CCAMLR Science, Vol. 3 (1996): 13-30

ENVIRONMENT-KRILL RELATIONS IN THE SOUTH GEORGIA MARINE ECOSYSTEM

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Abstract

Interannual variability in the Southern Ocean ecosystem has long been noted and physical factors appear to dominate the dynamics. There are, however, few ecological time series available to assess this variability and it is only recently that physical datasets have been generated for the Southern Ocean. In this study, time series of krill abundance (CPUE) indices were derived from Soviet fishing operations in the northeastern Scotia Sea around South Georgia for the period from 1974 to 1992. These indices were examined in relation to the variation in the physical environment. There are links between the ice, ocean and atmospheric components of the system, and there are also correlations with CPUE data. The CPUE index generally agrees with other data which give direct or indirect indications of krill availability, suggesting it can be a useful index for some regions. Associations with ice-edge position and atmospheric components were only expressed strongly in years of extreme conditions. The correlation with water temperature was more consistent, supporting suggestions that the variability in krill abundance around South Georgia is strongly influenced by the oceanographic regime of the Scotia Sea.

Résumé

La variabilité interannuelle de l'écosystème de l'océan Austral est reconnue depuis longtemps. Des facteurs physiques semblent en dominer la dynamique. Il n'existe toutefois que peu de séries chronologiques disponibles qui permettent d'évaluer cette variabilité et ce n'est que récemment que des jeux de données d'ordre physique ont été compilés pour l'océan Austral. Dans cette étude, des séries chronologiques d'indices d'abondance du krill (CPUE) ont été dérivées des opérations de pêche soviétiques menées dans le nord-est de la mer du Scotia, autour de la Géorgie du Sud, de 1974 à 1992. Ces indices ont été examinés en fonction de la variation de l'environnement physique. Il existe des liens entre les composantes du système - glaces, océan et atmosphère - ainsi que des corrélations avec les données de CPUE. L'indice de CPUE corrobore généralement les autres données qui donnent des indications, directes ou indirectes, sur la disponibilité du krill, ce qui laisse entendre son utilité potentielle dans certaines régions. Alors que la corrélation avec la position de la bordure glaciaire et avec les éléments atmosphériques n'est nettement marquée que les années où les conditions sont extrêmes, la corrélation avec la température de l'eau est, elle, remarquée plus fréquemment, ce qui conforte l'opinion selon laquelle la variabilité d'abondance du krill autour de la Géorgie du Sud est largement influencée par le système des eaux de la mer du Scotia.

Резюме

Межгодовая изменчивость в экосистеме Южного океана была замечена уже давно, и в ее динамике, по-видимому, доминируют физические факторы. Однако имеется мало исторических экологических данных для оценки этой изменчивости, и только недавно были подготовлены серии данных по физическим факторам Южного океана. Для данной работы временные ряды индексов численности криля (CPUE) были получены по результатам промысла СССР в районе Южной Георгии в северо-восточной части моря Скотия в период с 1974 по 1992 г. Эти индексы были проанализированы в зависимости от изменений в физической окружающей среде. Обнаружена связь между компонентами системы 'лед', 'океан' и 'атмосфера', а также корреляция с данными CPUE. Индекс CPUE в общих чертах имеет корреляцию с прямыми и косвенными показателями наличия криля, что говорит о возможности применения данного индекса к ряду районов. Связи между положением кромки льда и атомосферными параметрами были сильно выражены только в годы преобладания экстремальных условий. Корреляция с температурой воды была более последовательной, что поддерживает теорию о том, что на изменчивость численности криля в районе Южной Георгии сильное влияние оказывает океанографический режим моря Скотия.

Resumen

La variabilidad interanual en el ecosistema del océano Austral ha sido observada por largo tiempo y la dinámica está dominada aparentemente por factores físicos. Sin embargo, existen escasas series cronológicas de datos ecológicos disponibles para evaluar esta variabilidad, y recién acaban de elaborarse conjuntos de datos de parámetros físicos para el océano Austral. Las series cronológicas de datos sobre la abundancia de kril (CPUE) utilizadas en este estudio fueron derivadas de las operaciones de pesca soviéticas efectuadas en el noreste del mar de Escocia alrededor de Georgia del Sur durante el período desde 1974 hasta 1992. Estos índices fueron examinados en relación a la variación en el entorno físico. Existen vínculos entre el hielo, océano y los componentes climáticos del sistema, y también hay correlaciones con los datos de CPUE. El índice de CPUE generalmente concuerda con otros datos que dan una indicación directa o indirecta de la disponibilidad de kril, por lo que se supone puede ser un índice de utilidad en algunas regiones. Las asociaciones con la posición del borde de hielo y los componentes climáticos sólo demostraron ser fuertes en los años en que se dieron condiciones extremas. La correlación con la temperatura del agua es más fuerte, apoyando las suposiciones de que la variabilidad en la abundancia de kril alrededor de Georgia del Sur está fuertemente influenciada por el régimen oceanográfico del mar de Escocia.

Keywords: air transport, CPUE, CCAMLR, correlation, ice-edge position, interannual variability, krill fishery, sea-water temperature, South Georgia

INTRODUCTION

Large-scale fluctuations in the distribution and abundance of Antarctic krill (*Euphausia superba*) appear to be a characteristic feature of the South Atlantic sector of the Southern Ocean (Priddle et al., 1988). These variations are frequently accompanied by marked changes in the breeding population size and reproductive performance of seabirds and seals which feed predominantly on krill (Croxall et al., 1988). The general opinion is that these fluctuations are the result of large-scale changes in the physical environment. Mackintosh (1972) drew attention to the correlation between the size of the scientific catches of krill taken as part of the 'Discovery' expeditions and the occurrence of 'warm' or 'cold' years. In very cold seasons (e.g. 1927/28, 1930/31) krill catches were significantly greater than in warm seasons (e.g. 1936/37). Mackintosh (1972) developed this theme and highlighted a correspondence between water temperature, sea-ice conditions and krill biological characteristics. Later a relationship between the intensity of the atmospheric air transport and variations in density of krill aggregations was also suggested (Fedoulov et al., 1984; Maklygin, 1987) and Priddle et al. (1988) considered possible mechanisms.

For the eastern area of the Scotia Sea around South Georgia, it has been suggested that krill abundance depends on the intrusion into this area of cold water from the Weddell Sea (Bogdanov and Solyankin, 1970; Maslennikov et al., 1983). In reviewing the possible causes of these phenomena, Priddle et al. (1988) concluded that a large-scale breakdown of hydrographic structure caused by prolonged periods of southward air flow, and an associated southward displacement of warm surface water and pack-ice in the northern Weddell Sea, was a likely mechanism. As well as this possible direct physical effect on distribution, it has been suggested more recently that there is a link between the interannual variation in sea-ice conditions and krill recruitment (Ross and Quetin, 1991; Siegel and Loeb, 1995; Kawaguchi and Satake, 1994). It remains unclear, however, to what extent these are changes in abundance or distribution at one or more scales.

