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ESTIMATES OF CIRCUMPOLAR ABUNDANCE OF ANTARCTIC KRILL BASED ON RECENT ACOUSTIC DENSITY MEASUREMENTS

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Abstract

The total circumpolar abundance of Antarctic krill (*Euphausia superba*) is estimated using recent measurements of krill density from acoustic surveys and historical information on the overall range of krill. The biomass estimates fall between 60 and 155 million tonnes – at the low end of values that have been suggested in the past. The differences between our estimates and others can be explained by a number of factors such as: an underestimation of the range or the acoustic biomass estimates; the possibility of a large, undetected krill population; and the overestimation of the demand for krill by predators. Even if these low krill biomass estimates are correct, regional and total precautionary limits are still likely to rise as a result of new surveys because the method used to calculate precautionary limits uses a value of 11% of the estimated pre-exploitation biomass. Additionally, the current precautionary catch limits in the South Atlantic are set using a superseded acoustic target strength which has effectively underestimated the krill biomass by a factor of three, so the new survey of the South Atlantic in January 2000 may result in an effective biomass which is greater than the value used in the past. The seasonal and local consequences of large catch limits will have to be taken into account when managing an expanded krill fishery, and the appropriateness of using the existing statistical divisions as management areas will have to be considered.

Résumé

L'abondance circumpolaire de krill antarctique (*Euphausia superba*) est estimée à partir d'estimations récentes de la densité de krill fournies par des campagnes d'évaluation acoustique et d'anciennes informations sur l'intervalle général de densité de krill. Les estimations de biomasse varient de 61 à 155 millions de tonnes – ce qui correspond aux valeurs les plus faibles qui ont été suggérées par le passé. La différence entre nos estimations et d'autres peut s'expliquer par plusieurs facteurs tels qu'une sous-estimation de l'intervalle des estimations acoustiques de la biomasse, la possibilité qu'il existe une population nombreuse de krill non détectée et par la surestimation de la demande de krill des prédateurs. Même si ces estimations mettant en évidence une faible biomasse de krill se révèlent correctes, les limites de précaution régionales et totales sont susceptibles d'augmenter suite aux nouvelles campagnes d'évaluation, du fait que la méthode servant à calculer ces limites est fondée sur une valeur de 11% de la biomasse avant l'exploitation. De plus, les limites actuelles de précaution des captures du sud de l'Atlantique sont fixées en se basant sur une réponse d'intensité acoustique qui est dépassée et qui sous-estime la biomasse de krill par un facteur de trois, si bien que la nouvelle campagne d'évaluation du sud de l'Atlantique de janvier 2000 peut avoir pour résultat une biomasse plus importante que la valeur utilisée par le passé. Les conséquences saisonnières et locales des limites élevées de capture devront également être considérées dans la gestion d'une pêcherie de krill en expansion. Par ailleurs, il conviendra d'examiner l'à-propos des divisions statistiques existantes en tant que secteurs de gestion.

Резюме

В статье дана оценка общей циркумполярной численности антарктического криля (*Euphausia superba*) на основе последних оценок плотности криля по акустическим съемкам и ретроспективных данных по всему ареалу обитания криля. Оценки биомассы составляют между 61 и 155 млн. т, что соответствует меньшим из предполагавшихся до этого значений. Разница между нашими и остальными оценками может быть объяснена различными факторами: недооценкой диапазона акустических оценок биомассы; возможностью существования большой необнаруженной популяции криля; и завышенным потреблением криля хищниками. Даже если эти низкие оценки биомассы криля верны, по результатам новых съемок региональные и суммарные ограничения на вылов скорее всего возрастут, т.к. при расчете предохранительных ограничений на вылов используется значение 11% оценочной предэксплуатационной биомассы. Кроме этого, текущие предохранительные ограничения на вылов в южной Атлантике установлены на основе уже не используемой силы акустической цели, которая фактически недооценивала биомассу криля в три раза, поэтому новая съемка южной Атлантики в январе 2000 г. может дать реальную биомассу больше, чем использовавшееся в прошлом значение. При управлении возросшим промыслом криля надо будет учитывать сезонные и локальные последствия больших ограничений на вылов; также потребуется пересмотр целесообразности использования существующих статистических подразделений в качестве районов управления.

