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DO KRILL AND SALPS COMPETE? CONTRARY EVIDENCE FROM THE KRILL FISHERIES

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Abstract

Salp by-catch and krill discolouration ('green' krill) caused by active feeding on phytoplankton were analysed using logbook data from Japanese krill trawlers operating near the Antarctic Peninsula. Interannual and seasonal variability of the timing, duration and intensity of salp blooms and the presence of green krill were analysed. No relationship between salp density and the proportion of green krill in the catches was evident when both salps and krill were taken together. In the Livingston Island area, the proportion of green krill was high only when salp density was extremely low. However, no clear relationship was observed in the Elephant Island area. Possible reasons for these phenomena are discussed.

Résumé

La capture accessoire de salpes et la décoloration du krill (krill 'vert') causées par un approvisionnement actif de phytoplancton sont analysées à partir de données provenant des carnets de bord de chalutiers japonais pêchant le krill autour de la péninsule Antarctique. La variabilité saisonnière et interannuelle de l'époque, la durée et l'intensité des blooms de salpes et la présence de krill vert sont analysées. Lorsque les salpes et le krill sont capturés ensemble, il ne semble y avoir aucun lien évident entre la densité des salpes et la proportion de krill vert dans les captures. Dans la région de l'île Livingston, la proportion de krill vert n'est élevée que lorsque la densité des salpes est extrêmement faible. Il n'est toutefois observé aucun lien évident à cet égard dans le secteur de l'île Éléphant. Les raisons pouvant expliquer ces phénomènes sont discutées.

Резюме

Данные из промысловых журналов японских крилевых траулеров, работавших в районе Антарктического полуострова, использовались для анализа прилова сальп и так называемого зеленого криля, изменившего цвет в результате активного питания фитопланктоном. Была проанализирована межгодовая и сезонная изменчивость сроков, продолжительности и интенсивности цветения сальп, а также встречаемости зеленого криля. В уловах, содержащих как сальпы, так и криль, не наблюдалось взаимосвязи между плотностью сальп и долей зеленого криля. В районе острова Ливингстон доля зеленого криля была высокой только тогда, когда плотность сальп была исключительно низкой. В районе острова Элефант, однако, четко выраженной взаимосвязи не наблюдалось. Обсуждаются возможные причины этих явлений.

Resumen

Se analizó la captura secundaria de salpas y la descoloración del kril (kril verde) causada por su consumo activo de fitoplancton, de los datos de los cuadernos de pesca de arrastreros de kril japoneses que faenaron cerca de la Península Antártica. Se estudió la variabilidad interanual y estacional de la ocurrencia, duración e intensidad de las proliferaciones de salpas y la presencia de kril verde. Cuando las capturas incluyeron simultáneamente la presencia de salpas y de kril, no se observó una relación entre la densidad de las salpas y la proporción de kril verde. En el área de la isla Livingston, sólo se detectó una proporción elevada de kril verde cuando la densidad de las salpas fue extremadamente baja. Sin embargo, no se observó una relación definida en el área de la isla Elefante. Se discuten las posibles razones de estas relaciones entre las salpas y el kril.

Keywords: krill, feeding, phytoplankton, krill fishery, salps, by-catch, competition, CCAMLR

INTRODUCTION

Recently, an hypothesis of competition for primary production between salps and krill has been proposed (Siegel and Loeb, 1995; Loeb et al., 1997). This speculates that the consumption of primary production during early spring by salp blooms could deprive krill of sufficient food and retard krill gonadal development (Loeb et al., 1997). The timing and duration of salp blooms vary greatly between and within years (SC-CAMLR, 1997). Corroboration of this hypothesis requires the analysis of any available continuous data on salp density and krill feeding. Research vessels can cover wide areas but are usually limited in terms of continuity through the season. Krill trawlers are unable to cover wide areas, but they are useful for obtaining continuous data from a single location throughout the season. Some of the Japanese krill trawlers have accumulated a large amount of data on salp by-catch and on the occurrence of green krill. Local salp density could be calculated from salp by-catch data. Green krill are those individuals whose hepatopancreas has turned green because of the active ingestion of phytoplankton. The proportion of green krill in a sample is a relative indicator of the amount of phytoplankton available to krill. In this paper, we provide the results of an analysis of seasonal and interannual variability of salp by-catch and green krill and investigate the possible ecological relationships between krill and salps in the waters around the South Shetland Islands.