In this paper a time series of the catch per unit effort (CPUE) statistics from the USSR commercial krill fishery operating around South Georgia was derived and its usefulness as an index of abundance considered. In considering the hypothesis that fluctuations in the abundance of krill in the Scotia Sea area are related to environmental changes, correlations between selected physical environmental variables and CPUE indices were examined. It was concluded that the fishery statistics may be more valuable than was previously thought, and the analyses provided further evidence of the importance of large-scale physical processes in the interannual variability of krill around South Georgia.

METHODS AND DATA

Catch per Unit Effort

Some measure of catch rate from a fishery is often used as an index of abundance of the target organism. CPUE is not, however, necessarily a useful measure of abundance in all situations and there can be particular problems associated with pelagic shoaling species (Shepherd, 1988). Krill are highly heterogeneously distributed and simulation studies carried out through CCAMLR to consider the efficacy of various CPUE measures in krill fisheries suggested that simple application of such indices would not be useful (Butterworth, 1988; Mangel, 1988). However, those simulations were carried out using assumptions based on knowledge of fine-scale krill distributions from mainly open-water or ice-associated observations. Such assumptions probably do not apply in areas close to shelf regions where mesoscale physical processes are likely to dominate. This will be the case in the South Georgia area as indicated by the restricted spatial extent of whale catches taken in the early part of the century (Everson, 1984). Whales feed predominantly on krill, and the areas where they were taken are increasingly being identified as regions of high krill concentration (British Antarctic Survey, unpublished data). In such areas krill fishing will involve less time spent searching for krill. The use of simple CPUE indices is likely to be more useful in a situation where search time between large-scale krill concentrations is not a major factor. Within the regions where fishing occurs, the resource is fished by tows covering a much greater area than the size of a swarm, which suggests the regions may be fished more as traditional fishing grounds rather than fishing being directed at specific swarms. The usefulness of CPUE within a season may suffer more from the problems of spatial heterogeneity in krill distribution than from using the index between seasons where the changes we are interested in are large. As revealed by the simulation studies, CPUE may be reflecting changes in aspects of krill distribution such as swarm density or size changes rather than absolute abundance changes. This aspect is considered further below.

CPUE data (tonnes per day per vessel) from commercial krill fishing vessels were used to obtain an index of krill abundance (Anon., 1977-1992). The fishing data were obtained by processing information on catches while at sea; catch and effort data were available for the period 1974 to 1992. For the period 1974 to 1976 there was no information on the number of days spent fishing (days on which fishing actually occurred) or on the vessel owners. However, from 1977 to 1992 high resolution data were collected on the number of fishing days by each vessel type. There were no data available for 1982. Krill fishing was not significant in 1978 or 1984 (except during January) because of a reported absence of krill. These years were not included in correlation analyses. Only once during the entire period (1977) did Soviet vessels fish for krill during November or December, but catch data were not available for November.

The data from all vessels were combined according to their technical characteristics (vessel type) and shipowner. The analyses presented here are based only on the CPUE values of the large stern trawlers (3 800 GRT) which were the main type of vessel operating in the fishery. Average catch per day was calculated for each shipowner and this was used to calculate monthly mean values. Monthly CPUE indices were then calculated as a weighted average based on the number of days spent fishing by vessels of each shipowner. It should also be borne in mind that the intensity and duration of the krill fishery in the South Georgia area is influenced not only by the distribution and abundance of krill, but by other factors relating to the general economics of the fishery and the availability of other potential target species (e.g. finfish).

A range of indices was calculated based on various combinations of months in which fishing took place.

Sea-surface Air Transport

Quantitative analyses of atmospheric processes are usually based on various indices derived from surface pressure gradients. The vector of the air pressure gradient is decomposed into the zonal (along lines of longitude) and meridional (along lines of latitude) components. The direction of the sea-surface air transport is directly proportional to, and normal to, the atmospheric pressure gradient (Sverdrup et al., 1942). Thus, the zonal air transport (east-west) corresponds to the meridional pressure gradient and meridional air transport (north-south) corresponds to the zonal pressure gradient.

Monthly mean atmospheric pressure gradients were estimated for the area around South Georgia. The values were derived from standard meteorological charts of the South Atlantic for the 26-year period from 1965 to 1991. To produce comparable meridional and zonal pressure gradients, the pressure differences were divided by the distance between the points where the values of air pressure were estimated. The pressure gradients were expressed as millibars per equatorial degree. Daily gradients taken from meteorological charts were averaged for each month. These monthly mean values are referred to as the air transport index (AT). Z-AT represents zonal and M-AT represents meridional air transport indices.

The AT index characterises the predominant direction of air movement. Negative values of Z-AT indicate air transport to the east and negative values of M-AT reflect air transport to the north. In this study the Z-AT indices were calculated between 50°S and 60°S at 30°W and 40°W, while the M-AT indices were calculated between 30°-40°W and 40°-50°W at both 50°S and 60°S (Figure 1).

Ice-edge Position

Ice-edge position data were derived from sea-surface TV-satellite images (Soviet satellite 'Meteor') recorded at the Soviet Antarctic Station 'Molodezhnaya'. The ice-edge position (70% sea-ice concentration) was determined for each 10-day period. Block averages were calculated to

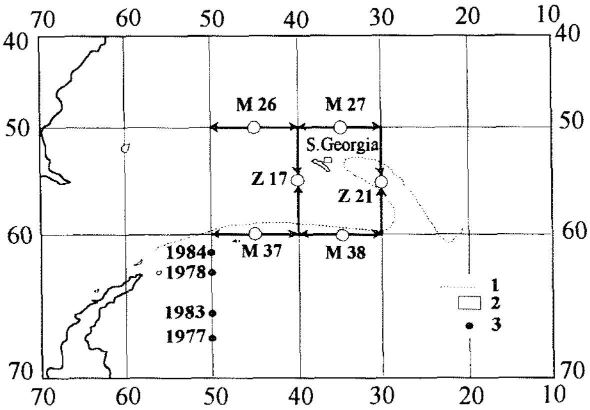

Figure 1: The lines (arrowed) over which the zonal and meridional air transport indices were calculated. 1 - mean position of the Weddell-Scotia frontal zone for 1967-1988 (Fedoulov and Shnar, 1990); 2 - area for which water temperature data were available; 3 - position of ice-edge in March of a particular year.

produce monthly mean values for the period 1979 to 1991 along longitudes 20°, 30°, 40° and 50°W. For the period 1973 to 1989, a further sea-ice dataset was available courtesy of Dr T.H. Jacka (Australian Antarctic Division). The two datasets showed a high degree of correspondence during the period of overlap (1979-1989). The Jacka data for the 1973-1978 period were, therefore, used to generate a series from 1973 to 1991.