Resumen

La abundancia circumpolar de kril antártico (*Euphausia superba*) fue calculada utilizando estimaciones recientes de la densidad de kril de prospecciones acústicas y de datos históricos sobre la distribución general del recurso. Se ha estimado una biomasa entre 61 y 155 millones de toneladas – estimación cercana al límite inferior del intervalo de la abundancia propuesto anteriormente. Las diferencias entre nuestras estimaciones y las demás pueden deberse a varios factores, tales como: una subestimación del rango de las estimaciones acústicas de la biomasa; la posibilidad de que exista una población abundante de kril que no ha sido detectada; y la sobreestimación de la demanda de kril por sus depredadores. Aún si estas estimaciones bajas de la biomasa de kril son correctas, es probable que los límites de captura precautorios a nivel regional y total aumenten como consecuencia de las nuevas prospecciones porque el método para calcular los límites de captura precautorios utiliza un valor correspondiente al 11% de la biomasa antes de la explotación. Además, los límites de captura precautorios que se aplican actualmente en el Atlántico sur se fijan en base a una potencia acústica del blanco obsoleta que, en efecto, ha subestimado la biomasa de kril por un factor de tres, de manera que la nueva prospección del Atlántico sur en enero del año 2000 puede producir una biomasa mayor que el valor utilizado anteriormente. En la ordenación de la pesquería de kril en desarrollo, se deberán tomar en cuenta las consecuencias, tanto a nivel temporal como regional, de una aplicación de límites de captura altos, y si es apropiado utilizar las divisiones estadísticas existentes como áreas de ordenación.

Keywords: Antarctic, krill, range, biomass, acoustics, precautionary catch limits, CCAMLR

INTRODUCTION

The total circumpolar biomass of Antarctic krill (*Euphausia superba*) has been estimated using a variety of techniques. These techniques include: extrapolation from local density estimates (Hampton, 1983); estimates based on predator consumption (Mackintosh, 1973); estimates based on primary productivity (Everson, 1977); estimates of secondary production (Voronia, 1983); P:B ratios (Ross and Quetin, 1988); and the abundance of krill larvae (Brinton, 1984). Many authors cite a total krill biomass figure of 500 million tonnes (Ross and Quetin, 1988), although there have been estimates reported that vary between 14 and 7 000 million tonnes (Miller and Hampton, 1989). More recently, a combination of fisheries and scientific data was used to arrive at a total estimate of krill biomass of 272 million tonnes (Voronina, 1998). Total circumpolar krill abundance has not been surveyed quantitatively, although the *Discovery Reports* provide information on krill over much of its range (Marr, 1962; Mackintosh, 1973), and historical large surveys, such as those of BIOMASS, examined significant portions of the distribution of krill (Miller and Hampton, 1989). Recent surveys such as BROKE (Nicol, in press) and the CCAMLR 2000 Krill Synoptic Survey of Area 48 provide large-scale data using modern acoustic techniques and refined survey designs, but have been regionally based.

Direct estimates of the total abundance of krill depend on a definition of the range of the species and an understanding of the typical density values within that range. In recent years there has been considerable research into the distribution and abundance of krill, mainly at a local scale (Azzali, 1992; Hewitt and Demer, 1994; Pauly and Higginbottom, 1994; Murray et al., 1995; Pauly et al., 1996; Brierley et al., 1997), however the overall picture of krill distribution has changed little. The distribution maps produced in the *Discovery Reports* (Marr, 1962; Mackintosh, 1973) support modern ideas of where krill are to be found and where the major concentrations lie, and this has been confirmed by fisheries operations in a number of areas (Ichii, 1990).

Over the last decade acoustic methods for estimating krill density and abundance have made great progress (Everson and Miller, 1994; Everson et al., 1990), and there are now representative estimates of krill density from a variety of locations made using standardised acoustic technology (e.g. Hewitt and Demer, 1994); these estimates can be used in combination with knowledge of the overall range of krill to produce some estimates of total krill biomass.

