf, and Coast sub-regions (Fig. 1). The NAP Slope sub-region included sampling stations offshore of the 750 m isobath along the continental shelf break, following the definition used by PAL LTER at the WAP (Martinson et al., 2008). The NAP shelf was defined as the area bounded to the northwest by the shelf break and to the southeast by the South Shetland Islands and another 750 m isobath along the edge of a submarine canyon. The NAP Coast sub-region included stations southeast of the South Shetland Islands and the canyon edge and was restricted to the east by the Antarctic Peninsula and the continental shelf break.

At each sampling station a tow was made using a 1.8 m Isaacs-Kidd Midwater Trawl (IKMT) equipped with a 505 µm mesh net. The net frame was also equipped with a General Oceanics flowmeter to determine the volume of water filtered during each tow. The IKMT was fished obliquely to either 170 m depth or 20 m above the bottom at stations <190 m deep using an attached pressure-sonde to determine net depth.

Aboard ship, zooplankton were sorted to species and enumerated. *Euphausia superba* post-larvae were identified by sex and maturity stage following Makarov and Denys (1981) and measured to the nearest 0.1 mm using Standard Length 1 (SL1) (Mauchline 1980). The SL1 measurement is taken from the anterior tip of the rostrum to the posterior tip of the uropod. From 1995 to 2011, euphausiid larvae were identified to species, staged and enumerated for each tow. Total euphausiid larvae (*E. superba* plus other species) were used for the analysis in this study, because larvae collected in the WAP were not identified to species. Annual *E. superba* and *Thysanoessa macrura* (another abundant euphausiid) larval abundances were compared to total euphausiid larval abundance using the available species-specific data from the NAP.

PAL LTER – WAP

The historical PAL LTER study region extends 400 km along the WAP from Anvers Island to Marguerite Bay and from coastal to slope waters approximately 200 km offshore (Ducklow et al. 2012) (Fig. 1). Sampling grid lines are spaced 100 km apart, with grid stations every 20 km along each grid line (Waters and Smith 1992).

Zooplankton were collected on PAL LTER annual research cruises during austral summer (approx. 01 January – 10 February) since 1993. From 1993-2008 tows were conducted at each PAL LTER grid station from the 600 to 200 lines, and since 2009 on an extended grid an additional 300 km further south with decreased sampling frequency (Steinberg et al. 2015). The sampling grid is divided into North, South, and Far South latitudinal sub-regions as well as Coast, Shelf, and Slope sub-regions (Steinberg et al., 2015). For this study, only data from the consistently sampled North and South sub-regions (600 to 200 lines) are included (Fig. 1).

Zooplankton were collected with two gear types on PAL LTER research cruises. Post-larval *E. superba* were collected with oblique net tows from 0-120 m using a 2x2 m square frame net with 700 µm mesh. Euphausiid larvae were collected with oblique net tows from 0-300 m using a 1x1 m square frame net with 333 µm mesh. Net depth was determined real time with a depth sensor attached to the bottom of the conducting hydro wire. Both nets were equipped with a General Oceanics flowmeter to record the volume of water filtered.

Post-larval *E. superba* were enumerated onboard, and a subsample of at least 100 randomly selected individuals were measured using SL1. Juvenile *E. superba* recruits belonging to age class 1 were defined as post-larval individuals < 31 mm in length (Saba et al. 2014; Atkinson et al. 2019). This same recruit definition was used for the WAP and NAP. Post-larval *E. superba* individuals with a visibly red thelycum were classified as mature females.

Once onboard, the 333 µm mesh net samples were preserved in 4% buffered formaldehyde and stored for subsequent laboratory analysis. A subset of samples was analyzed for larval euphausiid abundance: one Coast, one Shelf, and one Slope station on each of the 600, 400, and 200 grid lines from 1993-2013. The stations sampled on each grid line varied year-to-year within a 40-km radius. Preserved samples were sieved into three size fractions (> 5 mm, 1-5 mm, and 0.33-1 mm). The entire > 5 mm size fraction was enumerated, and the two smaller size fractions were subsampled as follows: the 1-5 mm size fraction was split with a Folsom Plankton Splitter (1-1/64 sample enumerated), and the 0.33-1 mm size fraction was subsampled using a Stempel pipet (1-1/180 sample enumerated; Postel et al. 2000). Samples were analyzed using an Olympus SZX10 dissecting microscope with dark/bright field illumination at 8-20x magnification. Larval euphausiids in this analysis include the calyptopis and furcilia stages. Euphausiid larvae collected at the WAP were not identified to species. Most samples analyzed were from daytime tows (hours of darkness are limited to < 4 h during our sampling period in January); there was no significant difference between the abundance of calyptopis or furcilia larvae collected in day ($n = 185$) compared to night tows ($n = 18$; Wilcoxon rank-sum $p > 0.05$).

Statistical analysis

WAP sampling locations were rounded to the nearest grid line and grid station. Abundance values were averaged when the same PAL LTER station was sampled multiple times in a given year. The following data processing steps were applied to NAP and WAP sampling sub-regions: When a life stage was absent at a sampling station, zeros were replaced with one-half the lowest non-zero abundance value in a given sub-region data set (O'Brien 2013). Sampling station abundance values were then $\log_{10}$-transformed prior to calculating annual mean abundance for the sub-region. Abundance anomalies were calculated by subtracting annual mean abundance from the climatological mean of the given time series (Mackas and Beaugrand 2010; O'Brien 2013; Thibodeau et al. in review). A difference of 1.0 in annual mean abundance or abundance anomaly indicates an order of magnitude difference. Although annual mean abundance cannot be compared across different gear types, temporal comparisons of abundance anomalies are appropriate. All statistical analysis was conducted with R version 3.5.1 (R Core Team 2018), and the significance level was set at 0.05 unless otherwise noted.

Spatial differences in annual mean abundance were examined among sub-regions within the NAP and WAP areas each. Linear mixed models (LMMs) were fitted using the nlme package by maximizing the restricted log-likelihood (Pinheiro et al. 2018). Annual mean abundance was the response variable, sub-region was included as a fixed effect, and year was included as a random effect to account for repeated sampling. This analysis was also conducted separately using *E. superba* larvae data available for the NAP. Tukey's honest significant differences tested for pairwise differences among individual sub-region means using the multcomp package (Hothorn et al. 2008).

Temporal synchrony in euphausiid larvae and *E. superba* recruit abundance across the study region was tested by calculating pairwise Pearson's correlations for the NAP Slope, Shelf, and Coast sub-regions as well as the WAP Coast, Shelf, and Slope. The same analysis was performed using available *E. superba* larvae data for the NAP. The significance level was set at 0.003 for this analysis according to the Bonferroni adjustment for multiple comparisons. The function 'acf' was used to test for autocorrelation in individual time series at the 0.05 significance level. This temporal analysis and all others described below were performed with data in anomaly form.