Sea-water Temperature

The sea-water temperature data were obtained from the AtlantNIRO hydrological database. These station data were collected using Nansen water bottles and Conductivity Temperature Depth (CTD) systems. The data were extracted for a region near South Georgia between 53.75°-54.25°S and 36.5°-35.5°W for the period between 1965 and 1990 (Figure 1). The mean water temperature was calculated over the upper 50 m of the water column. The greatest number of temperature observations were obtained during the austral summer between January and April. For further analyses, average temperatures were calculated for three periods: January-February, March-April, and June-July.

Data Processing

Statistical calculations were carried out using the computer programs MINITAB and STATGRAF.

RESULTS

Catch per Unit Effort

Fishing for krill in the South Georgia area usually took place from April-May to August-September (Figure 2), although the start and finish times varied greatly between years. The very high values obtained for the mean number of fishing days during February and March were the result of the large number of days spent fishing in those months during 1977. The monthly mean CPUE data suggest a seasonal pattern of low values between October and December and higher values between April and July. The data were least reliable during the first few years of exploitation when the fishery was developing. The relatively high CPUE values in January were the result of very high values obtained for 1974 and 1975 (64.8 and 51.5 tonnes respectively), and only in 1977 did krill fishing take place in November or December.

CPUE indices were calculated as either the mean CPUE over all months during a period or as the mean CPUE for those months in which fishing occurred, e.g. mean CPUE for all months from April to June is given by the index (April-June)/3 while the mean CPUE based on those months (n) when fishing occurred is given by the index (April-June)/n.

The different CPUE indices indicated generally similar interannual variability. Indices based on mean CPUE values for a fixed number of months (which can include zero values) tended to generate more variable series (Figure 3a).

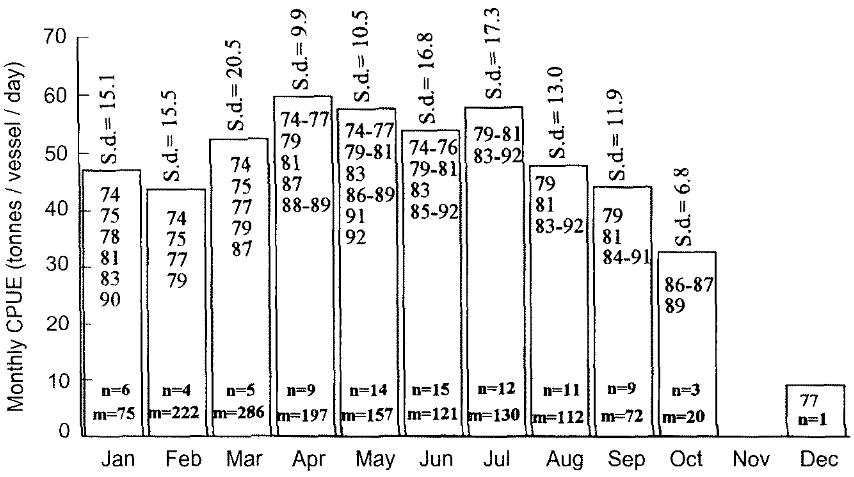

Figure 2: Seasonal variation in monthly mean CPUE index for the period 1974 to 1992 in Subarea 48.3 ('zero' CPUE values for 1978 and 1984 are excluded). n - number of years when krill fishing took place in the month (years are indicated inside the bars); m - monthly mean number of fishing days; sd - standard deviation.

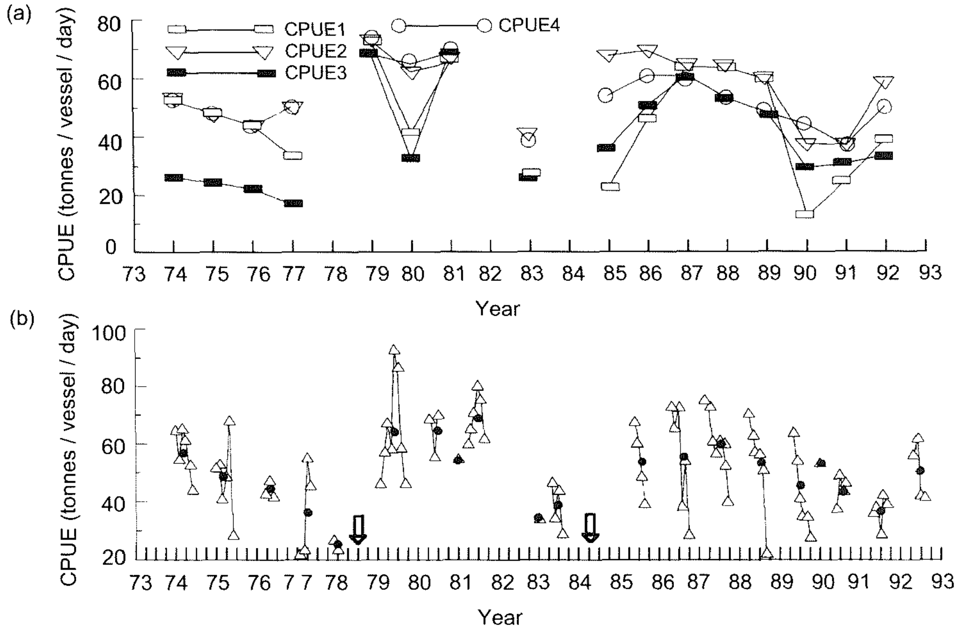

Figure 3: Variation in CPUE indices:

(a) interannual fluctuations of the CPUE indices: CPUE 1 - (April-June)/3; CPUE 2 - (April-June)/n; CPUE 3 - (April-September)/6; CPUE 4 - (April-June)/n (see text for definitions of indices).

(b) mean catch per unit effort by the Soviet krill fishing fleet for each consecutive period of months (solid circles) and monthly data on which the mean values were based (triangles). The arrows indicate periods when there was no fishery due to the reported absence of krill.

The first five years of the CPUE series were based on the mainly early season fishing between January and June (Figure 3b). These years showed a steady decline with an unfished stock in 1978. The CPUEs were then high again for three years. There were no data for 1982, then a low value was recorded again in 1983 followed by an unfished stock in 1984. Higher catch rates were again recorded in 1985, with another period of declining rates through to 1991 and a slight increase apparent in 1992. Over the late 1980s there was a distinct seasonal change in the CPUE, with high values recorded at the start of the season in April-June declining to lower levels by about September-October. The low catch rates during the mid-1980s and the late 1980s were reflected in lower overall catches from Subarea 48.3 (CCAMLR, 1991).

