16 Abundance and distribution of larval krill, *Euphausia superba*, associated with annual sea ice in winter

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ABSTRACT

Larval krill, Euphausia superba, *associated with annual sea ice were censused visually using SCUBA during three winter cruises to a region west of the Antarctic Peninsula. Sampling during September 1991 and June 1993 was restricted to a small number of stations off Adelaide Island. A more extended, mesoscale survey was conducted in September 1993. Larval krill were observed feeding on ice-associated biota at all sampling locations (n = 36) on each of the three cruises. Mean numbers of larval krill (individuals per m^2) per station for September 1991, June 1993 and September 1993 were 24.60, 2.04 and 16.72, respectively. Larval abundances were significantly greater during late winter (September) sampling periods. A majority of larval krill censused during late winter occurred in large aggregations (≥ 10^3 individuals). Large aggregations of larvae were not found in early winter. Eighty per cent of larvae were observed under a complex habitat provided by over-rafted and/or eroded ice floes, and were generally associated with upward facing ice surfaces. Larval krill were rarely observed on the downward facing surfaces of unilayer floes, though ice-algae were often visible in these areas.*

Key words: Antarctic Peninsula, ecology, Long-Term Ecological Research (LTER).

INTRODUCTION

Qualitative observations of larval krill, *Euphausia superba*, feeding on the undersides of sea ice (e.g. Guzman 1983, Stretch *et al.* 1988, Marschall 1988, Daly 1990) are suggestive of an important ecological coupling. Quetin & Ross (1991) suggested that the association is based on the need to feed on the ice-associated community, although sea ice may also provide a refuge from predation. The two scenarios are not mutually exclusive, and it is clear that the intricacies of the linkage are not completely understood.

Smetacek *et al.* (1990) suggested 'that the bulk of the krill population moves into the ice habitat upon its formation', but quantitative data needed to evaluate this claim are lacking. Direct measures of the abundance of krill associated with sea ice are few (O'Brien 1987, Marschall 1988, Hamner *et al.* 1989), and no systematic surveys of larvae have been reported to date. As part of our ongoing study on the ecology and physiology of larval krill during winter, we have quantified the abundance and distribution of larvae in the sea ice habitat during three cruises in the austral winter.

We intend to combine small-scale distributional data and behavioral observations to increase our understanding of how krill larvae exploit the ice habitat. Quantitative census data from early and late winter sampling periods provides additional insight into temporal variablity of krill associated with sea ice. Our results provide essential detailed information for formulating hypotheses and investigating further the krill/ice interaction.

METHODS

Larval krill associated with annual sea ice were censused visually with SCUBA during three winter cruises to a region west of the

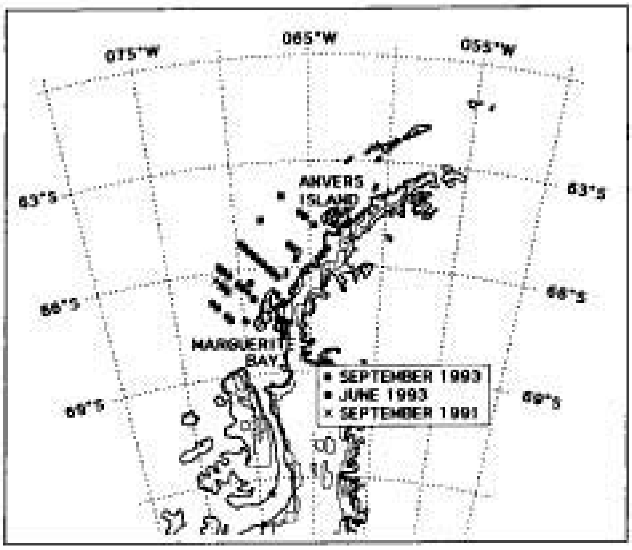

Fig. 16.1. Sampling stations occupied during each of the three winter cruises to the west of the Antarctic Peninsula in September 1991, June 1993 and September 1993. Adelaide Island is the large island north of Marguerite Bay.

Antarctic Peninsula (Fig. 16.1). During September 1991 and June 1993, sampling was restricted to a relatively small area offshore of Adelaide Island. During September 1993, a mesoscale survey was conducted between Anvers Island and Marguerite Bay. The mesoscale survey of the under-ice habitat for larval krill was conducted within the confines of the Palmer Long-Term Ecological Research (LTER) site (Waters & Smith 1992) and encompassed the sampling areas of the two previous cruises.