The relationship between total euphausiid larvae abundance and species-specific larvae abundance was investigated in each of the NAP sub-regions. Total euphausiid larvae abundance was compared to *T. macrura* larval abundance and to *E. superba* larval abundance using linear regression.

An information-theoretic approach was used to identify potential larval source areas impacting *E. superba* recruitment. This analysis was restricted to years with complete data coverage (1995-2010 for euphausiid larvae and 1996-2011 for *E. superba* recruits). All six individual sampling sub-regions were included as candidate larval source areas. The combined Shelf and Coast sub-regions for both the NAP and WAP were the recruitment areas of interest based on elevated *E. superba* recruit abundance in the LMM analysis described above. Separate linear regressions were fitted for each combination of larval source and recruitment area, with *E. superba* recruit abundance as the response variable and the previous year's euphausiid larvae abundance as the explanatory variable. Comparable linear regressions were also repeated for the NAP using available *E. superba* larvae data. The corrected Akaike Information Criterion (AICc) was used to assess support for individual linear regression models (Hurvich and Tsai 1989; Burnham et al. 2011) and calculated with the MuMIn package (Bartoń 2019). Models with ΔAICc < 2 were considered to have substantial statistical support. AICc weight approximates the probability that each candidate model is the best option given the set of models considered (Symonds and Moussalli 2011).

The functional relationship between larval euphausiid abundance and the following year's *E. superba* recruitment was assessed with thin plate regression splines. This analysis focused on larval abundance at the WAP Slope based on the above model selection procedure and our ecological interpretation of those results. Five additional years of larval abundance data were available from the WAP Slope for this analysis (1993-2013). *Euphausia superba* recruit abundance at the combined Shelf and Coast for both the NAP and WAP were the response variables in separate models. The previous year's larval euphausiid abundance at the WAP Slope was the only explanatory variable in each regression. Thin plate regression splines were fitted using restricted maximum likelihood with the gam function in the mgcv package (Wood, 2003). This non-linear technique alleviated problematic patterns in the residuals and reduced AICc compared to linear regression when using all available data. The basis dimension of the smoother term was set at 4 to avoid overfitting and confirmed to be adequate using the gam.check function. Model assumptions were verified by plotting residuals against fitted values, sampling year, and the explanatory variable (Zuur and Ieno, 2016).

Results

Spatial distribution of life stages

Larval euphausiid abundance was highest along the continental slope in both the NAP and WAP study areas. Annual mean larval euphausiid abundance was significantly different among sub-regions (LMM; NAP $p = < 0.0001$; WAP $p < 0.0001$) and was higher on the Slope than on the Shelf and Coast in both the NAP and WAP (Fig. 2A-B) (Tukey's test; $p < 0.0001$). Mean *E. superba* larval abundance was also different among

NAP sub-regions (Supplemental Fig. 1) (LMM; $p = 0.011$). With species-level data, *E. superba* larvae were significantly more abundant at the Slope than Shelf (Tukey's test; $p = 0.004$), while the Slope and Coast were not significantly different ($p = 0.10$). However, *E. superba* larvae were less abundant at the Coast on average, and two anomalous years drove the lack of a statistical difference (Supplemental Fig. 1).

In contrast to the larval distribution, *E. superba* recruit abundance was highest over the continental shelf in both the NAP and WAP study areas. Annual mean *E. superba* recruit abundance was significantly different among sub-regions (LMM; NAP $p < 0.0001$; WAP $p < 0.0001$), and within the NAP was higher on both the Shelf and Coast than on the Slope (Fig. 2C) (Tukey's test; $p < 0.00001$), and within the WAP progressively increased from Slope to Shelf to Coast (Fig. 2D) (Tukey's test; $p < 0.005$).

Mature female *E. superba* distribution was also consistent across the offshore sampling gradient in the NAP and WAP study areas. Annual mean *E. superba* mature female abundance differed among sub-regions (LMM; NAP $p = 0.0002$; WAP $p = 0.0008$) and was highest on the Shelf in both the NAP and WAP (Fig. 2E-F) (Tukey's test; $p < 0.02$).

Regional coherence

Larval euphausiid abundance was positively, significantly correlated between neighboring sub-regions from 1995-2011, but these correlations did not hold throughout the entire AP study region. There was a relatively weak positive correlation in euphausiid larvae abundance between the full WAP study area and the full NAP study area (Fig. 3A). Pairwise comparisons of individual sub-regions revealed larval abundance was strongly correlated between the adjacent Coast and Shelf sub-regions as well as the Shelf and Slope within both the NAP and WAP study areas (Table 1). The same result was found using *E. superba* larvae data for the NAP (Supplemental Table 1). There were no similarly strong cross-correlations between NAP and WAP sub-regions. Larval euphausiid abundance did not exhibit positive autocorrelation ($p > 0.05$).

Unlike larval euphausiid abundance, *E. superba* recruitment cycles were coherent across the AP study region. There was a relatively strong positive correlation in *E. superba* recruit abundance between the full WAP and NAP study areas compared to the euphausiid larvae time series (Fig. 3B). Recruit abundance in the WAP Coast sub-region was only significantly correlated with the WAP Shelf, an apparent exception to the pattern of synchronized recruitment throughout the AP study region (Table 1). Two to three successive years of positive *E. superba* recruit abundance anomalies were typically followed by two to three successive years of negative anomalies (Fig. 3B). Significant, positive autocorrelation at 5 to 6 years was identified in recruit abundance time series from all NAP sub-regions and the WAP Coast ($p < 0.05$).

Euphausiid larvae composition

The annual abundance of larval *E. superba* and *T. macrura* were both significantly, positively related to total euphausiid larvae abundance in all three NAP sub-regions ($p < 0.02$) (Fig. 4). Total euphausiid abundance was more strongly related to *T. macrura* larvae abundance than *E. superba* larvae abundance at the NAP Slope and Shelf.

Calyptopis stage larvae were numerically dominant compared to furcilia in the WAP samples. Calyptopes comprised 68% of larvae on average (median = 82%) in individual samples.