Air Transport

The Z-AT index showed a semi-annual oscillation with low absolute values in December-January and May-June and high absolute values in February-April and September-November (Figure 4). The index was always negative, so it characterises both the absolute intensity of atmospheric processes and the predominance of air transport in an eastward direction (westerly winds). M-AT values are nearly one order of magnitude less than Z-AT values. The M-AT index seasonal curves showed positive transport (i.e. from north to south) in February and August-November and negative transport (from south to north) in December-January and April-July with a maximum in May (Figure 4).

Interannual analyses of the air transport indices showed that there was substantial variability in both Z-ATs and M-ATs. There were indications of long-term change in both the Z-AT and the M-AT indices. For example, the Z-AT index declined from 1974 to 1987 indicating a period of increased westerly winds (Figure 5), while the M-AT index decreased after the mid-1970s indicating greater northerly air transport (Figure 5). The Z-AT indices were highly correlated between 30°W and 40°W in the same months with correlation coefficients within the range of 0.80-0.93. The M-AT indices were less well correlated between 50°S and 60°S with the correlation coefficients between 0.55-0.70. There was no consistent correlation between indices based on consecutive months.

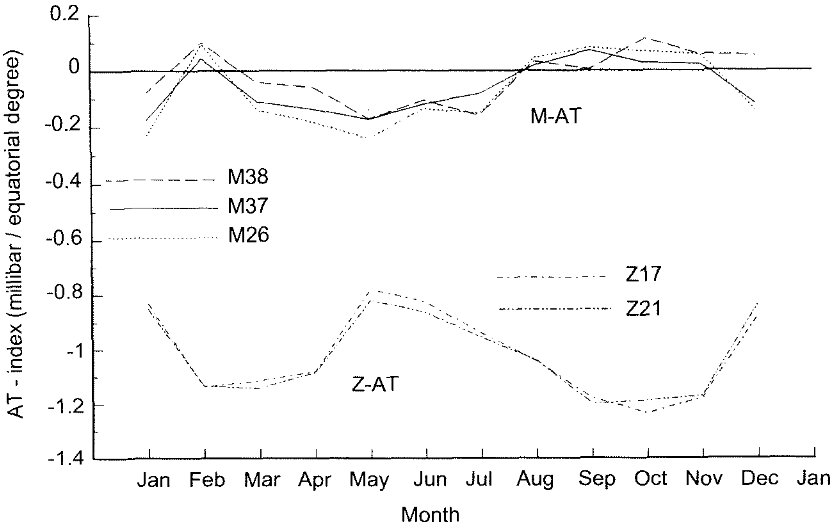

Figure 4: Seasonal variability in Z-AT and M-AT.

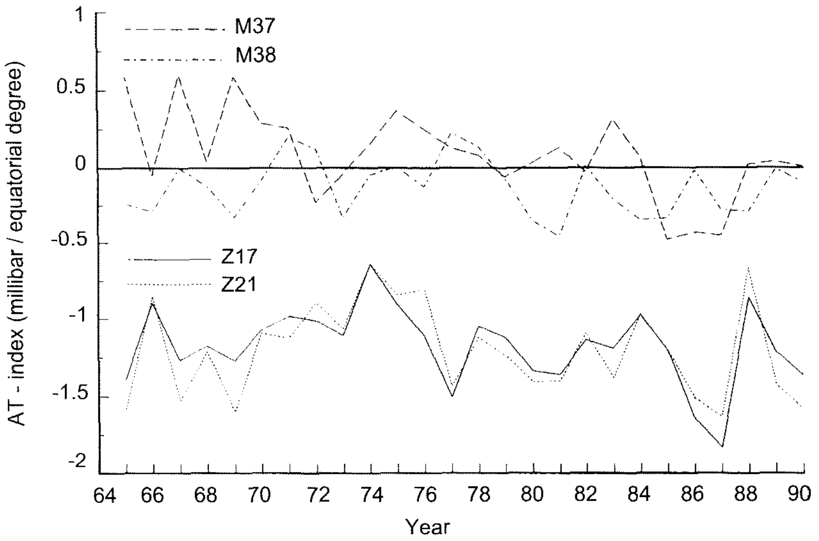

Figure 5: Interannual variation in Z-AT and M-AT. M37 - averaged for period April-July; M38, Z17, Z21 - averaged for period October-November.

Ice-edge Position

Over the 1973-1991 period the ice-edge attained its northern limit in the 20-50°W sector between August and October and reached its southern limit in February (Figure 6). The maximum rates of ice-edge retreat and advance occurred during January-February and April-June respectively. There was considerable interannual variability in ice-edge position (Figure 7). Thus, the October ice-edge reached 54°S (South Georgia) in 1980 and 1987 but did not exceed 58°S in 1977-1978, 1983 and 1989. Interannual variations in the ice-edge positions in March at 30-40°W and in October at 50°W (Figure 7) show a general correspondence: extreme northern (southern) position of the ice-edge in spring precedes an extreme southern (northern) position in the following autumn. The amplitude of seasonal ice-edge movements (latitudinal differences between northern and southern positions of the ice-edge in the same year) varies to a great extent from year to year. Figure 7 shows minimum amplitude in 1973, 1977-1978, 1983, 1990 and maximum amplitude in 1975-1976, 1981 and 1986-1987.

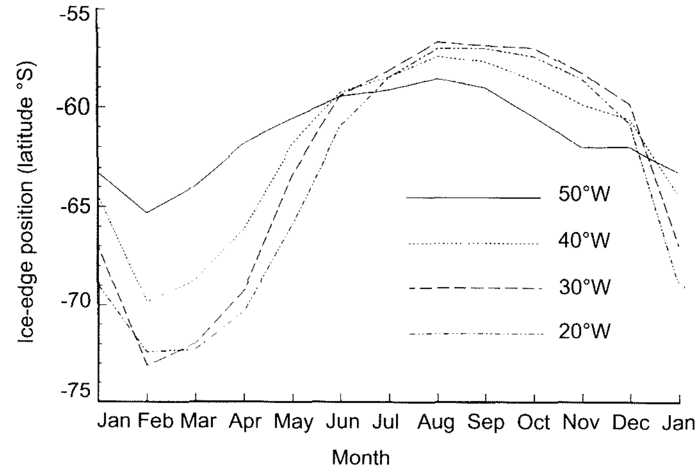

Figure 6: Seasonal variability of ice-edge position at different longitudes.

