A comparison of Antarctic krill *Euphausia superba* caught by nets and taken by macaroni penguins *Eudyptes chrysolophus*: evidence for selection?

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ABSTRACT: Using stomach lavage samples from macaroni penguins *Eudyptes chrysolophus* Brandt breeding at Bird Island, South Georgia and concurrent net samples caught within the penguin foraging range, we examined the potential selection of different length and maturity stages of Antarctic krill *Euphausia superba* Dana. Using Monte Carlo randomised simulation techniques, we also determined the probability of obtaining length-frequency distributions of krill different from that obtained in the net samples. The krill taken by the macaroni penguins differed significantly from those caught in the nets. Small krill (28 to 38 mm) were absent from the stomach samples, whereas large krill (58 to 62 mm) were more abundant. Random sampling using Monte Carlo simulation techniques produced length-frequency distributions that were statistically different from the original distribution of krill caught in nets on 76 out of 100 trials. Nevertheless, these differences were smaller than those found between the penguin samples and net samples. Comparison of krill maturity stages showed that krill taken by macaroni penguins contained 3 times as many female as male krill, whereas krill caught in nets contained nearly equal proportions. The differences in size and maturity of krill taken by penguins are discussed in terms of aggregated random sampling, prey selection by predators, and evasion by krill of predators and nets. We conclude that the differences are unlikely to be accounted for simply by sampling anomalies; the differences are more likely to relate to penguins selecting larger, nutritionally superior krill, but might also reflect differential escape responses of particular classes of krill when evading penguins or nets.

KEY WORDS: *Euphausia superba* · Antarctic krill · *Eudyptes chrysolophus*   Macaroni penguin · Predation · Selection

INTRODUCTION

Antarctic krill *Euphausia superba* are a major food source for many Southern Ocean marine predators (Croxall et al. 1985, Trathan et al. 1995). At the subantarctic island of South Georgia one of the most common avian predators dependent upon krill is the macaroni penguin *Eudyptes chrysolophus* with breeding populations of about 5 million pairs (Croxall & Prince 1979). The macaroni penguin, whose diet typically contains 98% krill and 2% fish by mass (Croxall

& Prince 1980, 1987, Croxall et al. 1988a), is estimated to take more than 50% of the krill consumed by marine top predators in the South Georgia region (Croxall et al. 1984).

Krill are also the target of an important commercial fishery which currently operates around South Georgia, mainly during the austral winter (Everson & Goss 1991) but also during the summer in some years (CCAMLR 1993). Commercial fishing during the breeding season may result in increased competition for resources and might therefore have important consequences for macaroni penguins, especially when they are foraging to feed chicks.

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Understanding the spatial and temporal distribution of krill and their interactions with natural and human predators is therefore of considerable importance. Information on the precise size and maturity of krill taken by natural predators as well as on the size and maturity of krill caught by fishing nets is necessary to understand any direct competition for resources. However, in making comparisons between krill caught in nets and krill taken by penguins, several biases must be taken into consideration. For example the following are likely to be important: spatial and temporal variability of predators and prey (Croxall et al. 1985), variability in the composition of krill swarms (Watkins 1986, Watkins et al. 1986), avoidance of nets (Everson & Bone 1986, Hovekamp 1989), avoidance of predators, selection of prey, as well as digestion of prey (e.g. Croxall et al. 1988b, Williams 1990, Jackson et al. 1992).

In this paper we attempt to address some of these biases in a study that compares krill caught by scientific sampling nets with krill taken by foraging macaroni penguins. The study was located to the northwest of South Georgia during the macaroni penguin breeding season. During this period stomach lavage samples could be collected at the same time that scientific nets were being used by the British Antarctic Survey research ship RRS 'John Biscoe'. Specifically we aimed to compare the precise characteristics of krill caught by nets with those taken by predators. Using Monte Carlo randomised sampling, we also attempted to examine

the probability of obtaining a sample distribution of krill that differed from the local population, particularly where variability exists in the composition of krill swarms.

METHODS

In this study, one of us (H.J.H.) made all maturity stage assessments and length measurements on all the krill caught by the nets and all the krill from the stomach lavage samples, thus eliminating observer variation between samples (cf. Watkins et al. 1985).