At each sampling station krill were censused along 2 m by 30 m long transects originating at the point of entry of the divers (Fig. 16.2). Observations were made to a depth of 3 m below the nearest ice surface, although larval krill were rarely observed more than 0.5 m away from any ice surface. Three replicate transects between 30° and 45° apart were generally completed at each station (32 of 36 total) during a single 30 to 60 minute dive. At the conclusion of each dive additional observations were recorded, e.g. estimated percentage of over-rafted ice in the sampling area and other fauna present.

Estimates of animal abundance *in situ* are influenced by such variables as visibility, sampling by different individuals and animal behaviour. The censuses reported here were completed by a single individual to eliminate between-sampler variability. Krill were censused during daylight hours. Visibility was generally greater than 30 m so it was easy to see individual krill to either side of the transect line. Larval krill associated with sea ice generally remain site-attached during a dive and do not exhibit an escape response into the water column when approached slowly by a diver; likewise, larvae do not exhibit directed movements along ice surfaces over any appreciable distance (<1 m). Even when disturbed by a diver with a collecting net, the integrity of the aggregation is soon re-established, generally at the collection site. For small aggregations, of less

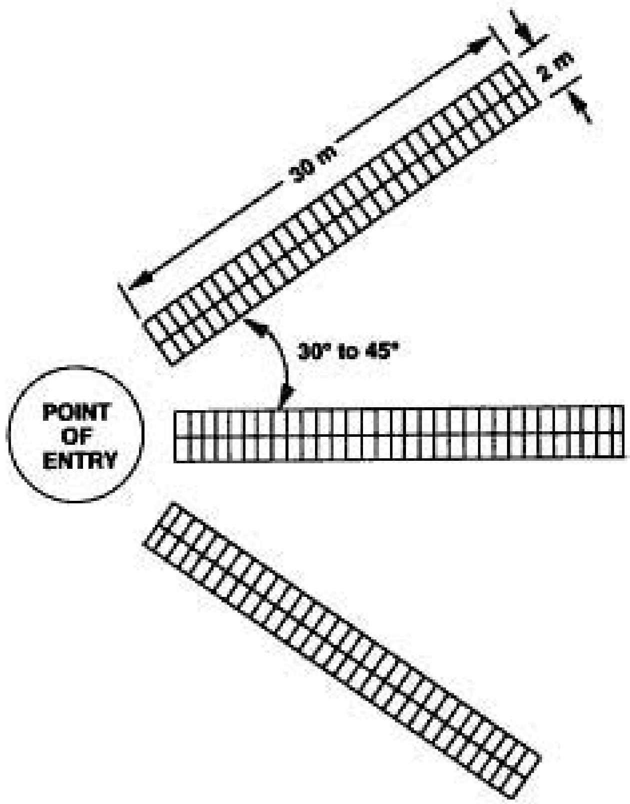

Fig. 16.2. Schematic depiction of diver transects at each sampling station. Krill larvae were censused continuously along replicate strip transects (30 m × 2 m).

than 50 individuals, absolute counts were possible. The total number of krill in larger aggregations was estimated by counting the number of volumes in an aggregation equivalent to a sub-volume with a counted number of individuals (10s, 20s, 50s).

Unless otherwise specified, larval abundances were calculated as the number of individuals per square metre and are reported as the mean of replicate transect counts at each sampling station. A Kruskal–Wallis non-parametric procedure with chi-square approximation (Sokal & Rolf 1981) was used to compare larval counts among sampling periods as variances were determined to be heterogeneous. For latitudinal comparisons the data from September 1993 were binned into one of three broad categories: (1) transect data collected at or north of 65° S, (2) transect data collected between 65° S and 66° S, and (3) transect data collected at or south of 66° S. Standard ANOVA procedures were used for the analysis.