The perception that there was an extremely large biomass of krill, and also a krill 'surplus', led to initial investigations into the feasibility of a krill fishery (Everson, 1977). In an era where most commercial stocks of marine living resources are either overexploited or are at the limits of sustainable exploitation, the prospect of an extremely large harvestable stock of krill in Antarctic waters becomes more and more attractive (Nicol and Endo, 1999). Consequently, there is a need to determine whether the extremely large krill biomass figures suggested in the past are still tenable, given the large amount of research that has been carried out around the Antarctic in recent years. This paper uses recent regional estimates of krill density together with historical information on overall krill distribution to arrive at a series of estimates of krill biomass to provide some upper and lower bounds for what might be realistic total krill abundance. These estimates are not intended to provide definitive figures for krill abundance, nor do we necessarily endorse any of them. Rather, they are presented in order to provoke further research into factors that might result in the observed discrepancy between at-sea measurements of krill abundance and those calculated from studies on land-based predators.

METHODS

The map of krill distribution produced by Marr (1962 – Figure 135, p. 394) was digitised to provide an overall range for *E. superba*. The range of krill distribution was estimated by joining the northernmost positive records of krill from the original map to indicate the northern limit of distribution and similarly, by joining the southernmost records to form the southern limit of distribution (Figure 1). This process resulted in an area of 8.4 million km^2, within which krill were reported in the *Discovery Reports* to occur during summer. This is only 62% of the estimate of the same area (13.6 million km^2) used by Miller and Hampton (1989) in a similar exercise using data from Mackintosh (1973). The area used in our calculations has not been smoothed and is therefore subject to some uncertainties, however it is likely to include all the major areas where krill are abundant in summer.

Acoustic surveys have now been carried out in a number of areas around the Antarctic (Table 2). These surveys have enabled us to subdivide the range of krill into a number of regions, some of which have been surveyed only once, but for some others there is a range of values from a number of surveys. The range of krill on the digitised map was subdivided into a number of areas. The boundaries of these areas were, in the first instance, chosen because they were the boundaries of individual acoustic surveys. For example, the boundaries of region 7 (southeast Indian Ocean) were defined by the area surveyed during the BROKE survey (Nicol, in press). Where recent large-scale survey results were not available, but where smaller-scale acoustic surveys had recently been conducted, the boundaries were set by reference to the boundaries of the CCAMLR statistical area. For example, region 5 (Peninsula) was bounded by the edges of Subarea 48.1 and includes a range of acoustic surveys which have been conducted in this subarea. For those statistical subdivisions where density information from acoustic surveys was not available, Subarea 48.6 and Area 88, the mean density from the recent BROKE survey was used. This density figure was chosen because it is the result of the only recent large-scale krill biomass survey in an area away from the known high-density areas of the South Atlantic. As such it may be an underestimate, however because it is the result of averaging over an extremely large area, it is likely to be the most appropriate figure to use for these extremely large unsurveyed areas. The estimated biomass of krill from each of the areas was then summed to give three overall biomass estimates: mean, high and low.

RESULTS

Density figures from recent acoustic surveys are highly variable, but for the South Atlantic subareas there is a large enough range of values to obtain maximum, minimum and mean figures (Table 2).

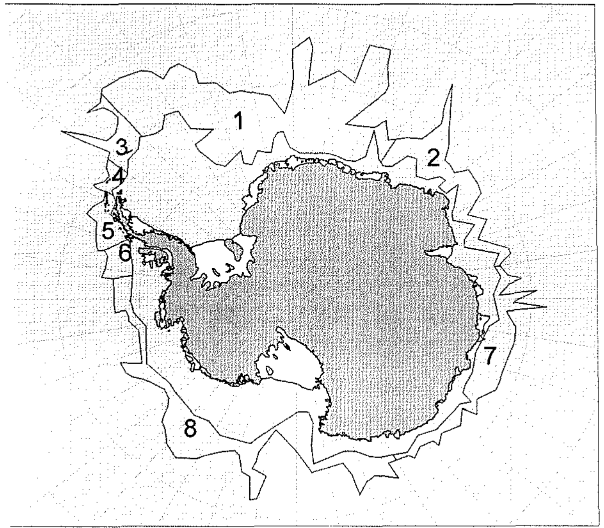

Figure 1: The distribution of *Euphausia superba* derived from digitising Figure 135, p. 394 in Marr (1962). The numbers refer to areas which were stratified for independent density estimation (see Table 1).