MATERIAL AND METHODS

Study Site and Data Source

Logbook data were collected by krill trawlers belonging to Nippon Suisan Kaisha (Ltd) from 1984/85 to 1992/93 (no data were available for 1989/90 and 1991/92). Data from the areas shown in Figure 1 were extracted and used in the analysis (6 911 hauls in total). All vessels were stern trawlers which fished with midwater trawls. Ten-kilogram subsamples were taken from each catch and the salps in the subsample weighed. Salp by-catch was expressed as catch per unit of towed volume. Also, 100 individual krill from every haul were subsampled and the number of green krill was counted. Green krill were determined visually by comparing their colour to a reference colour which gives a standard colour of green krill similar to that shown in the CCAMLR *Scientific Observers Manual* (CCAMLR, 1993). Sea-surface temperature in the logbook was also used in the analysis. Datasets from both the Livingston Island area and the Elephant Island area were analysed.

Statistical Analysis

An analysis of deviance was carried out using a generalised linear model (GLM) with an identity link function and binomial errors (Venables and Ripley, 1994), with the proportion of green krill as the dependent variable. Sea-surface temperature was used as a continuous independent variable. Salp density, month and area were used as categorical factors. Salp density d (g.m^{-3}) was categorised into four density bands as follows: $0 < d < 0.0001$, $0.0001 < d < 0.001$, $0.001 < d < 0.01$, etc.

RESULTS

Variability in the Proportion of Green Krill and the Presence of Salps

Monthly averages of the proportion of green krill and salp density are expressed in Figures 2 and 3. Generally, the highest proportion of green krill occurred in early summer (December/January) and decreased thereafter. However, the duration of the period of high proportion of green krill varied widely among years (Figure 2). Salp by-catch was relatively high in February and March during the period from 1985/86 to 1988/89 (Figure 3). However, in 1984/85 relatively high values of salp density were observed during January. In 1990/91 salp density was extremely low throughout the fishing season. These results show that although the highest salp density at the krill fishing ground was most often observed in February and March, the peak of salp blooms may occur in different periods in some years.

When comparing these two figures (Figures 2 and 3), it seems that there is a pattern of temporal mismatch. During the months when salp density was high (January 1984/85, February 1985/86, March 1986/87–1988/89, and February 1992/93), percentages of green krill were relatively low. On the other hand, relatively low salp densities were observed during months with relatively high percentages of green krill (February 1984/85, December 1985/86 and January/February 1990/91). Further statistical analysis was undertaken in order to study the relationship between the proportion of green krill and salp density.

Statistical Analysis

The results of the analysis of deviance (Table 1) show that each factor and interaction is statistically significant. The mean effect due to a given factor can be illustrated by plotting the predicted value of the dependent variable, and its standard error, for each level of the given factor, with the other factors held fixed.

Figure 4 shows the predicted proportion of green krill in each month. We can see the general trend in the proportion of green krill. In both the Livingston Island and Elephant Island areas the proportion of green krill was higher in early summer (November/December) and decreased thereafter. The predicted mean proportion of green krill for different salp densities is shown in Figure 5. The estimates for each area were standardised to February and an overall mean temperature of 1.59°C.

In the Livingston Island area (Figure 5a) the predicted proportion of green krill was significantly higher when salps did not occur. However, there was no correlation between the proportion of green krill and increasing salp density even over several orders of magnitude. This suggests that direct interaction between the proportion of krill and the salp density in terms of competition for phytoplankton appears to be negligible. The difference between the presence and absence of salps, however, indicates an effect on availability of phytoplankton to krill. In the Elephant Island area (Figure 5b) the predicted proportion of green krill was approximately the same value for different salp densities, except for one high value. This high value was for the low salp density 0.0001 to 0.001, but this may have been caused by the small sample size (n = 12). Therefore, we conclude that there is no apparent relationship between the proportion of green krill and salp density in the Elephant Island area.

Since the deviance from the month:area:sea-surface temperature interaction was larger than from the month:area interaction (Table 1), we focused on temperature and plotted the monthly average sea-surface temperature and salp density for both areas (Figure 6). The fluctuating pattern of salp density is similar to the temperature pattern in the Livingston Island area.

DISCUSSION

Seasonal Pattern of Green Krill

Results from the statistical analysis (Table 1) clearly show that month is the most important

Table 1: Analysis of deviance for the proportion of green krill.