RESULTS

Larval krill were observed in close association with sea ice at all under-ice stations during each of the three winter cruises where quantitative sampling was conducted (Fig. 16.3). The mean number of larvae per station did not differ between September 1991 and September 1993, but counts during the sampling period in June 1993 (early winter) were

Table 16.1. *Mean number of krill larvae per square metre (±standard error) for each of the three winter cruises. Sampling periods are ranked in order of increasing larval abundance (June 1993<September 1993=September 1991)*[1]

Sampling period	Larvae per m^2	Sampling stations	No. of transects
June 1993	2.04 (±1.32)	3	9
Sept. 1993	16.72 (±3.39)	26	73
Sept. 1991	24.60 (±12.42)	6[2]	21

Notes:

[1] The inequality is significant at the $p \leq 0.08$ level, Kruskal–Wallis test with chi-square approximation ($\chi^2=4.92$, df=2).

[2] One sampling station was occupied twice during September 1991.

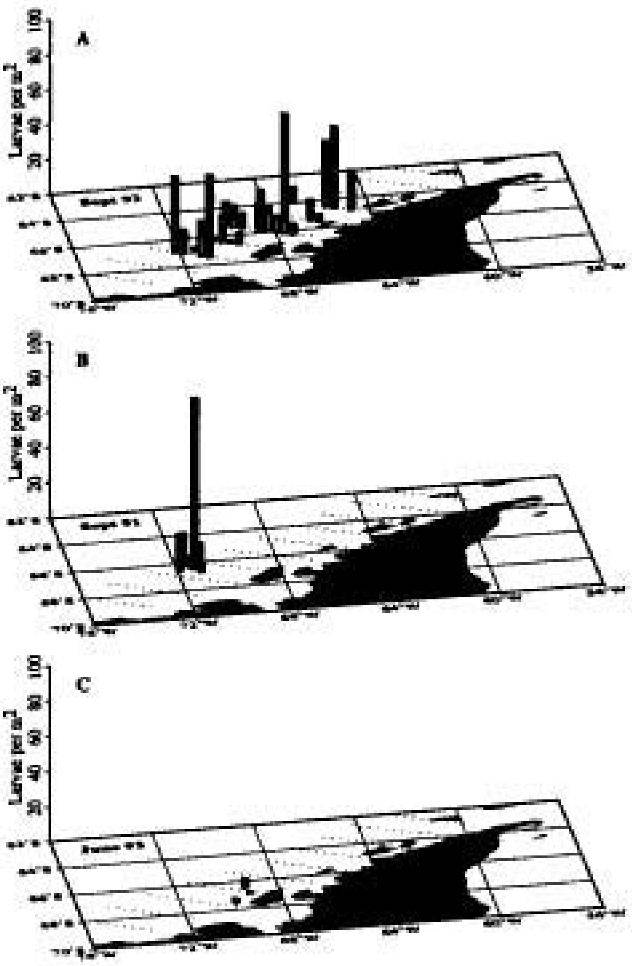

Fig. 16.3. Mean number of krill larvae per square metre at each sampling station for each of the three winter cruises: (A) September 1993, (B) September 1991 and (C) June 1993. All data are plotted with reference to established sampling locations within the Palmer LTER grid (Waters & Smith 1992).

significantly less than those from either late winter cruise (Table 16.1).

Large, distinct patches of larval krill (≥1000 individuals) accounted for less than 5% of the observations, but comprised 50% or more of the censused population (Fig.16.4). Large