Table 1: Areas of the regions where krill occur on the digitised map, and estimated krill biomass for these regions based on densities from regional surveys. A mean, intermediate value, and a maximum and minimum value from each area (see Table 2) have been applied where data are available. Where only a single-density value available, or where an extrapolated value is used, the same density figure is entered in the minimum, mean and maximum column.

Region (Numbers in brackets refer to digitised map sections)	Area (million km^2)	Mean Density (tonnes km^{-2})	Mean Biomass (millions of tonnes)	Maximum Density (tonnes km^{-2})	Maximum Biomass (million tonnes)	Minimum Density (tonnes km^{-2})	Minimum Biomass (million tonnes)
Peninsula (5)	0.271	53.0	14.4	131.0	35.5	8.0	2.2
South Orkneys (4)	0.111	26.0	2.9	64.5	7.2	17.1	1.9
South Georgia (3)	0.348	49.3	17.2	151.0	52.5	1.9	0.7
Southeast Atlantic (1)*	3.94	7.6	29.9	7.6	29.9	7.6	29.9
Southwest Indian (2)	0.968	2.3	2.2	2.3	2.2	2.3	2.2
Southeast Indian (7)	0.904	7.6	6.9	7.6	6.9	7.6	6.9
Pacific (8)*	1.711	7.6	13.0	7.6	13.0	7.6	13.0
Bellingshausen (6)	0.188	30.0	5.6	42.6	8.0	19.6	3.7
Total	8.4		92.1		155.2		60.5

* Using density estimate for surveyed area of Division 58.4.1 as mean for Pacific.

Table 2: Recent acoustic estimates of krill density from around the Antarctic.

Region	Survey or Vessel	Area Surveyed ($10^3 km^2$)	Average Density ($g\ m^{-2}$)	Time of Year	Reference
Southeast Indian Ocean Division 58.4.1	BROKE	873	7.65	February–March (1996)	Pauly et al., 1996
South Atlantic	FIBEX			January–February (1981)	Trathan et al., 1992
Area 48		0.75	48.9		
Subarea 48.1		2.83	37.24		
Subarea 48.2		2.42	64.52		
Subarea 48.3		0.25	59.73		
Subarea 48.6		5.76	8.03		
Southwest Indian Ocean Division 58.4.2	FIBEX	17.11	2.29	Summer (1981)	Trathan et al., 1992
South Orkneys Subarea 48.2	RV *Atlantida*	65.9	17.1 26.3 (corrected for vertical migration)	Summer (1996)	Kasatkina et al., 1998
South Georgia	Summary of 16 acoustic surveys, 1981–1998	various	1.87–150.99 mean 49.28	Various	Brierley et al., 1999
Elephant Island area	US AMLR Program	36.3 7.2 7.2 36.3	61.2 101.27 28.9 29.63	January February (early) February (late) March (1992)	Hewitt and Demer, 1993
Elephant Island area (18 surveys between 1983 and 1993)	US AMLR Program	17.4–43.5	8.4–134.5	November–March (1983–1993)	Hewitt and Demer, 1994
Bellingshausen Sea	STERNA	18.4 (approx.) 14.5 (approx.)	42.6 19.6	November December (1992)	Murray et al., 1995
South Shetland Islands	RV *Kaiyo Maru*	73.6		January–February (1992)	Ichii et al., 1998
Oceanic		44.0	8		
Frontal		17.2	36		
Inshore		10.3	27		
Close inshore		2.1	131		

Table 3: Areas of the CCAMLR statistical divisions and the percentage of these divisions in which krill are assumed to occur.

CCAMLR Statistical Area	Subarea/ Division	Area (km^2)	% of CCAMLR Area	% of Area Containing Krill*
48	48.1	595 490	1.8	45
	48.2	851 860	2.6	13
	48.3	1 029 000	3.1	34
	48.4	940 430	2.9	53
	48.5	1 519 610	4.6	0
	48.6	6 553 340	19.9	53
	Total	11 489 730	34.9	41
58	58.4.1	4 680 930	14.2	20
	58.4.2	1 038 820	3.1	93
	58.4.3	903 880	2.7	0
	58.4.4	2 484 500	7.6	0
	58.5	1 587 500	4.8	0
	58.6	835 050	2.5	0
	58.7	417 530	1.3	0
	Total	11 948 200	36.3	16
88	88.1	2 612 020	7.9	24
	88.2	4 600 180	14.0	24
	88.3	2 238 460	6.8	8.4
	Total	9 450 660	28.7	20
CCAMLR Area Total		32 888 590	100	25.5

* This percentage is derived from the area digitised from the *Discovery Reports* map.