Larvae-recruit relationships

The NAP and WAP Slope had substantial statistical support for impacting subsequent *E. superba* recruitment on the continental shelf in both the NAP and WAP (Table 2). According to AICc, the WAP Slope model was preferable to the NAP Slope model in both cases. The importance of remote larval supply to the NAP was further supported by the lack of statistical relationships between *E. superba* larvae abundance and subsequent recruitment in this area (Supplemental Fig. 2) (linear regression; $p > 0.31$). Larval abundance at the NAP Shelf was identified as the best model for recruitment at the combined WAP Shelf and Coast (Table 2), but it is unlikely that larvae follow this transport path given regional circulation patterns. There was not support for larval abundance at the NAP Coast, WAP Coast, or WAP Shelf driving subsequent krill recruitment (Table 2).

The functional relationships between larval abundance in the WAP Slope sub-region and subsequent *E. superba* recruitment on the continental shelf differed between the NAP and WAP. WAP Slope larval abundance was positively, linearly related with next year's *E. superba* recruit abundance at the combined NAP Coast and Shelf ($n = 18$; $p = 0.006$; deviance explained = 45%) (Fig. 5A). The larvae-recruit relationship at the WAP Coast and Shelf suggested a threshold response ($n = 21$; $p = 0.011$; deviance explained = 44%) (Fig. 5B). When larval abundance at the WAP Slope was below average (ranging two orders of magnitude), *E. superba* recruit abundance anomaly the following year was also negative but relatively stable. Following years with a positive larval abundance anomaly, *E. superba* recruitment increased with larval abundance.

Discussion

Spatial distribution of life stages

Two decades of time-series data confirm the importance of oceanic slope waters for larval euphausiid supply along the AP. Combined calyptopis and furcilia-stage abundance was elevated in the NAP and WAP Slope sub-regions. A January 2011 survey along the AP found *E. superba* calyptopes and furcilia were most abundant at the WAP continental slope, with a secondary peak at the NAP Slope (Siegel et al. 2013). A spatial analysis compiling *E. superba* data collected across the Southwest Atlantic sector from 1976-2011 showed calyptopes and furcilia were concentrated in waters deeper than 1000 m (Perry et al. 2019). A typical explanation for the offshore, oceanic distribution of *E. superba* feeding stage larvae is that embryos must sink to depths of roughly 1000 m without reaching the seafloor to successfully hatch (Hofmann et al. 1992). However, it is possible embryos can still hatch after reaching the benthos and it is uncertain where collected larvae were spawned.

Unlike larvae, *E. superba* recruits were concentrated in AP coastal and shelf waters, indicating persistent habitat partitioning. At the NAP and WAP, elevated *E. superba* recruit abundance coincided with low larval abundance in Coast and Shelf sub-regions. Concentration of juvenile *E. superba* in shelf and coastal waters is common along the AP and is consistent across the southwest Atlantic sector (Lascara et al. 1999;

Siegel et al. 2013; Perry et al. 2019). Elevated summer phytoplankton biomass along the coastal AP (Reiss et al. 2017, their Fig. 4A; Brown et al. 2019) promotes faster krill growth rates (Atkinson et al. 2006; Shelton et al. 2013) and makes these areas favorable juvenile habitat. Additionally, ontogenetic habitat partitioning may reduce food competition between krill larvae and recruits under limiting conditions (Siegel 1988; Ryabov et al. 2017), although we note adult *E. superba* are not phytoplankton food limited during summer at the WAP (Bernard et al. 2012).

Antarctic krill mature females were consistently most abundant in Shelf sub-regions along the AP. This distribution is consistent with the highest densities of krill embryos being concentrated on continental shelves (further inshore than feeding larvae) (Perry et al. 2019). The spatial mis-match between mature females and larvae suggests large numbers of embryos spawned over the continental shelf may fail to develop into feeding larvae. High mortality rates are likely in shallow shelf waters where embryos reach the seafloor before hatching (Hofmann et al. 1992; Thorpe et al. 2019). However, not all mature females are active spawners (Quetin and Ross 2001), and we did not distinguish by size or ovarian development stage. Adult krill on the AP shelf during summer are typically smaller than those further offshore (Lascara et al. 1999; Siegel et al. 2013; Siegel and Watkins 2016), and larger females typically produce larger embryo batches, although spawning output varies among individuals and years (Quetin and Ross 2001; Tarling et al. 2007). Therefore, the spatial distribution of mature females does not necessarily indicate the spatial distribution of reproductive output.

Regional coherence

Asynchrony in larval euphausiid abundance across the AP supports the existence of multiple localized *E. superba* spawning areas. The locations of these spawning areas are consistent with regional circulation patterns (reviewed in Moffat and Meredith 2018). The WAP's inner shelf is an isolated spawning area, and larvae that successfully develop in this area are likely retained locally by ocean currents and a longer sea ice season (Stammerjohn et al. 2008a; Piñones et al. 2013, Meyer et al., 2017). Larval abundance in the NAP is decoupled from the WAP further south, likely because the northern tip of the AP is influenced by water flowing from the Weddell Sea (Thompson et al. 2009) (Fig. 6). Inflow from the Antarctic Coastal Current and a cyclonic gyre appear to generally isolate NAP Coast, although its degree of exchange with the WAP remains unclear (Sangrà et al. 2017; Moffat and Meredith 2018). Larval abundance at the NAP may be coupled with downstream areas in the ACC as larvae are transported out of our study region and into the Scotia Sea (Thorpe et al. 2004; Fach and Klinck 2006) (Fig. 6). Differences in seasonal spawn timing (Spiridonov 1995) may also contribute to the lack of strong correlations between NAP and WAP summer larval abundances.

Unlike larval abundance, Antarctic krill recruit abundance was generally synchronized along the AP, indicating recruitment is a regional-scale process. A notable exception was the WAP Coast where *E. superba* recruits were abundant. Comparison of annual krill recruitment indices from the WAP, NAP, and South Georgia showed positive correlations among sampling areas from 1983 to 2000 (non-continuous time series) (Siegel et al. 2003). Although some studies suggest recruitment cycles became decoupled between the WAP and NAP from 2000 to 2008 (Loeb et al. 2010; Ross et al. 2014), our analysis shows recruitment remained synchronized until at least 2011, in agreement with recent work (Reiss 2016). Climate-scale environmental controls such as the El Niño Southern Oscillation (ENSO) and the Southern Annular Mode (SAM) that affect sea ice and primary production (Stammerjohn et al. 2008b; Loeb et al. 2009; Saba et al. 2014; Kim et al. 2016) likely synchronize krill recruitment throughout the region. ENSO and SAM indices are linked to krill recruitment success at the AP and throughout the southwest Atlantic sector (Loeb et al. 2009; Ross et al. 2014; Atkinson et al. 2019).