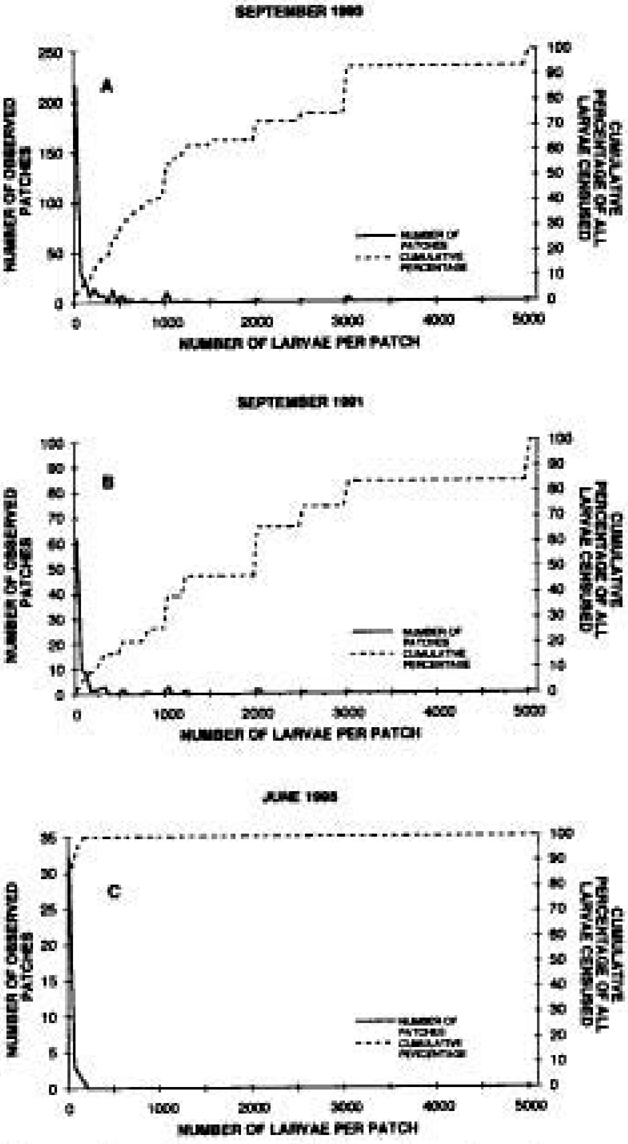

Fig. 16.4. Observed frequency of krill patches and cumulative abundance of individuals plotted against patch size for each of the three winter cruises: (A) September 1993, (B) September 1991 and (C) June 1993.

patches of larval krill were not observed on diver transects in June 1993. Early-winter sampling during both years was conducted in the same general geographic area west of Adelaide Island. Within the mesoscale sampling grid, there was no latitudinal gradient in krill abundance or distribution (ANOVA, df=2, $p \geq 0.05$). No cross-shelf gradients in abundance and distribution of larval krill were apparent (Fig. 16.3A).

Behavioural observations of larvae and the green coloration of their digestive gland indicated that most animals were feeding. However, larvae were not necessarily found in areas of highest plant pigment concentration. Greater than 80% of all larval krill were associated with over-rafted and/or eroded ice surfaces where plant pigment was rarely visible to the naked eye. Larval krill were less common on the downward facing surfaces of floes that were not over-rafted, although ice-algae were often visible in these areas.

DISCUSSION

Though sea ice had just recently formed in the northern portion of the mesoscale sampling grid in September 1993, larvae were observed at all stations with no statistical differences in abundance with latitude. This raises several questions: (1) do krill larvae inhabiting the water column stay with sea ice once it is formed, (2) did larvae sampled in the northern part of the LTER grid overwinter in ice-free water or (3) were they advected into the region prior to ice formation?

The distributional range of larval krill under sea ice during winter is not known. Nordhausen (1994) investigated the abundance and distribution of *E. superba* in ice-covered waters west of the Antarctic Peninsula. Although Nordhausen's study was restricted to the Gerlache Strait and inshore waters of Crystal Sound, no larvae were found during July 1992. This suggests that larval krill may, in general, overwinter in shelf and slope waters of the Antarctic Peninsula as observed and reported here. Comparative sampling in these distinctly different areas during the same year(s) would provide a test of the implicit hypothesis above.

Quantitative sampling of krill larvae is essential to evaluate spawning success and for subsequent predictions of year class strength and recruitment to the adult population. However, few quantitative studies of larval krill abundance and distribution have been conducted during the winter in the Southern Ocean, especially in the region covered by sea ice. One major difficulty is that in the complex ice habitat, larvae often occur on upward facing ice surfaces and net sampling is clearly not representative of larval abundance *in toto*. Quantitative surveys by divers are currently the best way to evaluate larval abundance and distribution in the sea-ice habitat.

The mesoscale survey during September 1993 covered a region large enough to allow estimation of the importance of sea ice to larval krill as a population. Larval krill were consistently found under the ice during September 1993, and a simple extrapolation of their mean abundance (16.72 larvae m^{-2}) yields a total estimate of 1.3×10^{12} larvae within the 200 km×400 km sampling region. Assuming that instantaneous rates of mortality (M) for all age-classes of post-larval krill are equal and ≤ 1.0 (cf. Priddle *et al.* 1988 and references therein, Siegel & Kalinowski 1994), and that recruitment is the same every year, then the larval concentrations in September 1993 are sufficient to generate an adult krill population on the same order of magnitude (Table 16.2). The projected number of adults within the sampling region would be 9.7–17.1 m^{-2}, with M values of 1.0 and 0.66, respectively (Table 16.2). These numbers compare favorably with Smetacek *et al.*'s (1990) estimate of 10–30 adults m^{-2} under sea ice at its maximal extent (based on population estimates by El-Sayed (1988)), and, if emigration is zero, suggest that larval concentrations immediately west of the Antarctic Penisula are not greater than necessary to maintain an average adult population. This would be counter to a generally held contention that the region west of the Antarctic Peninsula is an important nursery area for larval krill compared with other regions of the Southern Ocean.