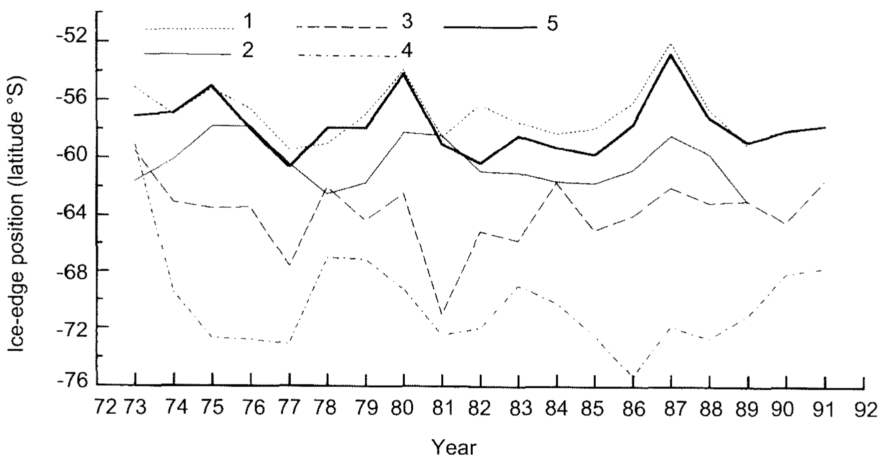

Figure 7: Interannual variation in ice-edge position. 1 - at 30°W in October; 2 - at 50°W in October; 3 - at 50°W in March; 4 - in March averaged for 30-40°W; 5 - in September at 40°W.

Monthly ice-edge positions were highly positively correlated between neighbouring longitudes and between nearby months with the correlation coefficients between 0.6 and 0.9 (Figure 8) and there were also consistent relationships between the ice extent in winter and in the previous autumn and the following summer (Figure 8). The later the ice started to retreat in the spring, the more to the north it advanced in the following winter and the further north it was in the following summer. These analyses support suggestions of strong regional and temporal coherence in the position of the ice-edge in the Scotia Sea and Weddell Sea (Pozdeeva et al., 1990; Murphy et al., 1995).

Sea-surface Temperature

The water temperature in the 0-50 m layer reached a minimum during September-October and a maximum during February-March (Figure 9). There was strong interannual variability in the mean sea-surface temperature during the summer-autumn period, however gaps in the data series limit the interpretation of longer-term changes (Figure 9). There were generally consistent positive correlations with water temperature at different times of the season. For example, a positive correlation was noted between the water temperature in early summer and early winter (r = 0.69; Figure 10a).

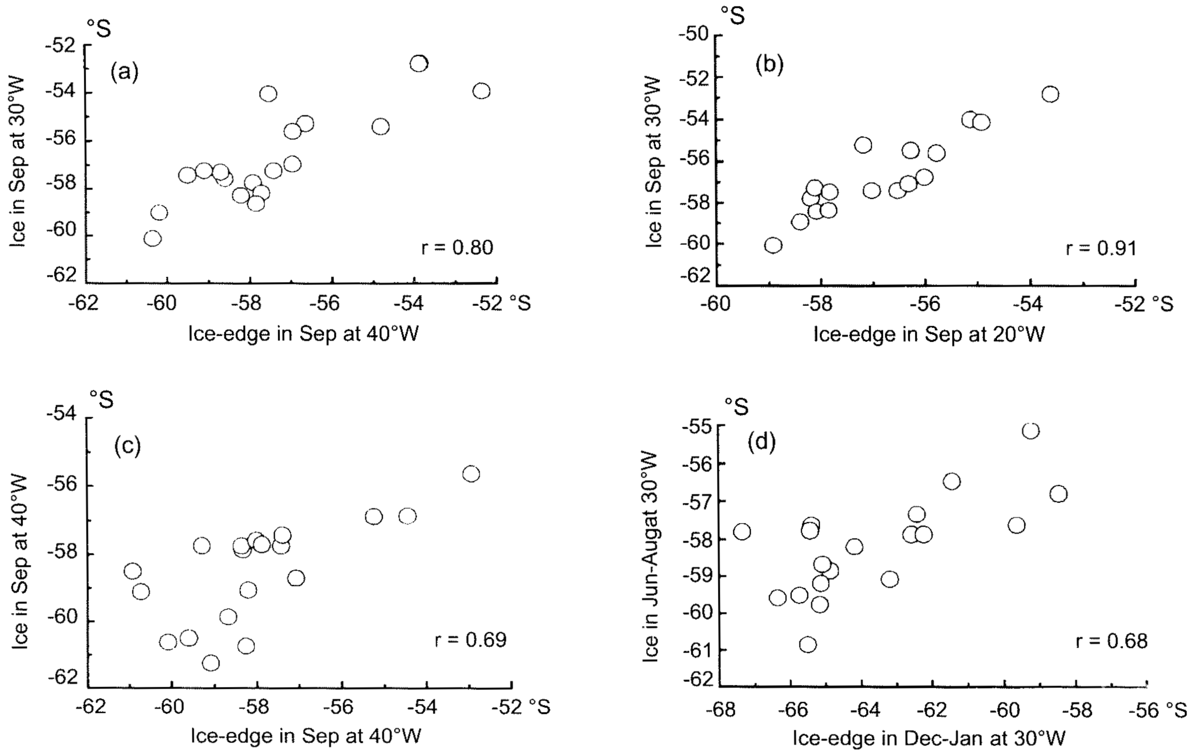

Figure 8: The relationship between ice-edge positions at different longitudes: (a), (b), (c) - in the same year; (d) - ice-edge position at 30°W averaged for December-January and at 30°W in the next June-August.

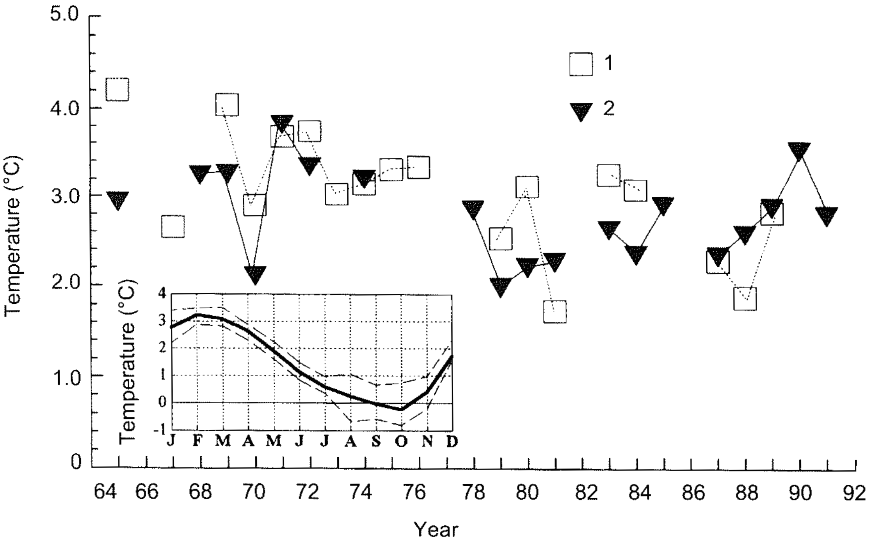

Figure 9: Interannual variation in sea-water temperature in the 0-50 m layer at the eastern South Georgia shelf (square: 53.75-52.25°S; 36.5-35.5°W): 1 - mean sea-water temperature for January-February; 2 - mean sea-water temperature for period March-April. Insert: seasonal variation in sea-water temperature in the 0-50 m layer (dashed lines - 95% confidence interval).