Factor	Df	Deviance	Res. Df	Res. Dev.	$Pr(\chi^2)$
NULL	6 910	185 293.90			
Month	5	65 402.14	6 905	119 891.8	0
Area	1	1 088.93	6 904	118 802.8	0
Salps	4	1 517.10	6 900	117 285.7	0
SST	1	1 577.60	6 899	115 708.1	0
Month:Area	4	1 142.82	6 895	114 565.3	0
Month:Salps	15	2 325.27	6 880	112 240.0	0
Area:Salps	4	2 051.42	6 876	110 188.6	0
Month:SST	5	2 640.84	6 871	107 547.8	0
Area:SST	1	576.41	6 870	106 971.4	0
Salps:SST	4	1 086.43	6 866	105 884.9	0
Month:Area:Salps	15	1 116.23	6 851	104 768.7	0
Month:Area:SST	4	3 495.62	6 847	101 273.1	0
Month:Salps:SST	15	412.49	6 832	100 860.6	0
Area:Salps:SST	4	243.69	6 828	100 616.9	0
Month:Area:Salps:SST	13	949.59	6 815	99 667.3	0

SST – sea-surface temperature

factor governing the proportion of green krill (highest deviance was observed for this factor). The general pattern of the proportion of green krill during the season (Figure 4) demonstrated that active ingestion of phytoplankton by krill generally occurs in early summer, and decreases in mid- to late summer. This result could be explained by the seasonal chlorophyll-*a* pattern around this area which shows high levels from December to January, and declines sharply thereafter (Priddle et al., 1995).

Competition for Food

Loeb et al. (1997) suggested that there is a degree of competition for primary production between krill and salps. If this is so, there must be interaction between salp density and the proportion of green krill because krill turn green as a result of actively ingesting phytoplankton. In our study, however, direct interaction between the proportion of green krill and salp density was not observed (Figures 5a and b). This suggests that there is negligible direct competition for phytoplankton between krill and salps.

Segregated distributing patterns of salps and krill (Nishikawa et al., 1995) might also suggest a low probability of competition for the same food source.

Ecological Implications of the Relationship between the Presence of Salps and Green Krill

Interestingly, our analysis also suggested that the presence of salps seems to indicate a lower level of greenness of krill in the Livingston Island area. Filtration rates of salps are known to increase exponentially with body length and are unaffected by changes in particle concentration (Harbison and Gilmer, 1976; Deibel, 1982). This unregulated filtration of all particles may lead to fatal clogging at concentrations of particles typical of neritic waters (Harbison et al., 1986). This would explain why salps are often restricted to oligotrophic offshore waters (Harbison and Gilmer, 1976; Harbison et al., 1986). The surface particle concentration around the South Shetland Islands ranged from 0.009 to 0.57 ppm during the austral summer in 1994/95 (Kawaguchi and Makita, unpublished data). The upper range of these values (>0.5 ppm) falls into the range that may cause clogging of salps' filtering meshes (Harbison et al., 1986). Particle concentrations between Antarctic coastal and north sub-Antarctic waters in the Indian Sector also ranged from 0.178 to 0.625 ppm ($1.78–6.25 \times 10^8 \mu m^3 l^{-1}$), and most of this variation was due to particles greater than 20 µm (Wright et al., 1996). Therefore, in our case, salps may have been excluded from the region when the phytoplankton concentrations were too high for them. These areas might also be active feeding grounds for krill, which effectively filters particles larger than 20 µm (Meyer and El-Sayed, 1983), thereby giving high percentages of green krill. Salp concentrations may form in areas with lower, more suitable densities of phytoplankton. Krill catches in those areas could be expected to contain a lower proportion of green krill. The phytoplankton concentration around the Elephant Island area may not be as high as the Livingston Island area on average (considering the low percentages of green krill compared to the Livingston Island area – Figures 5a and b), which explains the absence of any clear pattern in this area.