Table 16.2. *Projected numbers of post-larval krill within the 200 km × 400 km sampling region based on larval abundance estimates from September 1993*[1]. *The projected numbers will vary depending on the assumed instantaneous rates of mortality (M). Two different scenarios are given*

Age-class (year)	Mean number of krill per m^2	Total number of krill
age-class 1[1]	16.72	1.3×10^{12}
Projection 1 ($M = 1.0$[2])		
age-class 2–7	9.70	7.5×10^{11}
Projection 2 ($M = 0.66$[3])		
age-class 2–7	17.10	1.3×10^{12}

Notes:

[1] The larval population present at the end of winter (September 1993) and the one-year-old age-class are, for the purposes of this exercise, assumed to be the same. It is assumed also that the numbers of krill in age-class 1 are constant from year to year. Rates of immigration and emigration of post-larval krill into and out of the 200 km × 400 km sampling region are assumed to be equal.

[2] $M = 1.0$ is the average value assumed by Priddle *et al.* (1988).

[3] $M = 0.66$ is the lowest value expected by Siegel & Kalinowski (1994).

We recognize that larval numbers observed in September 1993 may not be representative of those in other years, but larval abundances in September 1993 were remarkably similar to those estimated during September 1991 and suggest otherwise. Continued censuses of larval krill associated with sea ice in late winter need to be interpreted relative to the variability of winter ice cover and the spawning success of the previous season to understand the population dynamics of krill in this region.

Larval krill were found to be most concentrated in areas of over-rafted sea ice with upward-facing ice surfaces. Although Smetacek *et al.* (1990) suggested that ice surface area would be greater by about one-third because of ridging of cover, estimates of over-rafting by divers west of the Antarctic Peninsula are generally less ($\leq 5\%$), particularly in early winter. More work is needed to understand the ecology of larval krill relative to habitat complexity. A lack of habitat complexity may explain, in part, patch characteristics and low counts of larval krill during early winter (Fig. 16.4A, Table 16.1). Little is known about krill's early-winter transition from the water column to the ice, but the fact that large patches of larval krill observed during late winter were not common during early-winter sampling is consistent with the hypothesis that sea ice facilitates aggregation and formation of krill swarms (Hamner *et al.* 1989). Since krill numbers and the frequency of large patches appear to increase over winter in the sea-ice habitat, estimates of larval numbers based on diver observations in early winter may not be valid.

Contrary to several schematic depictions of krill feeding on downward facing ice surfaces during winter (e.g. Garrison *et al.*

1986, Smetacek *et al.* 1990), larvae associated with sea ice are generally oriented with feeding appendages down and scraping the upward facing and eroded ice surfaces they tend to occupy. Since larval krill are generally not found in areas where plant pigment is most concentrated, structural characteristics of sea ice appear to be a primary determinant of krill abundance and distribution during winter. Larval krill appear to have an affinity for areas of over-rafted ice and the refuge it might afford. Unfortunately, there is a paucity of information regarding predator-prey interactions in the annual sea-ice zone during winter and direct observations of predation on krill larvae are few. Hamner *et al.* (1989) observed ctenophores and an amphipod feeding on furcilia and further suggested that larval krill might be a significant component of the diet of fishes and migratory invertebrates, particularly in winter. Several alternative hypotheses can be suggested to explain the apparent affinity of larval krill for areas of over-rafted sea ice: (1) Feeding costs may be less for larvae on upward facing ice surfaces since feeding on downward facing surfaces will entail the additional cost of maintaining contact with the ice surface against a negative buoyancy. (2) Upward facing surfaces may also act as sediment traps which concentrate food resources and/or provide a substrate for prefered food items (O'Brien 1987). The relative importance of food resources and shelter to larval krill, as provided by annual sea ice, merits further investigation.