The Antarctic krill life span (~6 years) coincides roughly with the period of its synchronized population cycles. One hypothesis suggests this long lifespan is an adaptive trait to deal with the environmental variability mentioned above, and it follows that successful *E. superba* recruitment would occur more frequently if environmental conditions were continuously favorable (Fraser and Hofmann 2003; Saba et al. 2014). An alternate view suggests *E. superba*'s relatively long lifespan causes periodic recruitment via intraspecific competition cycles that are independent of environmental variability (Ryabov et al. 2017). Regardless of the underlying mechanism driving periodic krill recruitment, climate-scale environmental forcing and larval dispersal are certainly important for its synchronization at the 1000-km scale of our study (Ripa 2000; Koenig 2002; Ryabov et al. 2017).

Euphausiid larvae composition

The grouping of all euphausiid larvae together is a limitation of our study. However, as our data analysis and interpretation depend upon relative temporal and spatial patterns, and are largely based on order of magnitude abundance differences between sampling years and sub-regions, we posit use of aggregated larval abundance is adequate. Larval euphausiid samples collected in autumn and winter 2001 at the WAP were numerically dominated by *E. superba* (typically > 95%) (Ashjian et al. 2008). The positive relationships between *E. superba* larvae and total euphausiid larvae abundance anomalies in all NAP sub-regions also support our use of aggregated euphausiid data to understand *E. superba* population dynamics. Contamination from *T. macrura* due to its high numerical abundance (Loeb and Santora 2015; Steinberg et al. 2015) is the most likely source of error. *Euphausia superba* larvae were present in 50%, and *T. macrura* larvae in 60%, of NAP samples from 1995 to 2009, but mean abundance was 37% greater for *E. superba* larvae compared to *T. macrura* (Loeb and Santora 2015). Larval *E. superba* and *T. macrura* abundance was positively correlated within and between years (Loeb and Santora 2015). The strong relationship between total euphausiid and *T. macrura* larvae abundance supports previous work showing both species are highly positively correlated with phytoplankton productivity (Steinberg et al. 2015).

The numerical dominance of calyptopes in the WAP larvae samples also supports their use in the study of *E. superba* population dynamics. Antarctic krill calyptopes were an order of magnitude more abundant than furcilia at the AP during January (Siegel et al. 2013) when *T. macrura* larvae are typically in furcilia stages (Makarov 1979; Nordhausen 1992).

Larvae-recruit relationships

The statistical link between larval abundance at the WAP continental slope and *E. superba* recruitment on the shelf suggests offshore larval production drives recruitment. Larvae are produced within our AP study area and further southwest in the

Bellingshausen Sea (upstream in the ACC) (Fig. 6). Above average phytoplankton biomass in the Bellingshausen Sea was associated with high larval euphausiid abundance at the WAP shelf break in autumn and strong *E. superba* recruitment the following summer (Marrari et al. 2008). Phytoplankton biomass and primary productivity are strong predictors of subsequent *E. superba* recruitment and post-larval abundance along the NAP (Loeb et al., 2009) and WAP (Saba et al., 2014; Steinberg et al. 2015). Importantly, early spawn timing also contributes to successful recruitment (Siegel and Loeb 1995). Additional time for larval development under high phytoplankton conditions likely increases overwinter survival (Ross and Quetin 1989).

The shelf is key habitat for later stage *E. superba* larvae despite lower numerical abundance compared to the slope. In autumn 2001 and 2002, *E. superba* larvae were more developmentally advanced and had improved body condition on the shelf where phytoplankton biomass is typically higher than offshore waters (Pakhomov et al. 2004; Daly et al. 2004). Therefore, the proportion of larvae that reach shelf waters may be more developed going into winter and thus have greater recruitment success (Ross and Quetin 1989; Daly et al. 2004). Shelf waters may include a mix of larvae spawned locally and offshore (Wiebe et al. 2011; Piñones et al. 2013), but our data show larval abundance is an order of magnitude lower on the shelf compared to the slope and suggest the importance of shoreward transport to drive subsequent recruitment.

Coupling between larval euphausiid abundance at the WAP slope and recruitment at the NAP suggests meridional links along the AP are direct and important (Fig. 6). These areas are connected by northeastward flow of the ACC, and larval transport onto the shelf is likely common at canyons (Orsi et al. 1995; Martinson et al. 2008; Martinson and McKee 2012; Piñones et al. 2013). From 1980 to 2004, *E. superba* larvae abundance at Elephant Island was positively correlated with the following summer's proportional recruitment (Loeb et al. 2009). In contrast, our analysis suggests local larval production was not driving periodic recruitment in the NAP from 1995-2011.

Regional warming has had divergent impacts on AP ecosystems. Phytoplankton biomass and diatom proportion decreased at the NAP but increased further south along the WAP from the 1980s to 2000s (Montes-Hugo et al. 2009), likely having localized impacts on larval production and survival. While the WAP has shifted from perennial sea ice coverage to seasonal sea ice coverage, the NAP is now ice-free for most of the year (Stammerjohn et al. 2008b; Montes-Hugo et al. 2009; Reiss et al. 2017). This latitudinal gradient in the ecosystem may have increased the importance of larvae from the WAP recruiting at the NAP during this period of rapid environmental change. One study found that *E. superba* abundance declined at the NAP while remaining stable or increasing along the WAP from the 1970s to 2010s (Atkinson et al. 2019). However, another study using the same database found no substantial decline in krill abundance (Cox et al., 2018), and an integrated model also showed variability but no directional trend in krill spawning biomass or recruit abundance at the NAP over the same time period (Kinzey et al. 2019). Recent winter surveys do suggest krill recruitment at the NAP is decoupled from local larval abundance (Walsh et al. 2020) and support the importance of remote larval supply.

Our results suggest krill recruitment fails following years of below average offshore larval abundance. Recruitment increases with larval abundance following above-average larvae years. Krill year-class failure is well-documented at the AP (Reiss et al. 2008; Ross et al. 2014), but the spawner-recruit relationship remains uncertain (Kinzey et al. 2019). Given that larval abundance, but not spawning biomass, has a clear one-year lagged relationship with recruitment, it appears individual spawning output and timing are key drivers of krill recruitment (Siegel and Loeb 1995; Saba et al. 2014). Our findings suggest total egg production or larval abundance estimates may provide valuable information about krill reproductive potential within the fishery management framework (Murawski et al. 2001; Kell et al. 2016).