Krill caught in nets. During February 4 to 24, 1986 a series of radial transects was carried out around Bird Island at the northwestern end of South Georgia. The survey encompassed the range of macaroni penguins foraging from the colonies at Bird Island (Croxall & Prince 1987), and comprised transects of approximately 140 km centred at 54°00.3' S, 38°10.2' W The distribution of birds at sea along these same transects has already been described by Hunt et al. (1992). During the survey period, a multiple 8 m^2 rectangular midwater trawl (RMT8) (Baker et al. 1973, Roe & Shale 1979) was used at night to sample for krill (Fig. 1). The RMT8 was towed at an average speed of 2.5 knots and used to sample the top 100 m of water (a few sampling to a depth of 130 m) thus including the dive depth range (median during day, 20 to 34 m with a maximum of 115 m; median during night, 5 m with a maximum of
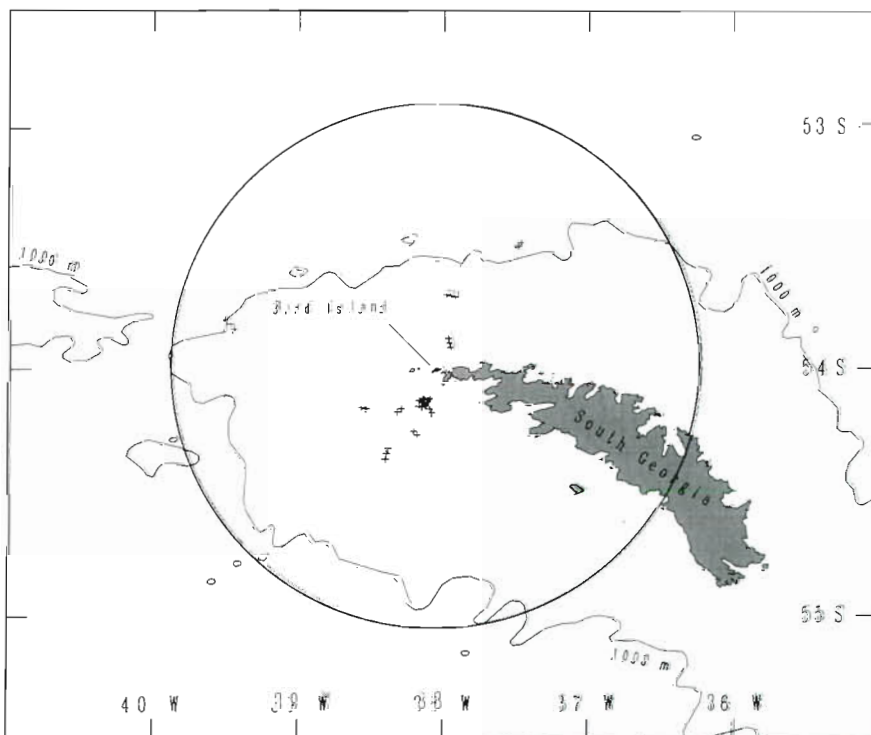

Fig. 1 Location of study site showing the maximum potential foraging range of macaroni penguins from Bird Island (120 km). Positions of RMT8 net samples are indicated by crosses

11 m) of macaroni penguins (Croxall et al. 1993). After every haul each net was randomly sampled and the krill fixed in 4% formaldehyde in seawater. In the laboratory the net samples were washed into a 350 µm mesh sieve and rinsed with freshwater. A random sub-sample of up to 100 intact, well preserved krill was taken (cf. Watkins et al. 1986). Krill maturity stage was assessed for each individual according to the key of Makarov & Denys (1981) but using the nomenclature of Morris et al. (1988). Total length (AT) was measured from the front of the eye to the tip of the telson, to the nearest millimetre below (Lockyer 1973). This is an accuracy of about 3.5% for the smallest measurement (28 mm), and is within the maximum of 5% suggested by Bird & Prairie (1985).

Krill caught by macaroni penguins. At weekly intervals during February 5 to 26, 1986 the complete stomach contents of 10 macaroni penguins returning to feed chicks at Bird Island, South Georgia were obtained using stomach lavage techniques (Wilson 1984). The lavaged material was drained into a sieve, weighed and fixed in 4% formaldehyde in seawater. In the laboratory the stomach samples were washed into a 350 µm mesh sieve, rinsed with freshwater and floated into a sorting tray. Prey items were picked out with fine forceps, identified and counted. Few krill were sufficiently intact to directly measure their AT length, so the removed carapace length (RC) measurement of Hill (1990) was used. To obtain the RC length measurements a subsample of up to 100 was randomly selected from all measurable krill in the sample. Two criteria were used to determine whether an individual krill was measurable: firstly, that it had an intact carapace, and secondly, that the first abdominal segment was still attached to the cephalothorax. For each selected krill, the carapace was detached and the RC length measured with a binocular microscope to the nearest eyepiece unit below (an accuracy of around 1%). The RC length measurements were then used to derive AT length using the regression method of Hill (1990). Hill (1990) provides a number of regression equations covering individual krill maturity stages, as well as a single equation covering all stages. The generic regression equation covers maturity stages not covered separately and was therefore used in this study. Thus, the regression equation $AT = 11.56 + [2.44 \times RC]$ was used to estimate AT length. The krill measurements used to calculate the regression equations in Hill (1990) were net caught animals taken in the vicinity of South Georgia during the same month and year as those in this paper. The maturity stage of each selected krill was also assessed (as described above for the net samples), but the stages FA2 to FA5 (females with spermatophores, gravid females and spent females) were not separated into individual classes.

Modelling predation by Monte Carlo randomised sampling. A computer simulation using the AT lengths obtained from the 35 nets which caught more than 30 measurable krill was carried out to investigate the consequences of different sampling protocols. For the purposes of the simulation the contents of the nets were assumed to represent the full size range of krill available to the macaroni penguins.