Some areas are only poorly covered (e.g. the Bellingshausen Sea and South Orkneys), so only two density estimates are available. Some other areas have only been surveyed once and others have never been surveyed. These surveys have associated with them coefficients of variation, however there is no consistency in their presentation in the publications from which these density figures have been extracted. Nonetheless, it is possible to allocate a density estimate or a range of density estimates to each of the defined areas, which is sufficient for the purposes of the exercise. Applying the reported density figures to each of the eight areas on the digitised map results in an overall mean biomass of 92.1 million tonnes (Table 1). Using the highest estimates of density from Table 2 for each region gives an overall biomass figure of 155.2 million tonnes, while using the lowest estimates of density from Table 2 for each region gives an overall biomass of 60.5 million tonnes.

In terms of the distribution of krill biomass, much of the uncertainty arises because of the lack of reliable data for the very large parts of the CCAMLR area for which there are no recent, reliable, standardised krill biomass estimates, viz. Subarea 48.6 (the Southeast Atlantic ~20% of the total area), and Divisions 88.1 and 88.2 (the Pacific Ocean sector ~22% of the CCAMLR area). These statistical subdivisions contain large areas where, according to the distributional maps in the *Discovery Reports* (Figure 1), krill is abundant (Table 3).

DISCUSSION

The estimates of total krill biomass that we calculated, and the earlier attempts to arrive at an estimate using similar techniques, are all less than the widely quoted figure of 500 million tonnes. Our estimate of the overall range of krill is not inconsistent with earlier approaches. We used density figures from small, krill-rich areas and extrapolated them to larger areas. This should yield an upper limit on the range of possibilities given present knowledge of krill density and range, but still results in a figure lower than 500 million tonnes. Given recent advances in understanding krill density and its distribution, these lower figures are probably more realistic.

Miller and Hampton (1989) extrapolated the FIBEX results over the zones where krill were reported in the *Discovery Reports* (13.6 million km^2), obtaining what they considered to be a conservative estimate of 41 million tonnes for total biomass. They also used the mean FIBEX density estimate of 2.49 g m^{-2} over the area enclosed by the 0°C isotherm (9.08 million km^2) (Naganobu, 1986) to give a biomass figure of 23 million tonnes. These figures would be some three times higher if more recent figures for krill target strength were used (Everson et al., 1990; Greene et al., 1991; Hewitt and Demer, 1991). The values from the calculations by Miller and Hampton (1989) are similar to ours (approximately 71–123 million tonnes corrected for the revised krill target strength value), and they go into considerable detail on the possible reasons for the discrepancy between their results and the estimated consumption of krill by predators (250 million tonnes year^{-1}). Possible reasons for this mismatch include: bias in the acoustics (partially rectified by the change in target strength (Everson et al., 1990)); the possibility of a large, undetected krill population that is either too deep, too shallow or too dispersed; and the overestimation of the demand for krill by predators (Miller and Hampton, 1989).

A recent estimate of total krill biomass was made using a combination of fisheries data, which were used to estimate the spatial extent of krill and to stratify the area according to density, and scientific net hauls to estimate density within the zones defined by the fishery data (Voronina, 1998). The estimate of krill biomass was 272 million tonnes, most of which was found in the 'zone of regular occurrence of dense concentrations'.

Two factors could seriously affect our estimates of total krill biomass: incorrect identification of the range of krill and inappropriate density figures.