Implications for fishery management and climate-driven change

Commercial krill catch at the NAP reached at least 94% of the 155,000 ton limit for this subarea of the Southwest Atlantic each year from 2013-2018 (CCAMLR 2018; Cavan et al. 2019). The Commission for the Conservation of Antarctic Marine Living Resources, which manages the krill fishery, has determined that the catch limit may only be increased further if the catch is spatially subdivided (see Hewitt et al. 2004 for example allocation strategies) to limit the potential that the fishery takes the entire interim catch limit of 620,000 tons from a single location. Strategies to distribute the catch spatially may result in increased fishing pressure in critical areas of recruitment or larval production and should be carefully considered. Other spatial management frameworks are also being considered for the AP region, and these include the delineation of a marine protected area (MPA) (Hindell et al. 2020). Implementing effective spatial management requires careful consideration of the target species' life history, distribution, and larval dispersal (Hilborn et al. 2004; Manel et al. 2019). Understanding whether upstream production of krill larvae in the WAP is responsible for recruitment and population dynamics in other areas is critical to understand in order to develop appropriate protected areas in a changing environment.

Our findings emphasize the importance of considering cross-shelf and alongshore krill population connectivity for MPAs or spatial management frameworks to achieve their conservation goals. In agreement with current krill life history models, recruitment in shelf and coastal waters along the AP is likely the product of larval production over the continental slope. The consistent relationship between krill larval abundance at the WAP and subsequent recruitment at the NAP suggests the ACC and other regional current flows play an important role in larval dispersal (Fig. 6). Clarifying the impact of larval production in the Bellingshausen and Weddell Seas remains a challenge. Additionally, recruits from the AP likely source the krill population near South Georgia where local recruitment is unsuccessful (Fach and Klink 2006; Tarling et al. 2007; Thorpe et al. 2007; Reid et al. 2010). Importantly, spatial catch distribution and MPA design should anticipate the impacts of continued climate-driven ecosystem shifts (Montes-Hugo et al. 2009; Flores et al. 2012; Atkinson et al. 2019; Hindell et al. 2020).

A management approach that distinguishes between successful and failed krill recruitment years may help achieve precautionary harvest rates and support ecosystem-based management goals. If held constant, the same fishery catch at the NAP is more detrimental to penguin performance during years of failed krill recruitment compared to successful recruitment years (Watters et al. 2020). Larval abundance estimates and length-based recruit abundance estimates effectively capture synchronized regional population cycles. Predator diet sampling as well as autonomous platforms equipped with optical and acoustic sensors can provide valuable information if ship-based surveys are not feasible. Fishery-independent time series provide the backbone for understanding krill ecology and population dynamics in a changing Southern Ocean.

Data availability statement

All post-larval krill abundance and length data up to 2016 are available in KRILLBASE at https://doi.org/10.5285/8b00a915-94e3-4a04-a903-dd4956346439. Additional U.S. AMLR data will be shared on reasonable request to the Director, U.S. AMLR Program, NOAA Fisheries, Southwest Fisheries Science Center, La Jolla, California. Post-larval krill data from PAL LTER are available in the Environmental Data Initiative Portal at https://doi.org/10.6073/pasta/03e6d72a78bc2512ef5bb327e686f8fa (abundance, 1993-2008), https://doi.org/10.6073/pasta/434b2f73803b9d3d8088cd094cf46cca (abundance, 2009-2019), and https://doi.org/10.6073/pasta/be42bb841e696b7bcad9957aed33db5e (length, 2009-2019). Larval euphausiid abundance data from PAL LTER (1993-2013) are available at https://pal.lternet.edu/data.

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Conflict of interest declaration

The authors declare no conflicts of interest.

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Table 1. Pearson's correlation coefficients across study sub-regions for annual euphausiid larvae abundance from 1995-2011 (*n* = 17 years) (above the diagonal) and annual *Euphausia superba* recruit abundance from 1993-2011 (*n* = 19 years) (below the diagonal). Values in italics indicate $p < 0.003$.

	WAP Coast	**WAP Shelf**	**WAP Slope**	**NAP Coast**	**NAP Shelf**	**NAP Slope**
WAP Coast	-	*0.68*	0.61	0.15	0.38	0.31
WAP Shelf	*0.68*	-	*0.81*	0.08	0.39	0.50
WAP Slope	0.26	*0.75*	-	0.20	0.40	0.56
NAP Coast	0.47	*0.76*	*0.66*	-	*0.69*	0.57
NAP Shelf	0.50	*0.84*	*0.79*	*0.89*	-	*0.88*
NAP Slope	0.38	*0.65*	0.54	*0.83*	*0.86*	-

Table 2. Summary of model selection statistics from linear regression models assessing the relationship between euphausiid larvae abundance (1995-2010) and *Euphausia superba* recruit abundance (1996-2011) in the following year (n = 16 years). AICc: corrected Akaike Information Criterion; ΔAICc: difference from lowest AICc; AICc weight – relative model support or probability. Italics indicate models with ΔAICc < 2.

	NAP Coast & Shelf *Euphausia superba* recruits			**WAP Coast & Shelf *Euphausia superba* recruits**		
Explanatory variable (1-yr lag)	**AICc**	**ΔAICc**	**AICc weight**	**AICc**	**ΔAICc**	**AICc weight**
NAP Slope euphausiid larvae	*25.9*	*1.39*	*0.28*	*36.1*	*1.37*	*0.19*
WAP Slope euphausiid larvae	*24.5*	*0.00*	*0.56*	*35.5*	*0.78*	*0.26*
NAP Shelf euphausiid larvae	28.1	3.56	0.09	*34.7*	*0.00*	*0.38*
WAP Shelf euphausiid larvae	30.0	5.50	0.04	38.2	3.52	0.07
NAP Coast euphausiid larvae	32.2	7.74	0.01	37.6	2.87	0.09
WAP Coast euphausiid larvae	31.5	6.97	0.02	40.4	5.73	0.02