Hauls were fished for only a short duration and each net contained krill from 1 or a very limited number of swarms. Therefore, in the simulation the distribution of krill caught by an individual net was assumed to represent the distribution in a single swarm. Thus, these data were used to simulate the effects of predation on a krill population subdivided into heterogeneous assemblages with differing length and maturity stage characteristics. However, variation between swarms with respect to length-frequency distribution and maturity stage distribution has been shown to be considerable (Watkins et al. 1992) and 35 nets (taken as being equivalent to swarms) may not represent adequately the full amount of subdivision found within the real population. Furthermore, as each net may have sampled more than 1 swarm, there may be a further underestimation of the degree of subdivision in the real population. Thus, the actual degree of swarm segregation may be different from that represented by the nets. Despite this possible underestimation, the net data can still be used to determine whether subdivision has important consequences for predator foraging, even though it cannot necessarily be used to determine the magnitude of the importance.

Small numbers of macaroni penguins have been recorded in multi-species feeding aggregations (Harrison et al. 1991) and penguins from a single aggregation may take prey which are more alike than prey taken by penguins from different aggregations. If stomach lavage samples were taken from penguins which were foraging in the same feeding aggregation, then the degree of variability in the prey population would be underestimated. In the absence of data describing the membership and size of feeding aggregations of macaroni penguins, and the degree to which these associations vary, we have assumed that these factors were random. Given the number of stomach lavage samples (n = 39) in relation to the size of the macaroni penguin population at Bird Island (ca 90 000 breeding pairs), this assumption is probably reasonable. In the simulation, the size of the macaroni penguin aggregation was restricted to a maximum of 10 birds, the number of stomach lavage samples taken on the majority of sampling dates.

Hence, from the sample population of 35 swarms a single swarm was selected and randomly sampled (with replacement) for 75 krill; this was repeatedly carried out a random number of times (maximum 10)

in order to simulate the size of the predator feeding aggregation. Subsequently, other swarms were selected and sampled until a total of 3000 krill had been taken, a number approximately equal in size to the combined macaroni penguin stomach samples. This process was carried out 100 times. In order to test the results of the simulation, Kolmogorov-Smirnov 2-sample tests were used to compare the length-frequency distributions generated by the simulation program with the length-frequency distribution derived from the original combined net samples.

RESULTS

Length of krill caught in nets and by macaroni penguins

During the period February 4 to 24, 1986 68 nets were fished in the vicinity of South Georgia. Some of these nets contained very few krill, so a sample size of 30 measurable krill was chosen as a compromise between including as many samples as possible, and not biasing the samples with distributions from very small sample sizes. Of the 68 nets, 35 provided more than 30 measurable krill (n = 3395) and were within the 120 km near-maximum foraging range of the Bird Island macaroni penguins (Croxall & Prince 1987). The mean AT length from the 35 nets was 53.1 mm (SD = 5.36, range = 28 to 65 mm).

During the same period, 39 macaroni penguin stomach lavage samples were taken that contained krill; of these 31 provided more than 30 krill from which RC measurements could be made (n = 2519). After transformation of the RC length by regression, the mean AT length was 55.4 mm (SD = 4.21, range = 39 to 64 mm).

The large numbers of krill measured from the nets and from the stomach samples allowed a valid comparison of their length-frequency distributions (Fig. 2). Small krill in the range 28 to 38 mm were absent from the macaroni penguin stomach samples, whereas larger krill in the range 58 to 62 mm were more frequent than in the nets. A Kolmogorov-Smirnov 2-sample test indicated that the length-frequency distribution of krill caught in the nets was significantly different ($D = 0.24$, $p < 0.01$) from the length-frequency distribution of krill taken from the stomach samples.

The variation in AT lengths of krill caught in individual nets, or taken by individual macaroni penguins, is shown in Fig. 3a, b respectively. In addition, the relative magnitude of the variance components calculated for krill caught in nets and krill taken by pen-
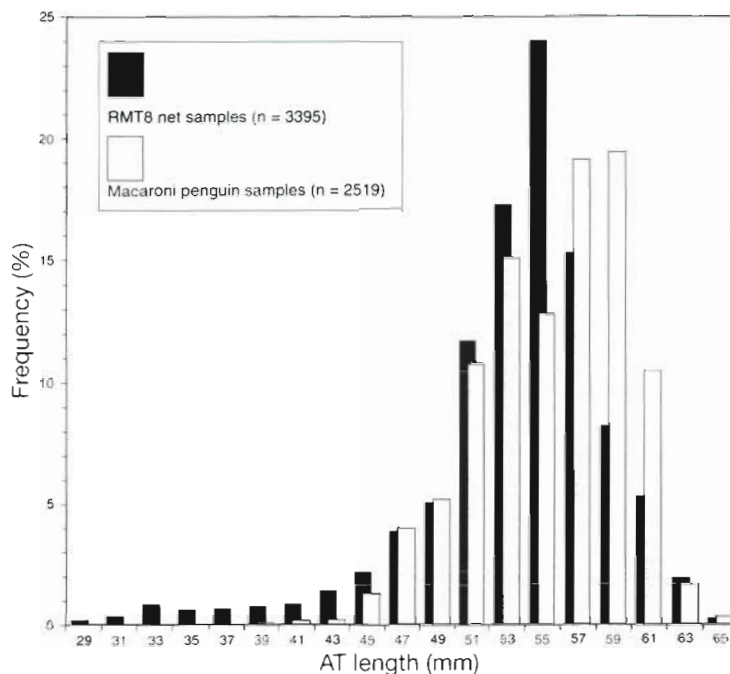