There might be another reason for this, based on the community structure and environmental factors. Although salps are commonly present in the oceanic biological community, including the neritic zone, their position in the food web is not very prominent (Siegel and Piatkowski, 1990). The oceanic community comprises the group of species inhabiting the area influenced by the West Wind Drift (which may be dominated by South East Pacific Basin Surface Water described in Heywood, 1985), which has a notable warm surface layer in the summer (Piatkowski, 1989). If the increase of sea-surface temperature that we observed indicates an increased influence of the West Wind Drift, a synchronised pattern between salp density and sea-surface temperature (Figure 6) could also be explained by the variation of the relative dominance of the West Wind Drift in the study area. We cannot further extend the discussion relating to other water properties (such as nutrients, etc.) from the sea-surface temperatures. However, salps are known to exhibit explosive population growth under certain conditions (Fortier et al., 1994), and according to our results it may be interpreted that the occurrence of salps is linked with temperature variability, which may be an indicator of favoured conditions for salp growth.

This leaves the question as to why this pattern is absent in the Elephant Island area. Kawaguchi et al. (1997) analysed the long-term trend of CPUE in commercial krill fisheries and reported larger inter- and intra-annual variation within the Elephant Island area compared to the Livingston

Island area. The Elephant Island area is close to the Weddell–Scotia Confluence which shows substantial inter- and intra-annual variations in its position (Sahrhage, 1988). The water properties around the Elephant Island area therefore are very complex which might have made the relationship between sea-surface temperature and salp density unclear.

Further studies on krill and salps, especially in relation to environmental factors, are needed to understand the dynamics of the Antarctic Ocean pelagic ecosystem.

CONCLUSIONS

(i) The proportion of green krill is generally high in early summer, and declines thereafter.

(ii) Although the highest salp density at the krill fishing ground is most often observed in February and March, the peak of salp blooms may occur in different periods in some years.

(iii) Results of the GLM analysis suggested that there is no substantial competition for phytoplankton between krill and salps.

(iv) The proportion of green krill was significantly higher when there was no salp by-catch, than in hauls containing salps at any density. Concentration of particles in the seawater or the degree of the influence of oceanic water were considered as possible explanations.

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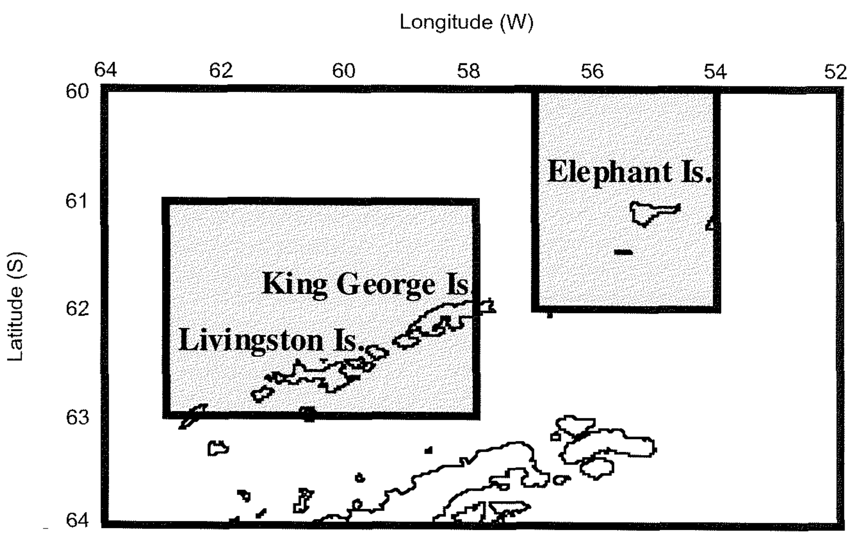

Figure 1: Areas considered in the analysis of data.