Range of Krill

It is unlikely that the area of high krill abundance has been greatly underestimated in our calculations. Acoustic surveys in a number of areas (Bellingshausen Sea, Antarctic Peninsula, South Georgia, Enderby Land, Prydz Bay, Wilkes Land, Ross Sea) have confirmed that *E. superba* is largely found in the shelf/slope front area except in the Weddell–Scotia Arc (Table 1). This has been confirmed by information from the fishery (Ichii, 1990). There have been no reports of significant concentrations of krill being regularly found in areas that were not identified in the *Discovery Reports*. Much of the CCAMLR area north of 62°S (with the exception of the Weddell–Scotia Arc) appears devoid of significant concentrations of krill. It would take a doubling of the range at high levels of density to obtain a biomass estimate greater than 500 million tonnes and this is probably unrealistic.

The largest recent survey in the Convention Area was the survey of CCAMLR Division 58.4.1 (Pauly et al., 1996). This survey covered an area of 873 000 km^2, which was the portion of Division 58.4.1 in which *E. superba* was found to be abundant and can be considered to be a conservative estimate of the summer range of krill in the southeast Indian Ocean sector. The digitised section of the *Discovery Reports* map indicated that in the southeast Indian Ocean sector krill were found over 940 000 km^2, an estimate of range that is only 8% larger than that estimated from the acoustic survey. This general agreement between surveyed area and the area digitised from the *Discovery Reports* map indicates that the approach used to arrive at an estimate of the summer range of krill may provide a realistic result, and that the stratified krill biomass estimates may be similarly realistic, particularly for those areas where recent krill density estimates are available.

Mackintosh (1973) provides some estimates of the range of krill by season. His estimate for the zone within which krill occur from October to December is 19.24 million km^2, whereas he envisioned it contracting to 15.43 million km^2 from January to March. Mackintosh also indicated an 'area of higher density' of 3.23 million km^2. Miller and Hampton (1989) cited a figure for the range of krill of 13.6 million km^2 derived from Mackintosh (1973), yet a much greater distributional range of up to 32 million km^2 is often cited.

The summer range of krill defined by fishery data (Voronina, 1998) suggests that krill are 'abundant' in an area of 3.84 million km^2, krill concentrations are 'rare' in a further 8.64 million km^2, and krill are 'in low abundance' in the remaining 19.5 million km^2 south of the Polar Front. The densities defined for these three areas are: 60.1 tonnes km^{-2}, 3.3 tonnes km^{-2} and 0.8 tonnes km^{-2} respectively. Our estimate of the region where krill is abundant is 8.4 million km^2, although the range of densities we have used would probably include much of the area defined as the 'zone of rare occurrence of krill concentrations' (Voronina, 1998), and this is confirmed from the map in Figure 1. The comparable area, encompassing the two highest density zones, is 12.44 million km^2, some 50% above our estimate of range derived from the *Discovery Reports*. The overall biomass figure of 272 million tonnes from the fishery-derived range is thus higher than our stratified estimates.

Some of the larger estimates of krill biomass have resulted from the use of a range which is probably too great. The earlier viewpoint that krill were found in high density throughout the region to the south of the Antarctic Convergence (some

35.8 million km^2) resulted in biomass estimates of the order of 600 million tonnes (Hampton, 1983). Since this estimate of range is some four times the area that we used in our calculations, it is not surprising that our estimates of total krill abundance are a quarter of those that used this larger range.

Density

The estimates of density used are the best available and take into account the range of values from recent surveys in numerous areas. Acoustic surveys have been conducted regularly in some areas for nearly 20 years, and there is now a good appreciation of the range of acoustically estimated densities that are found in these areas (Hewitt and Demer, 1994; Brierley et al., 1999). To alter the total biomass figure upwards would require that the density in the areas where krill is most abundant is being underestimated by a considerable amount, either because of errors in the acoustic methodology itself or through inappropriate survey design. There is no direct evidence of systematic errors in either of these two factors but current research may help to clarify their precision and accuracy. The only current alternative to the acoustic estimates of density is estimates derived from nets, and these generally give even lower biomass values (Miller and Hampton, 1989), although densities derived from scientific nets were also used in a recent estimate of total krill biomass (Voronina, 1998). Surface swarms of krill have been reported to contain up to 154 kg m^{-3}, however most estimates fall between 10 and 1 000 g m^{-3} (Miller and Hampton, 1989). Even so, these sorts of densities are higher than those regularly recorded by acoustics even within dense subsurface swarms. Underwater photographs of subsurface aggregations of krill reveal that they can be closely packed (Guzman, 1983; Hamner et al., 1983), but few attempts have been made to relate acoustic measurements of krill density with those obtained by photographic means. Acoustic estimation of krill abundance has been subject to considerable research over the last 20 years (Greene et al., 1998), and it is difficult to imagine that this technique is underestimating krill density by a factor of 2 to 4, which is what would be necessary to match the predator demand to our lower estimates of total krill abundance.