Inter-relationships between Physical Variables

Z-AT values did not show any correlation with ice-edge positions through the year. There were no consistent correlations between the M-ATs at 50°S (M26, M27, Figure 1) and the ice-edge position. However, there were consistent high positive correlations between the M37 index during the early winter period and the ice extent throughout the whole of the winter and the following spring; this was the case for all latitudes from 20°W to 50°W (Figure 10b). The M38 index, which is based on gradients to the east of M37 (Figure 1), did not show any general correspondence with ice-edge position. This suggests that a predominance of southerly M-ATs in the area of the Weddell outflow region during the autumn-winter months (May-July) preceded a more northern ice-edge position throughout the whole region in the following spring (September-November). The M37 index appears to give a good indication of the process of ice formation and atmospheric interaction.

There was a general weak positive correlation between the winter ice extents and the water temperatures around South Georgia throughout the year, which indicates that higher water temperatures were associated with a more southern ice-edge position. The most consistent and strongest of these relationships were based on winter ice extents and the water temperatures in the following spring-summer, but these were dominated by the extreme years of maximum ice extent associated with much colder water (Figure 10c). There was also a generally weak positive correlation between the various atmospheric indices and the indices of water temperature around South Georgia. The M37-AT index again appeared to be most consistently correlated, i.e. low temperatures near South Georgia in June-July corresponded to the prevalence of southern air transport in M37-AT in May-July (Figure 10d).

Relationships between Physical Variables and CPUE

Given the consistent correlations between the various physical variables shown above, we would expect correlations between any one physical variable and the CPUE data to be reflected to some extent in correlations between the CPUE and the other physical variables. Correlations were calculated between the physical data and the CPUE in the same year and the CPUE in the following year. There was a consistent correlation between the various CPUE indices and ice-edge positions (Figure 11a). The further south the ice-edge occurred during winter-spring, the lower the CPUE values were in the following fishing season. This relationship does not appear to be linear, in other words once the ice got closer to South Georgia, as indicated by the 70% ice concentration at about 56-57°S, there were no further increases in CPUE associated with greater ice extents. The most extreme expression of this relationship was the lack of a fishery in 1978 and 1984 where the ice did not extend far north during the previous winter (Figure 7). In 1978 and 1984, the ice-edge in March had reached its northern limit at 50°W in March, preceding high CPUE values in 1979 and 1985 (Figure 3). The southernmost March position of the ice-edge was observed in 1981, but unfortunately we have no CPUE or other krill data for 1982.

These relationships of reduced CPUE in years following a winter-spring when the ice-edge was found further south were most consistently and strongly expressed during September and October along 40°W when the ice reached its maximum extent. The indices which best emphasised this relationship were based on mean CPUE calculated over all months on which the index was based, as opposed to just those months in which fishing occurred. This emphasises that there was no strong relationship between ice extent and catch rate in the same or the following season (Figure 11b). The inclusion of months in which no fishing occurred tended to generate low catch rates in years when the ice was furthest south, as there were more months in which fishing did not occur in the area. This may reflect a genuine increase in the number of months in which there were uneconomic catch rates in the South Georgia area, but may also be due to the fishery preferentially operating elsewhere in months when the ice was further south. There were also significant correlations between air transport in late spring and the CPUE in the the next year. For example, the prevalence of southerly meridional air transport in M38 preceded high CPUE values (Figure 11c), but again the indices which best emphasise this relationship were not based on 'realised' catch rates, i.e. catch rates realised by the fleet rather than catch rates calculated as a mean over a fixed period of time.

There was a consistent relationship between CPUE and water temperature based on all indices. Warm water in the South Georgia shelf area in

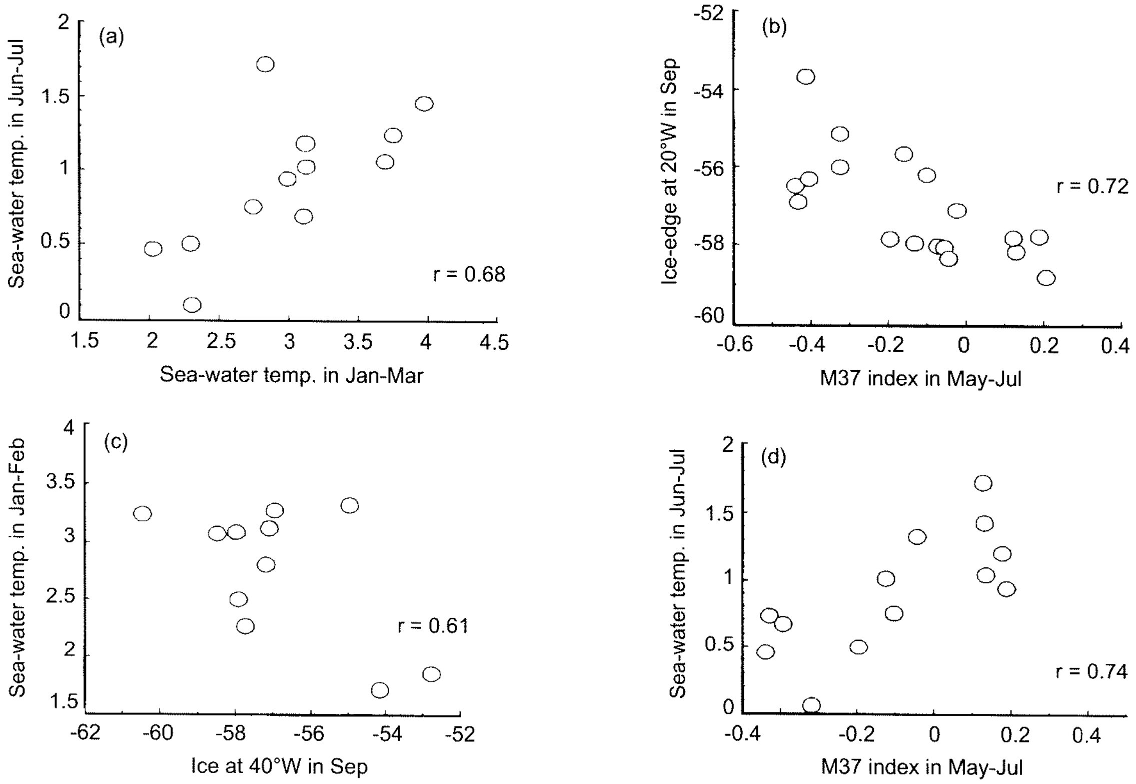

Figure 10: The relationships between the ice-edge position, sea-water temperature and M-AT index. (a), (b), (d) in the same year; (c) temperature in the next year.