Fig. 2. AT length-frequency distribution of krill from samples where the sample size >30 krill for RMT8 net samples and macaroni penguin stomach lavage samples

guins are shown in Table 1. The variance of krill caught in nets was greater than that for krill taken by penguins, but in each case more variation was observed within nets, or penguins, than between them. Although the percentage of variation between nets, or penguins, was low, it was possible to examine this component in more detail. Thus, for the net samples it was possible to calculate the variation within hauls, as up to 3 nets were fished in a single haul, as well as the variation between hauls. Both levels of variation were found to be significant. For the macaroni penguin stomach samples, it was possible to calculate the variation between the 4 sampling dates, as well as between the 2 penguin sexes. The difference between sampling dates was found to be significant, whereas the difference between penguin sexes was not. These results suggest that small scale spatial (and/or temporal) variability was important in both the net samples and the penguin stomach samples. Such heterogeneity has been found for krill caught in other areas, for example the Bransfield Strait (Watkins et al. 1986)

As the nets sampled slightly different depths, it was possible to test whether vertical variability was also important. No evidence of structured vertical stratification was found when the mean AT lengths for individual nets were compared to the minimum, maximum and mid-depth of fishing. For example, in the mid-depth, classified into the ranges 0 to 50, 50 to 75 and 75 to 125 m, the mean AT lengths of krill were respectively
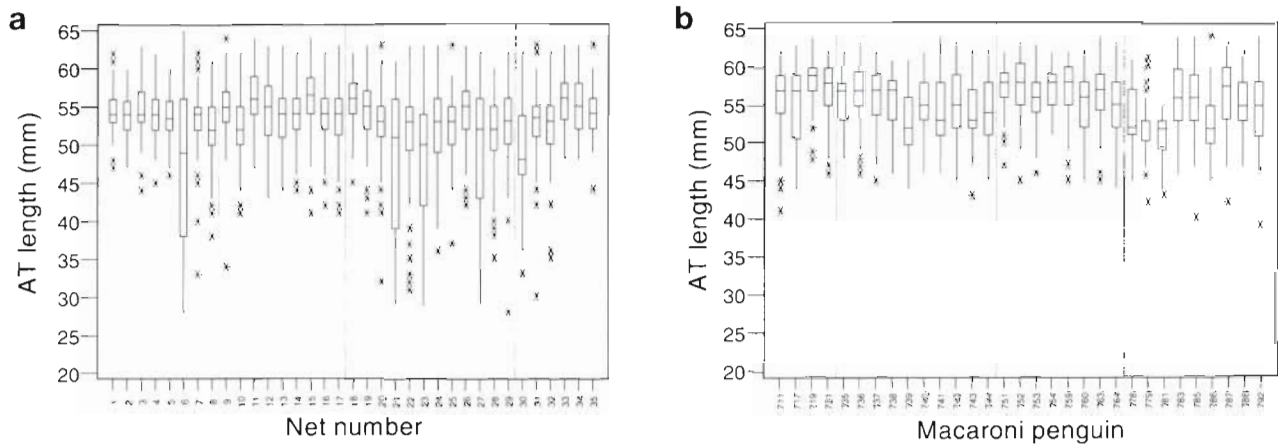
Fig. 3. AT length from krill samples where the sample size >30 krill. Thin vertical lines divide the samples into weekly groups. (a) RMT8 net samples and (b) macaroni penguin stomach lavage samples. The horizontal line across each sample represents the median, the bottom of the box is at the first quartile (Q1) and the top is at the third quartile (Q3). The whiskers extend to the lowest and highest observations still inside the regions defined by Q1 – 1.5 (Q3 – Q1) and Q1 + 1.5 (Q3 – Q1) respectively. Outliers beyond these limits are shown as asterisks

52.3 (SD = 5.77), 53.7 (SD = 4.75) and 52.7 (SD = 5.85) mm. Similarly, as the nets were sampled at different distances from Bird Island, it was also possible to test whether structured horizontal variability was important. No evidence of stratification was found when the mean AT length of krill sampled from nets fished close to Bird Island was compared with that from nets fished further offshore. Thus, dividing samples into those taken closer than 30 km and those taken further away than 30 km, the mean AT lengths of krill were respectively 52.9 (SD = 5.39) and 53.4 (SD = 5.27) mm.

Modelling predation by Monte Carlo randomised sampling

Kolmogorov-Smirnov 2-sample tests showed that on 24 of the 100 runs of the simulation program the generated length-frequency distribution was not signifi-

cantly different from the original net samples, with $D < 0.03$ and $p > 0.05$; however, on 76 runs a statistically significant difference was found, with $D > 0.03$ and $0.01 < p < 0.05$ (4 runs) or with $D \geqslant 0.03$ and $p < 0.01$ (72 runs). The maximum absolute difference recorded was $D = 0.20$, which was much lower than the maximum absolute difference found between the length-frequency distribution of krill caught in nets and the length-frequency distribution of krill taken from stomach samples (see above).