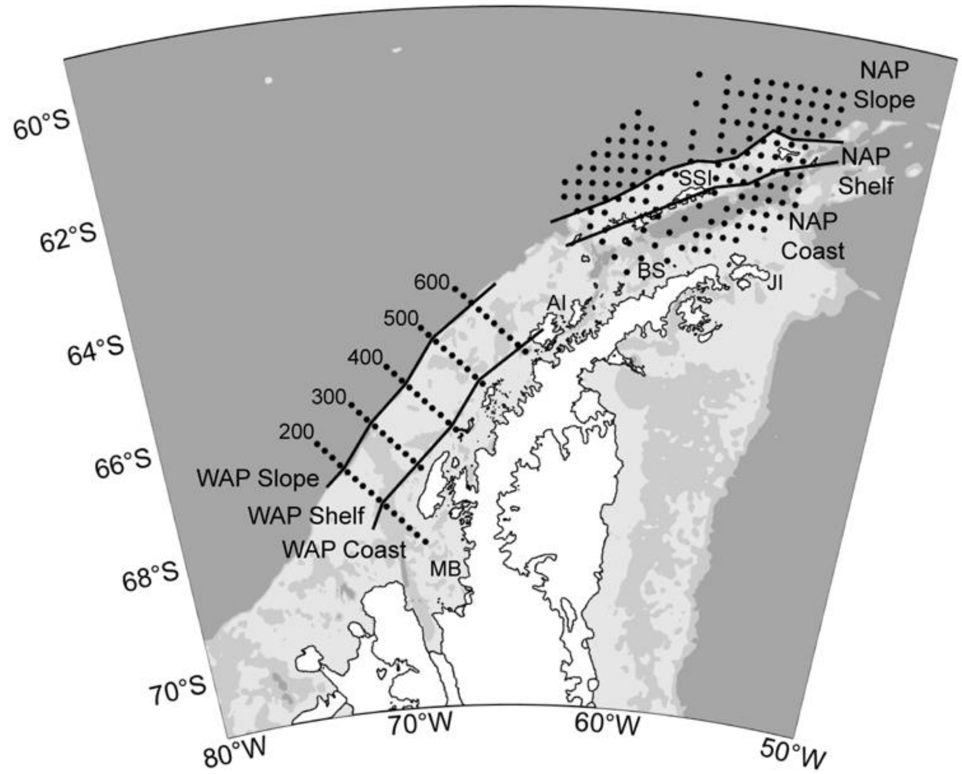

Figure 1. Map of the study area indicating U.S. AMLR sampling sub-regions in the North Antarctic Peninsula (NAP) and PAL LTER sampling sub-regions in the West Antarctic Peninsula (WAP). Bathymetric shading indicates 0-500, 500-1000, and > 1000 m depth intervals. Black dots indicate sampling stations, the occupation of which varied through time. SSI: South Shetland Islands, JI: Joinville Island, BS: Bransfield Strait, AI: Anvers Island, MB: Marguerite Bay, 600-200: PAL LTER sampling grid lines.

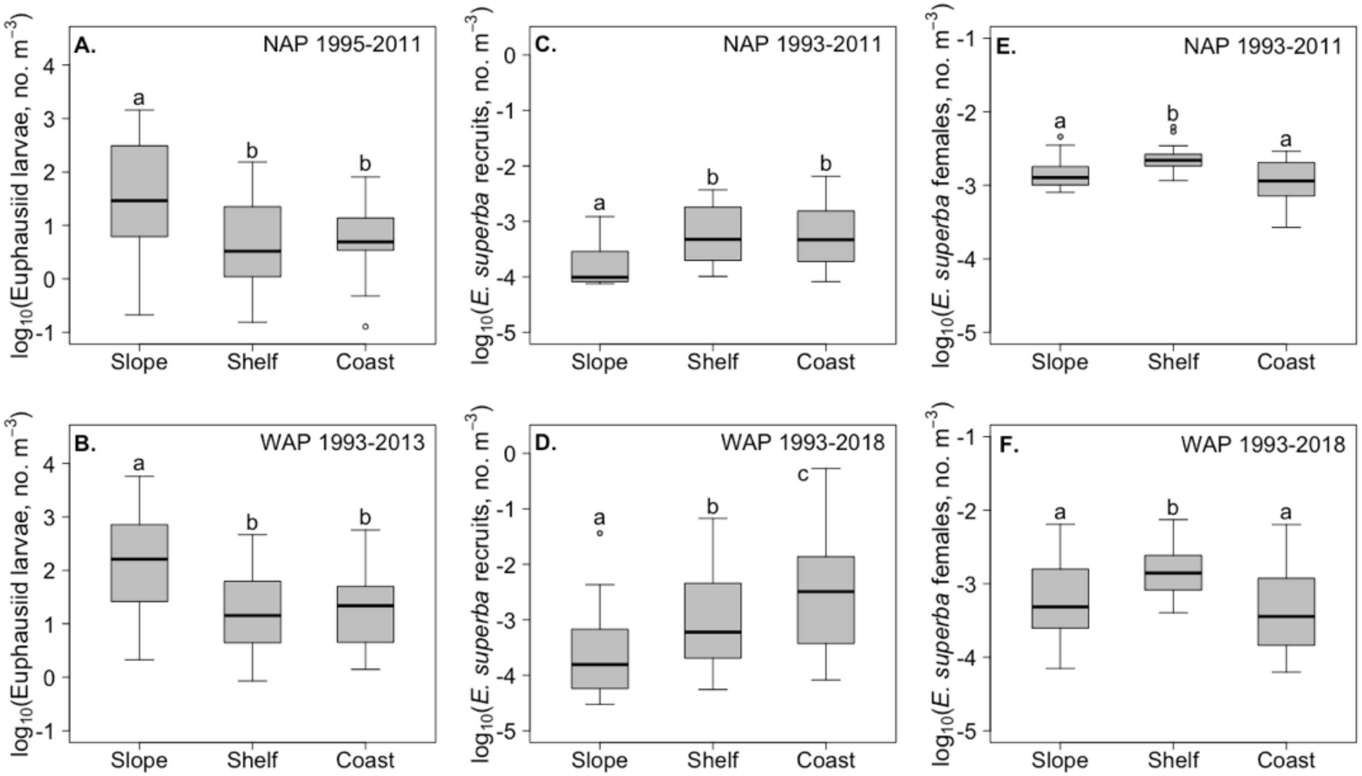

Figure 2. Spatial abundance comparisons. Annual mean $\log_{10}$-adjusted abundance for (A-B) euphausiid larvae, (C-D) *Euphausia superba* recruits, and (E-F) *E. superba* mature females at the North Antarctic Peninsula (NAP) Slope, Shelf, and Coast sub-regions (A, C, E) and West Antarctic Peninsula (WAP) Slope, Shelf, and Coast sub-regions (B, D, F). Thick black line indicates the median, gray box indicates the interquartile range, and whiskers indicate the range excluding outlier values indicated as points. Different lowercase letters indicate statistically different group means. Note different scales although abundance is not directly comparable across plots due to different sampling methods. Sample size n = 17-26 years.