There are a number of other factors that could affect the estimate of either the range or density of *E. superba*.

'Background Krill'

It has been argued that krill occur throughout the CCAMLR area in very low densities which may not be detected by acoustics (Miller and Hampton, 1989). If we assume that the background level is of the order of 1 tonne per km^{-2}, which is not an especially low density, then the addition to the total biomass estimate for the CCAMLR area from this 'background krill', if it were regularly distributed, would only be 33 million tonnes. It would require a 'background density' of krill in the oceanic areas greater than the estimates of density in the shelf/slope region of the southeast Indian Ocean sector to make sufficient difference such that the estimate of overall krill biomass approached 500 million tonnes. This seems unlikely.

Krill Refuges

It is possible that a significant proportion of the krill population remains under fast-ice and ice shelves during summer and is thus not surveyed by conventional hydroacoustic surveys and was not surveyed by nets during the 'Discovery' expeditions. Ice shelves and fast-ice occupy only 4 million km^2, so the biomass estimates would only increase marginally if these ice-covered areas indeed served as refuges – even if krill there were at high density. There is mounting evidence, however, that in more coastal areas *Euphausia crystallorophias* replaces *E. superba* as the dominant species of euphausiids (Nordhausen, 1992; Hosie and Cochran, 1994), so it seems unlikely that residual fast-ice is a significant refuge for *E. superba* in summer.

Surface Krill

E. superba is known to form surface swarms (Marr, 1962; Mackintosh, 1966; Hampton, 1981) and in some areas it also performs pronounced diurnal vertical migrations which bring it into the surface layer at night – out of the range of downward, hull-mounted acoustic transducers (Arimoto et al., 1979; Everson, 1983; Marschoff et al., 1998). There is evidence that vertical migration by krill may differ between seasons or regions (Pauly et al., in press). Attempts have been made to correct the results of acoustic surveys to account for this potential bias (Demer and Hewitt, 1995), but there is no general consensus on the magnitude of this potential bias, which would tend to result in an underestimate of regional density. The surface layer is also the region which is of greatest importance to land-based krill predators (Croxall et al., 1985; Boyd, 1996), so underestimation of krill abundance in this layer has important implications.

Indirect Approaches to Estimating Krill Biomass

A variety of approaches, including P:B ratios, have been used to estimate total krill production from estimates of primary production, krill consumption and larval abundance (Ross and Quetin, 1988). Ross and Quetin were able to narrow the estimates of production from 75–1 350 million tonnes per year (a factor of 20) to 100–500 million tonnes per year (a factor of 5). An earlier combination of estimates of secondary production with a stratification of the Southern Ocean into krill-dominant areas and krill-poor areas resulted in a total biomass estimate of 60–100 million tonnes (Voronia, 1983).

Predators

Over the last decade there has been considerable research into the size of land-based krill predator populations, the diets of these predators and overall krill requirements in certain areas (Croxall et al., 1990; Everson and de la Mare, 1996; Woehler, 1997). Although there has been some evidence that many species feed on species other than krill, there has also been a consolidation of knowledge about those predators which do consume large quantities of krill, both locally and totally. There has not, however, been any recent attempt to refine the estimates of total krill consumption by land-based predators. A major gap in knowledge is the consumption of krill by marine-based animals: cetaceans, pack-ice seals, fish, and squid and other invertebrate predators. Mackintosh (1973) worked backwards from the area in which he saw krill being available for whales (16.7 million km^2), and, using an estimate of krill consumption by baleen whales (175.1 million tonnes), arrived at a production of krill of 10.5 g m^{-2} over the whole feeding season. Calculations of the estimated annual consumption of krill by the Antarctic population of minke whales (*Balaenoptera acutorostrata*) produced figures between 35.5 million tonnes (Armstrong and Siegfried, 1991) and 140 million tonnes (Ichii and Kato, 1991). Some of the krill consumed by minke whales may in fact be *E. crystallorophias* rather than *E. superba*, particularly in areas such as the Ross Sea (Ichii et al., 1998), but these consumption figures still amount to a significant portion of the biomass of krill that we have estimated. A better estimate of pack-ice seal abundance will result from the results of the Antarctic Pack-Ice Seals (APIS) Program, and this will hopefully result in a better estimate of annual krill consumption. Consumption of krill by squid and fish is unlikely to be better quantified in the near future.