The large number of simulation runs that showed a statistically significant result suggest that the subdivided structure of both the krill population and the macaroni penguin population imposes limits on the validity of comparing the krill caught in nets and the krill taken by penguins. In the sea, where the levels of variation are potentially greater than those found in our samples, random predation coupled with simple behavioural patterns may generate significant differ-

Table 1. Analysis of variance of krill AT lengths from RMT8 net samples and macaroni penguin samples

Factor	df	SS	MS	F	p	% variation
RMT8 nets						
Between hauls	13	12699.8	976.9	40.86	<0.001	13.0
Between nets within hauls	21	4271.7	203.4	8.51	<0.001	4.4
Residual (within nets)	3360	80338.0	23.9			82.6
Totals	3394	97309.6				100.0
Macaroni penguins						
Between sampling dates	3	3078.2	1026.1	68.7	<0.005	6.9
Between sexes of penguins	1	198.2	198.2	13.3	NS	0.4
Between penguins	26	4178.2	160.7	10.8	<0.001	9.4
Residual (within penguins)	2488	37167.1	14.9			83.3
Totals	2518	44621.7				100.0

ences between the length-frequency distribution of prey taken and the length-frequency distribution of the prey population.

Distribution of male, female and juvenile krill

The ratio of male krill to female krill was very different when the krill caught in nets were compared to the krill taken by the macaroni penguins (Table 2). Similar numbers of males and females were caught in nets (1:0.9), but the number of females was much higher (1:2.7) for the krill caught by penguins. Krill with juvenile characteristics were all smaller than 53 mm and comprised only a small percentage of the samples.

The AT length distributions of male, female and juvenile krill caught in nets and caught by macaroni penguins are shown in Fig. 4a, b respectively. The plots indicate that female krill were generally longer than male krill, and also that a greater proportion of females were taken by the penguins than were caught in the nets. Krill sampled in the AT length range of 46 to 62 mm provided at least 30 measurements in each length class, and the proportion of males to females in each class is shown in Fig 5. This plot indicates that for the AT length classes without krill with juvenile characteristics (i.e. greater than 53 mm), macaroni penguins consistently took a higher proportion of female krill than were caught in the nets, even in those length classes where the proportion of female krill was low. A sign test showed that for krill greater than 53 mm, the difference between the 2 distributions was highly significant ($p < 0.01$, $n = 10$).

The maturity stages of krill caught in the nets and taken by the macaroni penguins were different ($\chi^2 = 868.34$, $df = 4$, $p < 0.001$), with very few adult male krill (MA) in the stomach samples (Table 3). Thus, even though subadult male krill (MS) were found in similar
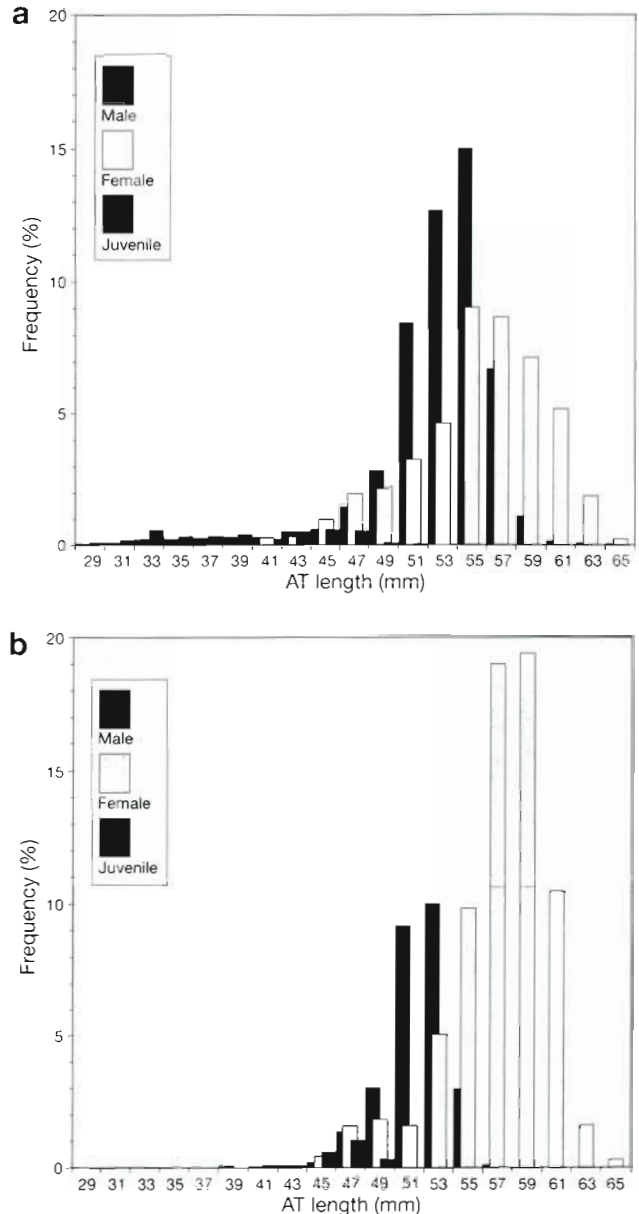

Fig. 4. AT length-frequency distribution of male, female and juvenile krill from samples where the sample size >30 krill. (a) RMT8 net samples and (b) macaroni penguin stomach lavage samples. Subadult and adult maturity stages have been combined in order to simplify the comparison (males = MS + MS1 + MS2 + MS3 + MA1 + MA2; females = FS + FA1 + FA2 + FA3 + FA4 + FA5; juveniles = J)

proportions in the net samples (22%) and in the stomach samples (25%), they represented 93% of all males taken by penguins compared to only 43% of males caught in nets. Using a Kolmogorov-Smirnov 2-sample test, the difference between the length-frequency distribution of MS krill caught in the nets and the length-frequency distribution of MS krill taken from the stomach samples was significant ($D = 0.20$; $p < 0.01$).