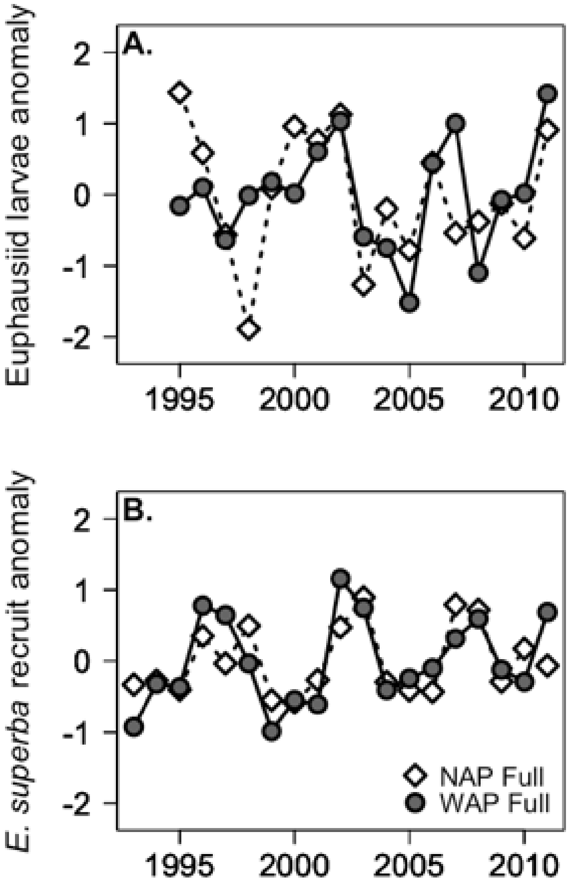

Figure 3. Annual abundance anomaly time series. (A) Euphausiid larvae abundance anomalies in the full NAP sampling area (dashed line, white diamonds) and the full WAP sampling area from 1995 to 2011 (solid line, gray circles) ($n = 17$; $p = 0.05$; Pearson's $r = 0.47$). (B) *Euphausia superba* recruit abundance anomalies for the same study areas from 1993 to 2011 ($n = 19$; $p = 0.0004$; Pearson's $r = 0.72$).

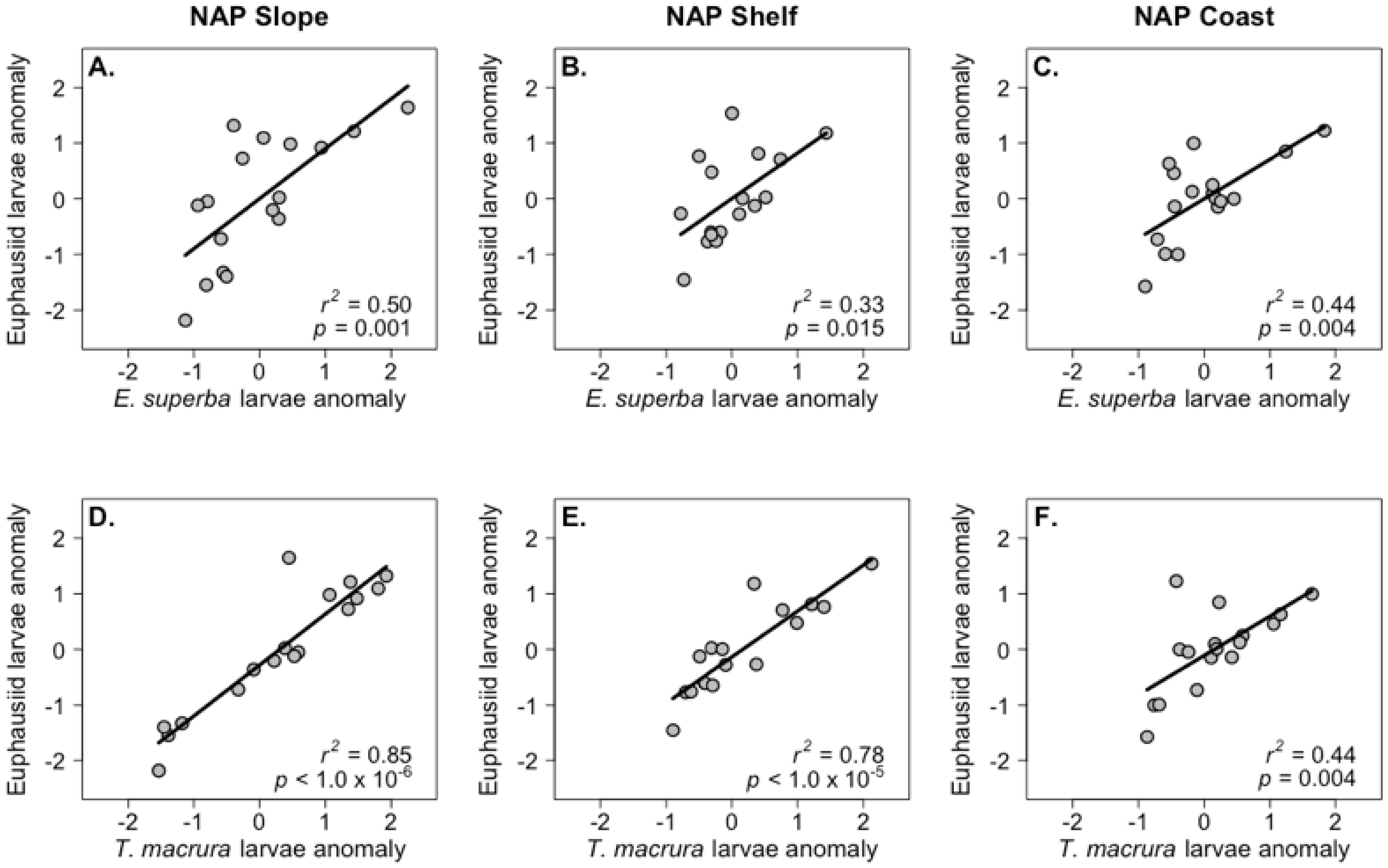

Figure 4. *Euphausia superba* larvae abundance anomaly (A-C) and *Thysanoessa macrura* larvae abundance anomaly (D-F) versus total euphausiid larvae abundance anomaly in the NAP Slope (A, D), Shelf (B, E), and Coast (C, F) sub-regions from 1995 to 2011 (*n* = 17 years). Black line indicates linear regression fit.