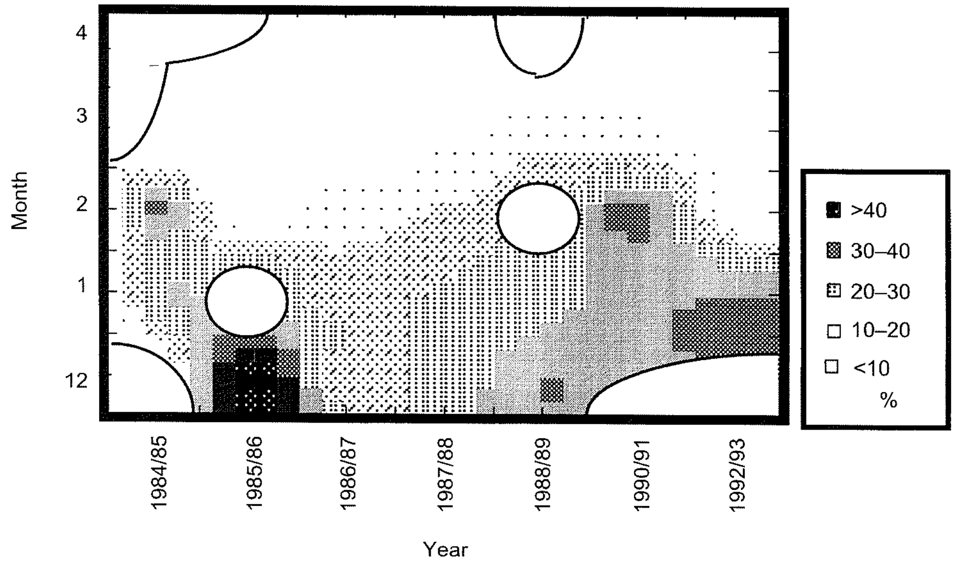

Figure 2: Seasonal variability of average proportion of green krill at the fishing ground fror 1984/85 to 1992/93.

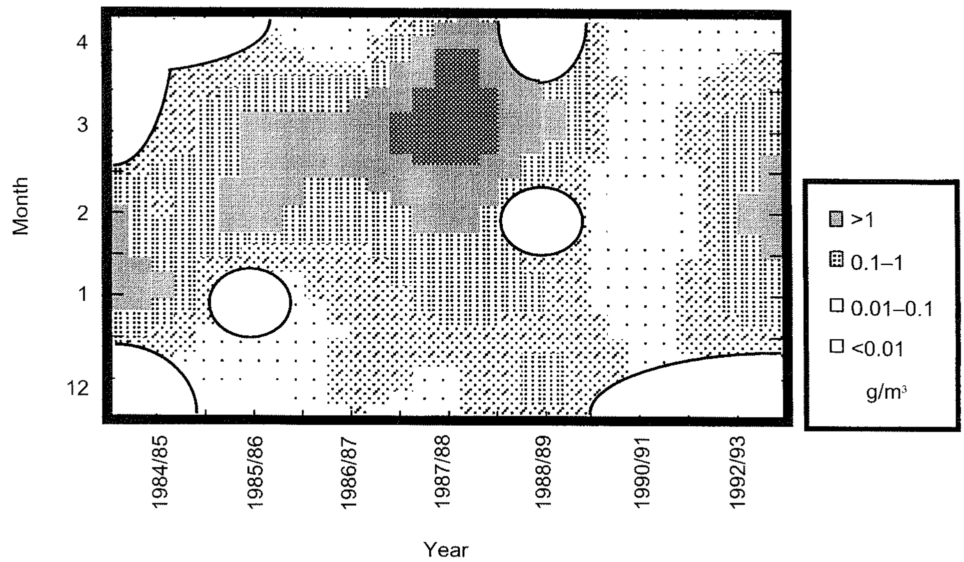

Figure 3: Seasonal variability of average salp density at the fishing ground from 1984/85 to 1992/93.