Table 2. Mean AT length and frequency of occurrence of male, female and juvenile krill from RMT8 net samples and macaroni penguin samples

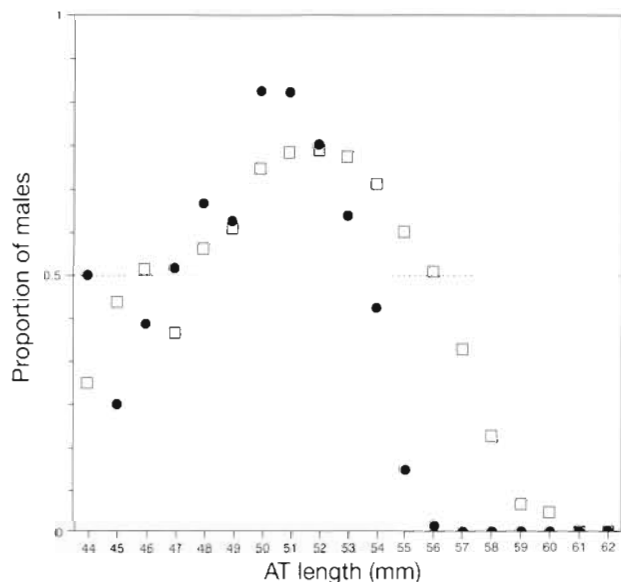| Class of krill	Count	%	Mean AT (SD)
RMT8 nets			
All	3395	100.0	53.1 (5.36)
Males	1724	50.8	52.3 (4.10)
Females	1535	45.2	55.1 (4.51)
Juveniles	136	4.0	39.2 (5.52)
Macaroni penguins			
All	2519	100.0	55.4 (4.21)
Males	673	26.7	51.3 (8.86)
Females	1793	71.2	56.0 (3.48)
Juveniles	53	2.1	44.9 (2.57)

Fig. 5. Ratio of male to female krill with respect to AT length class from samples where the sample size >30 krill; (□) RMT8 net samples and (●) macaroni penguin samples

DISCUSSION

Our results indicate that macaroni penguins take krill which are significantly larger than those caught in nets, and also that they take krill which have a significantly different maturity stage composition. However, to determine whether macaroni penguins sample krill in an unbiased way requires that the nets provide an accurate description of the krill accessible to predators in the water column. In this study we consider a comparison with krill sampled by the frequently used RMT8 scientific net. No net samples the water column perfectly, however, and therefore net samples are subject to bias. Macaroni penguin stomach lavage samples may also be biased, with variability arising from a number of sources. In both sampling methods some of the factors introducing variability can be eliminated or taken into account; however, other factors cannot be controlled. Hence, any comparison between krill caught in a series of nets and krill taken by a group of predators relies upon a number of assumptions. Here we examine the effect some of these biases and assumptions will have on our results.

Differences between macaroni penguins

During the study period, both sexes of macaroni penguins were foraging to provide food for their chicks at Bird Island. Male penguins were also feeding in order to regain body mass lost during the brooding period. Macaroni penguins are sexually dimorphic and the female, being smaller by 10%, has an energy expenditure over the whole season which is 3.5% above that of the male (Davis et al. 1989). Thus, the different requirements of the female and male parent may influence their choice of prey (either directly, or through use of different foraging areas); however, with regard to the size of krill taken, no evidence for such a difference was found.

Differential digestion of krill

The observation that smaller krill were more numerous in net samples than in the macaroni penguin stomach samples may have been the result of differential digestion. For example in well-digested samples, small carapaces from badly damaged krill could not be measured. In addition, eyes from small, broken up krill were apparent in well-digested samples, but in the absence of the necessary morphological relationships, quantitative counts could not be made. Thus, if small prey are digested more rapidly than large prey, they may be under-represented in the stomach lavage samples. Several seabirds have chitinolytic enzymes present in their digestive tract (Jackson et al. 1992), and Spindler & Buchholz (1988) suggested that the resulting chitinolytic activity contributes more to the mechanical breakdown of prey, allowing faster digestion of softer parts, than to the digestion and assimilation of the chitin itself. Krill also generate chitinolytic enzymes (Nicol & Hosie 1993) and chitinolytic activity of dietary origin, particularly from smaller krill which have shorter inter-moult periods, may also contribute to increased chitin digestion within the predator. In our study, krill smaller than 40 mm were almost totally absent from the stomach lavage samples; however, they have been recorded in greater numbers in other years