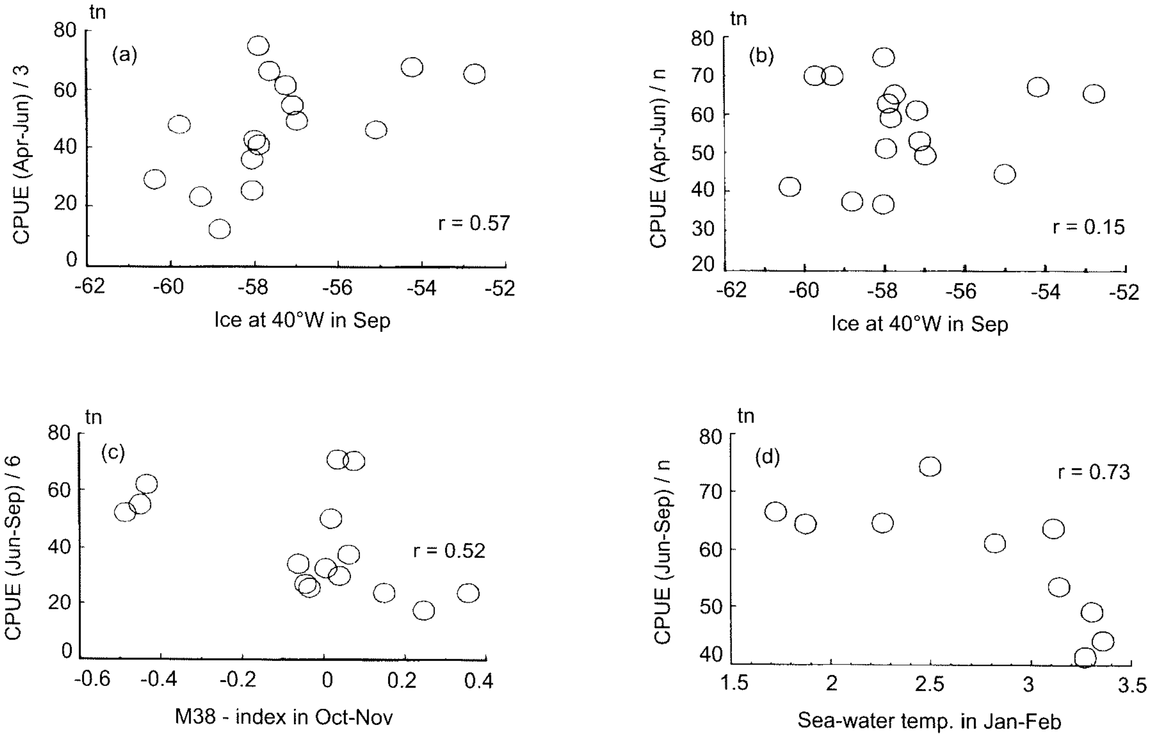

Figure 11: The relationships between ice-edge position at 40°W, M-AT indices in M38, sea-water temperature and CPUE indices.

January-February corresponded to lower CPUE values in the same year (Figure 11d). Lower catch rates were also associated with higher water temperatures around South Georgia in the following spring-summer.

DISCUSSION

CPUE as an Index of Changes in Krill Abundance

There are strong indications that the CPUE index is reflecting changes in the local availability of krill. The two pieces of evidence which support this suggestion are, firstly, that there appears to be consistency between years with declining values over a number of years until very low levels are reached and commercially unviable stocks occur which are not exploited. These values are followed by a return to high CPUE levels. The second piece of evidence is that where the fishery consistently operated from late summer through to the end of winter (April-May to September-October), there was a consistent decline in the CPUE. This was shown particularly clearly over the mid to late 1980s. At the start of the following season the CPUE levels had increased.

The seasonal pattern observed suggests that the CPUE declines as the stock is fished over the winter season and then the combination of growth and recruitment leads to a recovery in CPUE levels in the following season. This interpretation suggests that years of good and poor recruitment can be identified. Applying this idea suggests that over the period from 1974 to 1978 there was little recruitment, reflected in the continuous decline in CPUE. This was followed by good recruitment between 1979 and 1981, poor recruitment in 1983 and 1984, followed by consistent but not high levels of recruitment over the period from 1985 to 1989, peaking in about 1987. This was followed by poor recruitment in 1990 and 1991 and, possibly, some level of recruitment in 1992.

Is there any evidence to support these suggestions and the observed pattern of CPUE? Time series of various indices of population dynamics have been generated for colonies of birds and seals breeding during the summer months on Bird Island, South Georgia (Croxall et al., 1988; Lunn et al., 1994; Croxall and Rothery, 1995). The available information cannot provide a sensitive index of prey availability, however it is clear that some of the indices do reflect overall changes in the availability of prey and this in turn reflects years of high or low krill abundance around South Georgia. In 1978 and in 1984 some predator species suffered from very low prey availability and a range of indices of breeding performance indicated that there was very poor performance. Some species also fared quite badly in 1990/1991. Research vessel work in these years (Bonner et al., 1978; Hempel et al., 1979), as well as in 1984 (Anon., 1984; Heywood et al., 1985; Everson, 1992), has confirmed that they were years of low krill abundance in the South Georgia area. In general terms, the CPUE series indicate that the krill fishery is not carried out in the area when catches are at very low levels or krill availability is low. For areas around the Antarctic Peninsula, there is evidence that there are years of weak and strong recruitment (Siegel and Loeb, 1995). This may also be the case in the South Georgia area, but as yet there is no relevant information available. The CPUE data do not show a substantial decline in catch rates over the last 10 to 15 years.

It is possible that economic factors or operational changes may have occurred in the fishery. The fishery may have moved to exploit krill in other areas of the Scotia Sea or the Southern Ocean and economic factors may be important. The above suggests, however, that larger fluctuations in CPUE do reflect changes in the local availability of krill.