CONCLUSION

This is the first quantitative account of larval krill associated with sea ice during austral winter and observations using SCUBA have proved to be a requisite method for investigating the the krill/ice interaction. The data reported here are essential information for the formulation of hypotheses and further study of this ecologically important linkage.

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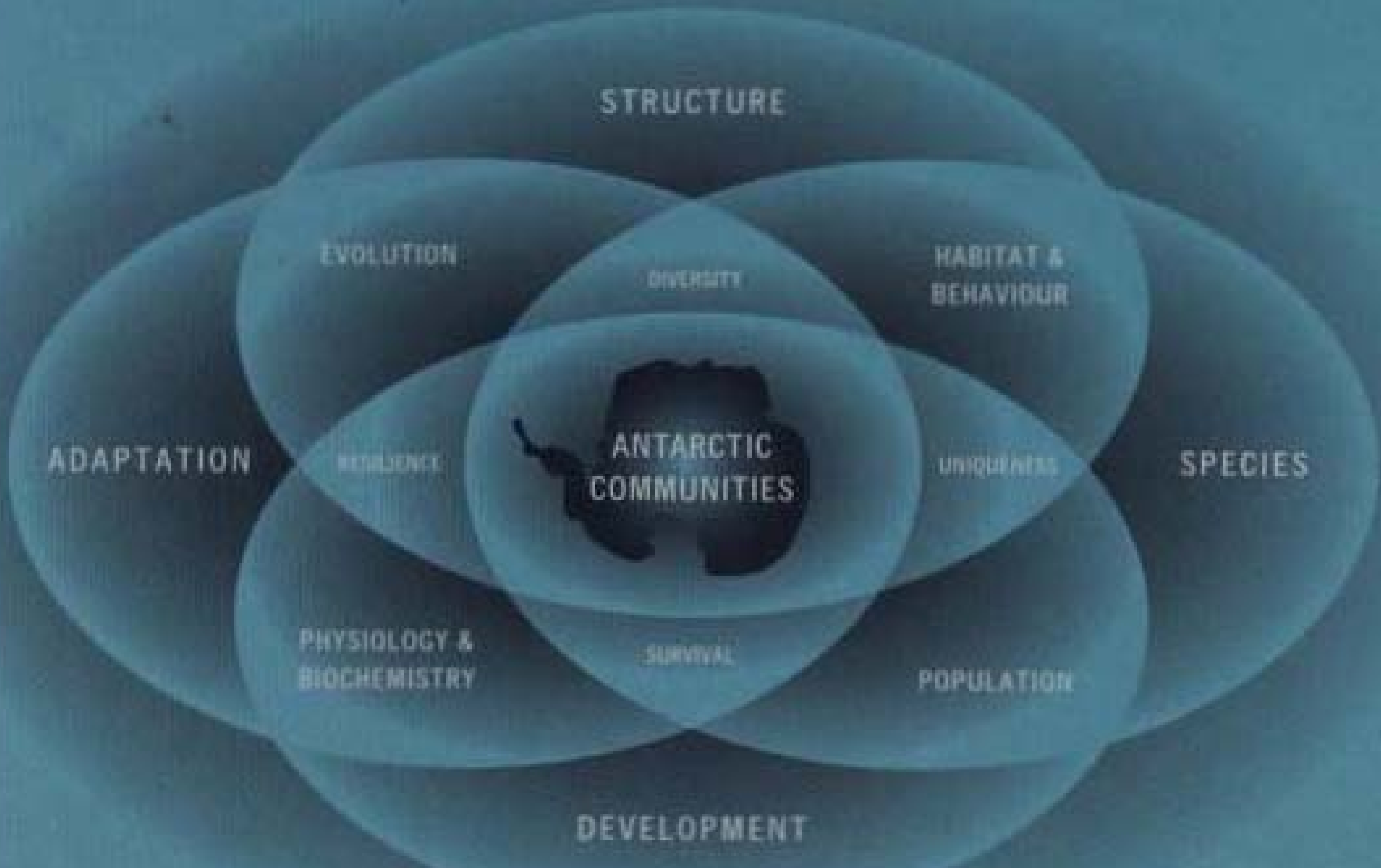

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