Table 3. Maturity stage of krill from RMT8 net samples and macaroni penguin samples. Maturity stages have been combined in order to simplify the comparison (MS = MS + MS1 + MS2 + MS3; MA = MA1 + MA2; FS = FS; FA = FA1 + FA2 + FA3 + FA4 + FA5)

Maturity stage	Count	% of ♂ or ♀	% of all krill (n)
RMT8 nets (n = 3395)			
MS	741	43.0	21.8
MA	983	57.0	29.0
FS	187	12.2	5.5
FA	1348	87.8	39.7
Macaroni penguins (n = 2519)			
MS	628	93.3	24.9
MA	45	6.7	1.8
FS	88	4.9	3.5
FA	1705	95.1	67.7

(Croxall et al. 1985, British Antarctic Survey unpubl. data). Thus, though differential digestion may occur, it is unlikely to be the major factor causing the reduced number of small krill in the macaroni penguin samples.

Consideration of heterogeneous krill swarm structure

Although our results indicate that krill taken by macaroni penguins are larger than krill caught in RMT8 nets, differences between krill swarms could introduce significant variability. The time, depth and location of all krill caught by nets is accurately known, but the location of swarms found by foraging penguins is not. Thus, it is possible that macaroni penguins were sampling at different locations from the nets. However during the period of our study, Hunt et al. (1992), recorded large numbers of macaroni penguins to the northeast and southwest of Bird Island, the same position as many of the net samples used in this study (Fig. 1). Hence, it is likely that the nets and the penguins sampled krill from the same concentrations of swarms, although not necessarily from the same swarms (cf. Croxall & Pilcher 1984).

Most diving by macaroni penguins occurs during the day (Croxall et al. 1988a, 1993), whereas all of our nets were fished at night. Therefore, as krill may undergo a diurnal migration (Everson 1982), it is possible that macaroni penguins feeding by day sampled a different krill population to that sampled at night (by both nets and penguins). However, BIOMASS (1991) examined net data from a large number of cruises and found only small differences between the length-frequency distributions of krill sampled during the day and those sampled at night. Hence, BIOMASS (1991) suggested that differences between day and night were not biologically significant. Therefore in this study it is likely that the characteristics of krill in swarms sampled by both nets and penguins at night were similar to the characteristics of krill sampled through the day by penguins alone.

Krill exhibit significant inter-swarm differences, even over relatively short distances (Watkins 1986). Thus, samples from individual swarms are unlikely to reflect the characteristics of the local population (Watkins et al. 1986). Our Monte Carlo analyses indicate the importance of this factor, showing that statistically significant departures from the population length-frequency distribution often result from sampling a restricted group of swarms. Furthermore, we have no information about the number of krill swarms that foraging macaroni penguins encounter and therefore no knowledge about the extent to which a single stomach lavage sample integrates population characteristics. The largest departure from the population length-frequency distribution encountered during the 100 Monte Carlo simulation trials ($D = 0.20$) was less than that found in the comparison between the length-frequency distribution obtained from the net samples and the macaroni penguin samples ($D = 0.24$). This may reflect the small number of krill swarms encountered by the penguins, or an extreme degree of heterogeneity in the krill population not sampled by the nets, or it may reflect non-random sampling within the krill swarms encountered by the penguins.

Comparison of length and maturity of krill caught in nets and taken by macaroni penguins

It is possible that the size differences between the krill caught in nets and the krill taken by macaroni penguins were the result of larger krill escaping capture by nets (but not by penguins) and/or smaller krill not being taken by foraging penguins (Fig. 2). Hence it is possible that the inefficiency of the sampling process generated selection. For nets these biases may be the result of a number of factors. For example, different net types have been shown to sample different maturity stages and different length-frequency distributions (BIOMASS 1991). Similarly, vibration from leading bridles or turbulence from the net itself has been shown to lead to net avoidance by targeted species (Hovekamp 1989). Everson & Bone (1986) have suggested that net avoidance may also be affected by swarm density, with greater opportunity for avoidance in lower density krill swarms, particularly near the surface. For the related species *Euphausia pacifica*, net avoidance may also vary as a function of animal size, with larger animals evading nets more successfully (Hovekamp 1989). Light levels have also been shown to have an important effect upon the distribution of animals in the water column and thus to have an effect upon which animals are caught (Hovekamp 1989). Such factors probably affect all nets to some degree. In considering the sampling efficiency of the RMT8, Everson & Bone (1986) concluded that because net avoidance was greatest during the day, krill mainly use visual cues to avoid nets. In our study, the net system was relatively large and the nets were all fished at night to a depth of approximately 100 m. Hence, every attempt was made to minimise visual avoidance of nets and to reduce surface interference.

Though all attempts were made to reduce the biases associated with net sampling, it remains a possibility that net biases could have lead to the result that larger krill were relatively more numerous in penguin stomach samples than in net samples. However, we consider that net biases were unlikely to have lead to the observation that macaroni penguins took considerably more adult female krill and considerably less mature

male krill than were caught in the nets (Table 2). The magnitude of these differences were sufficiently large that they suggest macaroni penguins were taking a non-random sample of krill from the local population. Here we consider 2 (not mutually exclusive) possibilities: that adult male krill were much better at evading capture (subadult males proportions were very similar), or that macaroni penguins were actively selecting adult female krill (subadult female proportions were also very similar) (see Table 3).