Precautionary Catch Limits

The model used by CCAMLR to set precautionary catch limits currently uses a figure of 0.116 of the estimated pre-exploitation biomass as the annual allowable catch (Everson and de la Mare, 1996). Current precautionary catch limits for the entire CCAMLR area total 2.725 million tonnes per year. The precautionary catch limit (1.5 million tonnes per year) for Area 48, based on surveys in Subareas 48.1, 48.2 and 48.3, has not been corrected for the revised target strength estimate, but if it were it would be 4.5 million tonnes. The current precautionary catch limit of 1.5 million tonnes for Area 48 would result from a biomass of krill in this area of only 12.9 million tonnes, one third of the 34.5 million tonnes – the mean value derived from estimates of known density. Krill biomass in the southern Atlantic will be clarified as a result of the CCAMLR 2000 survey of Area 48, which will provide synoptic estimates of krill density and distribution throughout much of the South Atlantic and will result in the calculation of new precautionary limits for this area. If the results of our calculations are borne out through the survey, then a precautionary catch limit of around 4.5 million tonnes for Subareas 48.1, 48.2 and 48.3 is not impossible.

A summed precautionary catch limit for the krill fishery throughout the CCAMLR area is likely to be very large, even if our lower estimates of overall biomass are correct, with values of between 7 and 18 million tonnes per year. Given the way in which the precautionary catch limits are calculated and the large (though perhaps somewhat less large than previously thought) size of the krill stock, the allowable catches are also always going to be large. The key to management of this fishery, then, will be in the way in which the fishery effort is distributed – both by area and by season – to ensure that large quantities of krill are not taken out of restricted areas to the long-term detriment of the ecosystem.

Currently, the krill fishery is managed by instituting precautionary catch limits by statistical division. These divisions can vary markedly in area and in the proportion of each area in which krill occurs (Table 3), and it is apparent that in many cases the statistical divisions are much larger than is appropriate for the purposes of managing the krill fishery. In most of the areas currently fished, and in those areas which have been fished in the past, we know enough about the distribution of krill to begin the process of subdividing these large areas into more suitable management areas (Everson and de la Mare, 1996). Such a process of subdivision would go some way to ensure that the basic principles outlined in Article II of CCAMLR's Convention are not being violated.

CONCLUSIONS

The calculations presented, based on the available estimates of krill distribution and abundance, seem to indicate that a total krill biomass of under 155 million tonnes may be more realistic than one as high as 500 million tonnes. This is actually consistent with many other estimates of total krill abundance which have resulted from density or production estimates and realistic assumptions of the range of krill. In January 2000, krill biomass and distribution in the South Atlantic will be clarified as a result of the CCAMLR survey of Area 48, which will clarify estimates of krill density and distribution throughout much of the South Atlantic and will result in the calculation of new precautionary limits for this area. Our results indicate that the calculated precautionary catch limit is likely to be higher than the current 1.5 million tonnes per year. Further, our results confirm the discrepancy between estimated krill abundance and estimated predator demand on a global scale, but are unable to determine whether the cause of this discrepancy is a result of underestimates of krill abundance or overestimates of krill consumption. Suggested areas where significant improvements in estimates of total krill abundance can be made include: further ground-truthing of acoustic estimates of density, quantification of the proportion of krill in the surface layer, determination of acoustic biomass and distribution patterns for krill in large unsurveyed areas (i.e. Subareas 48.6, 88.1 and 88.2), refined Antarctic-wide estimates of land-based predator krill consumption and improved estimates of crabeater seal, fish and squid abundance and krill consumption.

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