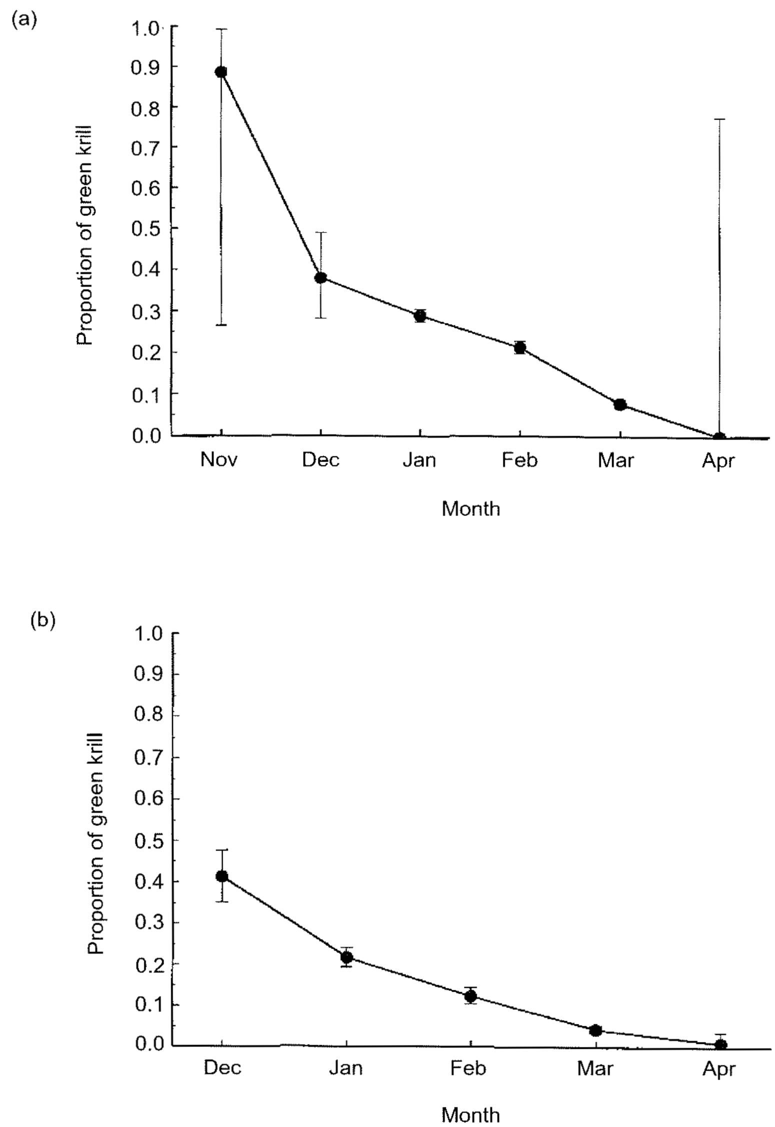

Figure 4: Predicted proportion of green krill in each month. The estimates for (a) Livingston Island area and (b) Elephant Island area are standardised to February and a mean temperature of 1.59°C.