The above analyses were based on only one type of vessel, and the available evidence does not suggest any systematic changes in the fishing operations that would have generated the observed changes. The question of whether or not the CPUE relates directly to changes in abundance for all concentrations of krill requires further study, although the above series provides some justification for using a measure of catch rate as an index. Changes in swarm density, swarm size or krill 'quality' may be occurring, but the above suggests that these would have to be systematic both within season and between years. The absence of a fishery in years when ice was well to the south may be associated with a shift in the fishery, which could be examined by considering catch rates in other areas; presumably the catch rates would be higher in the more southern areas. The fishery, which is known to track the ice-edge retreat during the summer (Everson and Goss, 1991), may be exploiting some aspect of krill aggregation associated with the ice-edge. This would still reflect a real change in local availability with lower catch rates when the ice-edge was further south in winter as reflected in the lack of krill indicated by research surveys and predator monitoring.

The Physical System of the Scotia Sea and the Transport of Krill to the South Georgia Area

Links between the ice, ocean and atmospheric components of the Southern Ocean have been revealed by a range of studies (Gloerson, 1995; Murphy et al., 1995; Stammerjohn and Smith, 1995). From the above a prevalence of more southerly meridional air transport during the winter-spring months was associated with a more northern ice extent across the Scotia sea throughout the winter and with lower sea-water temperatures. The opposite effect was also observed, i.e. a predominance of northerly meridional air transport was related to a more southern ice-edge position in the winter-spring season and a higher sea-water temperature at the beginning of the year.

How does this system affect krill distribution? Priddle et al. (1988) discussed in detail some of the possible mechanisms. The catch rate changes in relation to sea-water temperature support the suggestion that water mass changes may be occurring, enabling us to concentrate on the circulation patterns. The general consensus is that krill do not undertake large-scale directed migrations and are transported over long distances by the prevailing water currents. Both the Antarctic Circumpolar Current (West Wind Drift) and the flow of the Weddell-Scotia Confluence (WSC) water can contribute to the formation of the krill stock around South Georgia. However, krill are usually more abundant in the southern Scotia Sea along the WSC, so it is likely that the WSC current plays a key role in krill transport to South Georgia.

The WSC is a region where cold Weddell Sea waters in the south mix with the relatively warm water of the Scotia Sea to the north (Patterson and Sievers, 1980; Fedoulov and Shnar, 1990; Whitworth et al., 1994) and is an area of relatively high current velocities (Orsi et al., 1993). The WSC zone extends northwards into the eastern Scotia Sea where colder water penetrates along the southeastern shelf of South Georgia (Figure 1; Bogdanov et al., 1980; Maslennikov et al., 1983). The position of the WSC is thought to be determined by the intensity of the Weddell gyre, which in turn is driven by the formation of dense and cold Weddell Sea water (Fedoulov and Yakovlev, 1986; Fedoulov and Shnar, 1990). The main factor in the creation of the cold Weddell Sea water is the increased salinity resulting from ice formation (Foster and Middleton, 1980). The thickness of the sea-ice is proportional to the number of degree-days of frost (Zubov, 1938) suggesting that a very warm or cold year reflects the intensity of the Weddell gyre and consequently the general position of the WSC. As yet there is very little information available to investigate the connection between ice extent and ocean frontal systems. There is some evidence that the WSC was located in the extreme south in the Scotia Sea during the summer of 1983/84 (Anon., 1984) when the ice was in a more southerly area during winter, but this requires a more focused study. The interaction of ice-edges and fronts is an understudied aspect of Southern Ocean dynamics and is likely to be crucial in the operation of the ecosystem, one aspect of which is the observed interannual variability of krill in the South Georgia area.

It is unclear whether ice influences the movement and distribution of krill aggregations directly, but the current systems are likely to be a major factor in generating the final distribution. If the main transport of krill takes place in the WSC, it is reasonable to suppose that ice starts to influence krill distribution when it is close to or covers this area. The ice-edge attains 60°S (i.e. latitude of South Orkney islands) in 'normal' years in June and retreats to the same latitude in November-December. It is likely that it is during this period that favourable (northern ice-edge position) or unfavourable (southern ice-edge position) conditions for krill transport to South Georgia will be important. Ice cover modifies the mechanism of drift current formation by changing the atmosphere-ocean energy transfer but it is not yet fully understood how this can modify large-scale circulation patterns in the Southern Ocean.

There is some anecdotal information relating to this subject. In years when there were virtually no krill near South Georgia (1978 and 1984), large concentrations of krill were found in the open Scotia Sea (Anon., 1977-1992). In 1978 the USSR fleet fished krill in the area to the north of the South Orkney Islands during February and March. In April krill began to be dispersed over larger areas and the density of krill concentrations diminished, resulting in the cessation of fishing. Reasonably dense concentrations of krill were also observed in the southeastern part of the Scotia Sea during a krill trawl survey in March-April

1984 (Anon., 1984). The database available at present is inadequate to pursue these questions further.

As shown above, the variation in catch rates does not appear to be simply related to ice extent, apart from in years of extreme ice conditions. The water temperature relationship appears to be more direct, suggesting that there are both spatial and temporal links which will be important. The extent to which the changes in local availability reflect a shift in the krill distribution associated with the sea-ice or water mass distributions or the effects of population dynamics (Seigel and Loeb, 1995) may be resolved, in part, by further analyses of fisheries data. A more mechanistic approach is now required to understand the underlying physical connections.

ACKNOWLEDGEMENTS

We thank Dr Jacka for providing the sea-ice position dataset, C. Symon and C. Mitchell for their assistance in the early stages of work, E. Berezina for help in arranging the manuscript and Dr J.P. Croxall, Prof. Antezana and Dr S. Nicol for valuable comments on an earlier draft of the manuscript.

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Figura 7: Variación interanual en la posición del borde de hielo. 1 - en el meridiano 30°W en octubre; 2 - en el meridiano 50°W en octubre; 3 - en el meridiano 50°W en marzo; 4 - en marzo promediada para el intervalo de 30-40°W; 5 - en septiembre en el meridiano 40°W.

Figura 8: Relación entre la posición del borde de hielo en distintas longitudes: (a), (b), (c) - en el mismo año; (d) - posición del borde de hielo en el meridiano 30°W promediada para el período de diciembre a enero y en el meridiano 30°W en el próximo período de junio a agosto.

Figura 9: Variación interanual de la temperatura del agua de mar en el estrato de 0-50 m en la zona al este de la plataforma de Georgia del Sur (cuadrícula: 53°75'-52°25'S; 36°5'-35°5'W): 1 - temperatura promedio del agua de mar en enero-febrero; 2 - temperatura promedio del agua de mar de marzo a abril. Inserción: variación de la temperatura promedio del agua de mar en el estrato de 0-50 m durante la temporada (líneas punteadas - intervalo de confianza del 95%).

Figura 10: Relaciones entre la posición del borde de hielo, la temperatura del agua de mar y el índice M-AT. (a), (b), (d) en el mismo año; (c) temperatura en el año próximo.

Figura 11: Relaciones entre la posición del borde de hielo en el meridiano 40°W, índices M-AT en M38, temperatura del agua de mar e índices de CPUE.