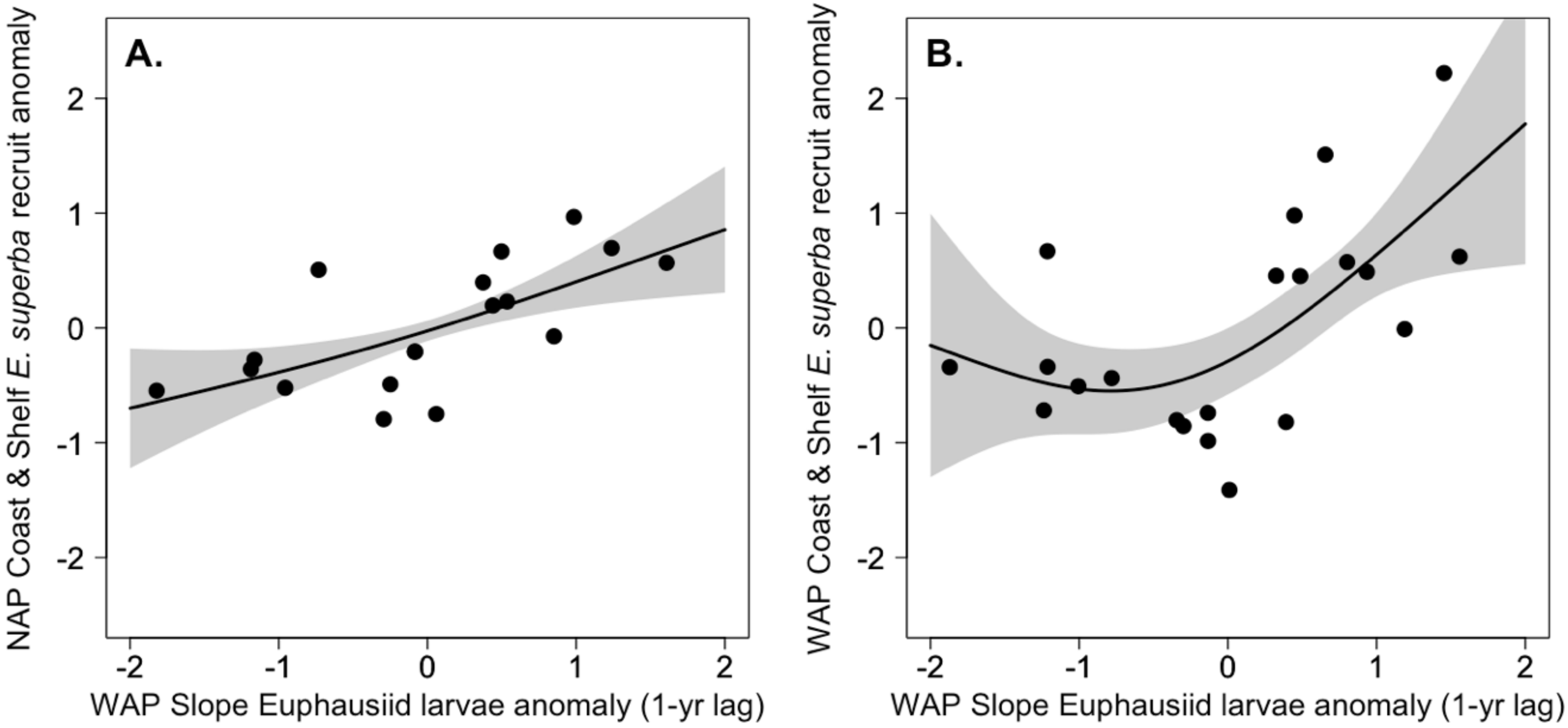

Figure 5. WAP Slope euphausiid larvae abundance anomaly versus the following year's *Euphausia superba* recruit abundance anomaly in the (A) combined NAP Coast and Shelf sub-regions from 1994 to 2011 (*n* = 18 years), and (B) combined WAP Coast and Shelf sub-regions from 1994 to 2014 (*n* = 21 years). Black line indicates the mean regression spline fit, and gray shading indicates the 95% confidence interval.

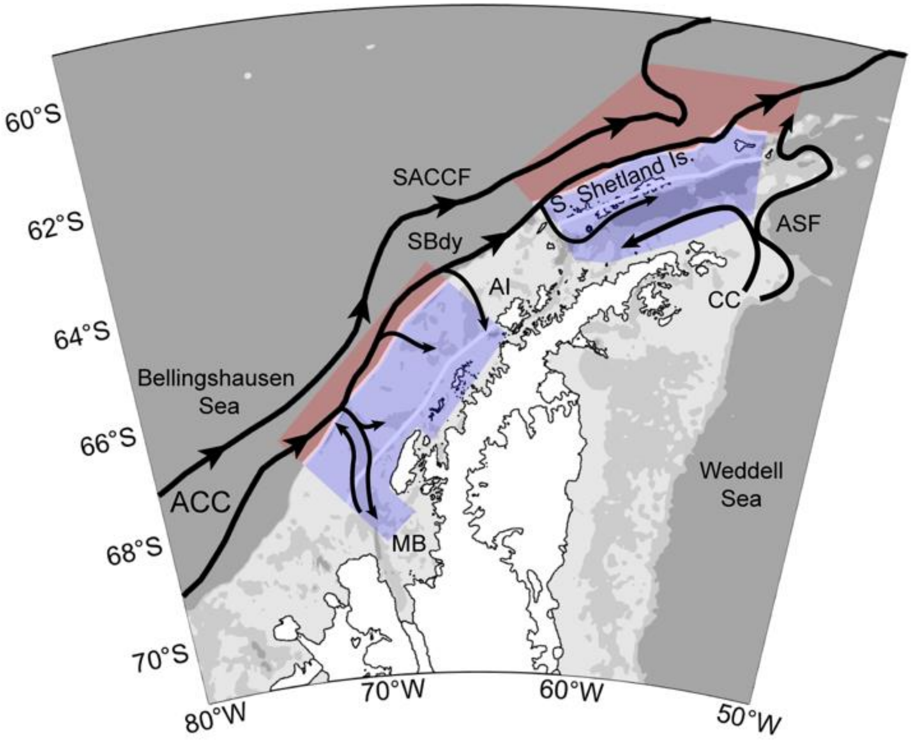

Figure 6. Conceptual diagram illustrating how regional ocean circulation relates to areas of relatively high krill larval abundance (red sub-regions) and recruit abundance (blue sub-regions) along the Antarctic Peninsula. The Antarctic Circumpolar Current (ACC) flows from the West Antarctic Peninsula to the North Antarctic Peninsula. Cross-shelf transport connects oceanic waters of the ACC to the Antarctic Peninsula shelf. Although not sampled in this study, the Bellingshausen and Weddell Seas likely influence krill population dynamics at the Antarctic Peninsula. Similarly, krill reproduction and recruitment at the Antarctic Peninsula likely impact abundance to the northeast in the Scotia Sea (not shown). See Fig. 1 for sampling sub-regions shown in this diagram. Ocean current locations and

illustrations are from Orsi et al. 1995, and Moffatt and Meredith 2018. SACCF: Southern ACC Front, SBdy: Southern ACC Boundary, ASF: Antarctic Slope Front, CC: Antarctic Coastal Current, AI: Anvers Island, MB: Marguerite Bay.