Krill usually swim using their pleopods, but their escape response involves rapid backward propulsion called tail swimming. Kils (1979) reported that velocity is size dependent and may represent 11 times the body length per second, with average speeds of up to 50 cm s^{-1} that may be maintained for several metres. Kils (1979) also indicated that acceleration may be high, with krill able to reach speeds of 100 cm s^{-1} in 55 ms. The tail swimming speed of male krill has not been reported separately but there are several aspects of the morphology of male krill which may confer an advantage when trying to evade an active predator. For example, male krill have a longer abdomen than female krill (Makarov & Denys 1981) and thus have a greater muscle mass which may provide a faster, or more prolonged, escape response. In addition the body of a male krill is narrower than that of a gravid female, and as a consequence of the decreased water resistance, tail swimming may be more efficient. Kils (1979) also reported that krill have directional control during their escape response, and it could be that the compact body of the male krill is more agile during evasion. Another possible advantage over female krill is that the eyes of males are larger for the same body length (Makarov & Denys 1981); hence, they may have better vision, allowing them to detect a predator sooner, or at lower light levels. This may be particularly important during tail swimming, when the stalk eyes are held high above the body, enabling the krill to see in the direction of travel (Kils 1979).

The nutritional value of gravid female krill is greater than that of males or subadults, particularly with regard to lipid (Clarke 1984) and protein (Clarke 1980) content. Although seasonal differences in lipids are known to occur (Quetin et al. 1994), the relative advantage before assimilation, calculated from the Model alpha regression equation of Morris et al. (1988), would be approximately 53% for a 55 mm gravid female compared to a male. Thus, a macaroni penguin that consistently caught adult female krill would have an overall advantage, provided energy expenditure was the same in catching both sexes. In our study, this benefit would accrue regardless of whether penguins were actively selecting large krill (or gravid females), or whether males were better at escaping capture.

To understand fully the mechanics of evasion or selection, further work investigating the relative swimming and predator detection capabilities of male and female krill would be necessary. The relationship between the ability of penguins to select large krill that are nutritionally superior, and the ability of certain maturity stages of krill to escape capture, will probably require video film of penguin-krill interactions of sufficient quality to allow discrimination of krill sex and general maturity categorisation. To understand how such results compare with the reactions of male and female krill in response to nets (Table 2) or to larger predators such as baleen whales (Mackintosh 1974), which operate at a different scale to penguins and which may therefore evoke a different response (cf. O'Brien 1987), similar high definition video film will also be required.

Comparisons with other studies

A number of studies have examined the size of krill taken by foraging predators. These studies have explored different aspects of predator ecology, considering differences in prey in terms of sexual dimorphism within a single predator species (e.g. Ainley & Emison 1972), ecological segregation between closely related species (e.g. White & Conroy 1975, Lishman 1985), ecological segregation between unrelated species (e.g. Croxall & Prince 1980), and potential competition between predators and commercial fishing (e.g Lishman 1985). However, a number of authors (e.g White & Conroy 1975, Croxall & Pilcher 1984) have cautioned that a temporal and spatial mismatch in sampling methodology could also lead to significant differences in results for both krill maturity and krill length.

Thus, a number of studies suggest that a variety of marine top predators, utilizing a range of foraging techniques, take krill that differ in mean size and/or maturity to that available in the local population; however, only a few studies present an independent assessment of krill available in the water. While it may be plausible (and even anticipated) that predators maximise ecological segregation, or maximise foraging efficiency, most studies cannot discount the possibility that differences in krill length-frequency distribution could have arisen due to spatial and temporal variability within the krill population. Our results from the Monte Carlo simulation confirm the importance of this.

The recent at-sea study of Nicol (1993) did report results from concurrent sampling. Nicol (1993) compared krill taken from spontaneous regurgitations of Antarctic petrels *Thalassoica antarctica* with krill caught in research nets in the Prydz Bay region of

Antarctica, and reported that petrels took larger krill. Thus, Nicol (1993) suggested that krill taken by seabirds do not necessarily represent an unbiased description of the length-frequency distribution of krill available locally. This result is confirmed by the present study, which also extends this result to the maturity of krill. The present results are particularly important as they relate to krill taken during the breeding season and within the known foraging range of breeding birds.

Given the magnitude of the differences found between krill caught in nets and those taken by penguins, particularly the differences in sex and maturity stage, we believe it is unlikely that in our study sampling biases were the predominant cause. It is more likely that differences in length, sex and maturity stage of krill were the result of macaroni penguins selecting particular classes of prey, or that certain maturity stages of krill were better able to avoid capture due to a superior escape response. Both these mechanisms, which are not mutually exclusive, provide macaroni penguins with a subset of krill which also happen to be nutritionally superior. To understand the relative importance of these 2 mechanisms, very detailed work will be required, including similar projects to the current study, but at times when multiple AT length modes of krill are present in the local population. Such projects should also ensure that the size and number of predator stomach samples are adequate to fully characterise the prey, given that the greater part of the variance for both krill caught in nets and krill taken by predators may be within, rather than between, samples (cf. Watkins 1986).

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