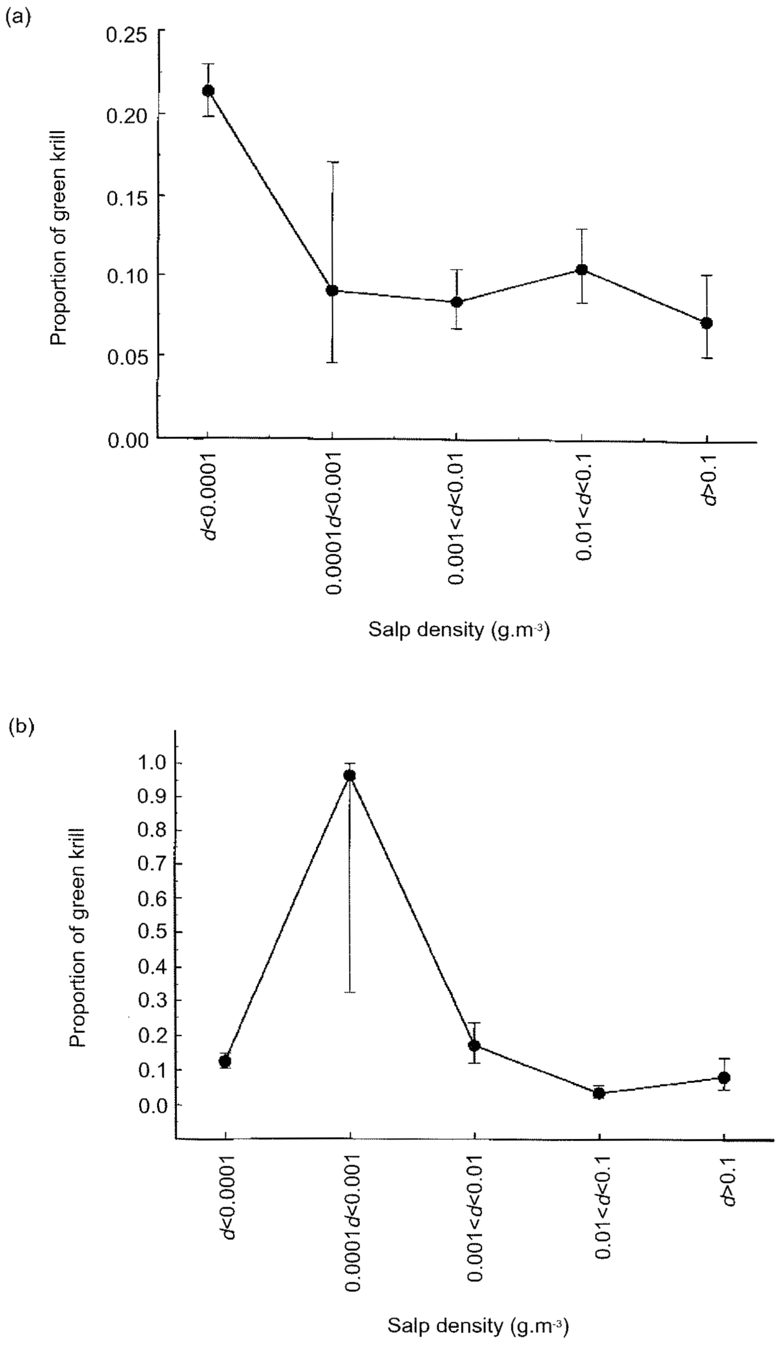

Figure 5: Predicted proportion of green krill for different salp densities. The estimates for (a) Livingston Island area and (b) Elephant Island area are standardised to February and a mean temperature of 1.59°C.

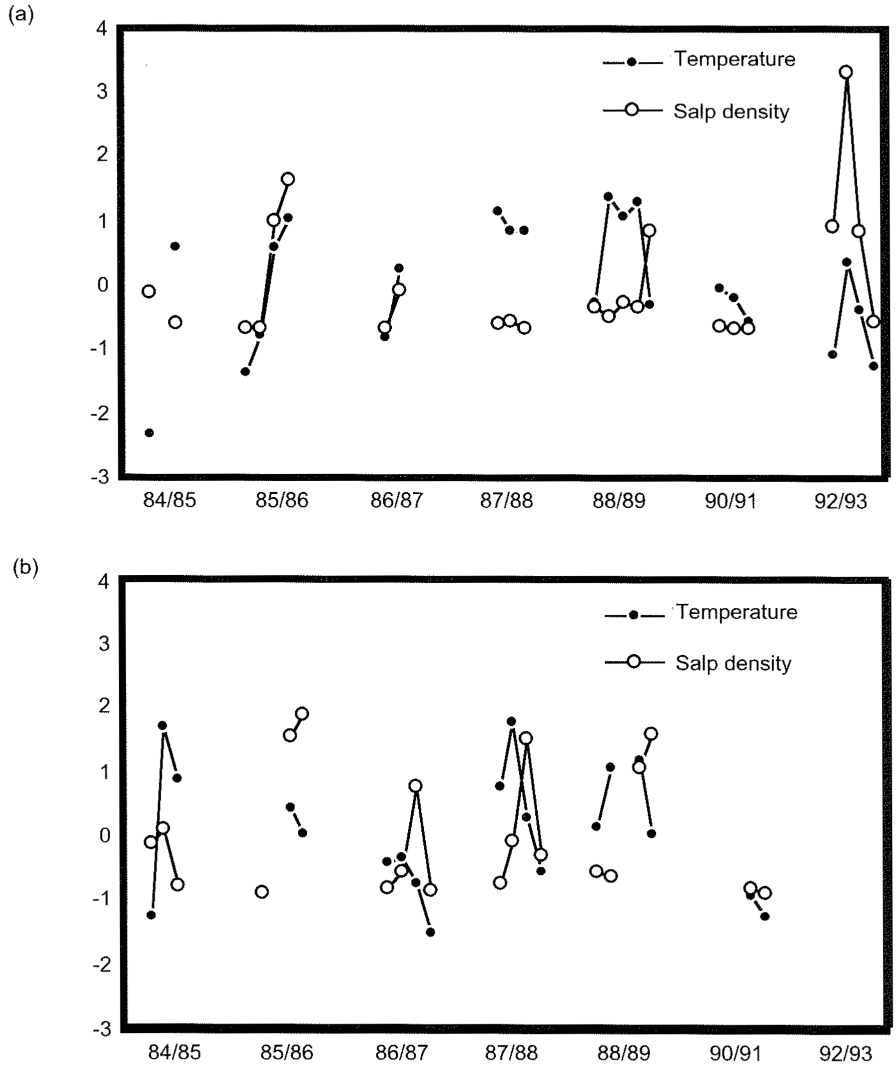

Figure 6: Monthly averages of temperature and salp density in (a) Livingston Island area and (b) Elephant Island area. The values are standardised by the deviance from the average value. November to April of each fishing season are plotted.

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