

CONSIDERATION OF MAJOR ISSUES IN ECOSYSTEM MONITORING AND MANAGEMENT

I. Everson
British Antarctic Survey
Natural Environment Research Council
High Cross, Madingley Road
Cambridge CB3 0ET, United Kingdom
Email – iev@pcmail.nerc-bas.ac.uk

Abstract

This paper outlines the requirements of an ecosystem approach to the management of Southern Ocean resources and highlights the need for information on harvested and dependent species, their interactions and the manner in which their populations vary naturally. Large-scale interactions are catered for in the Krill Yield Model (KYM). Smaller-scale interactions centre around three main categories: the availability of krill, variation in vital rates of the dependent species and the overlap between commercial fishing and predator foraging. The CCAMLR Ecosystem Monitoring Program (CEMP) provides a good framework within which to investigate krill availability. Vital rates can be investigated directly and also by means of CEMP. The overlap between fishing and predator foraging is being monitored. A mechanism for bringing these various components together as an ecosystem approach to management is discussed.

Résumé

L'auteur indique les conditions requises pour que l'approche de la gestion des ressources de l'océan Austral tienne compte de l'écosystème, et souligne la nécessité de disposer d'informations sur les espèces exploitées et dépendantes, leurs interactions et la manière dont leurs populations varient à l'état naturel. Le modèle de rendement du krill (KYM) tient compte des interactions à grande échelle. Celles à plus petite échelle sont classées en trois catégories principales : la quantité disponible de krill, la variation des taux démographiques des espèces dépendantes et le chevauchement de la pêche commerciale et de l'alimentation des prédateurs. Le programme de contrôle de l'écosystème de la CCAMLR (CEMP) forme un cadre approprié à l'étude de l'abondance du krill. Les taux démographiques peuvent être étudiés directement ou par le biais du CEMP. Le chevauchement de la pêche et de l'alimentation des prédateurs fait l'objet de contrôles. L'auteur traite la question d'un mécanisme qui lierait ces divers éléments pour en faire une approche de la gestion qui tienne compte de l'écosystème.

Резюме

В статье обрисовываются требования экосистемного подхода к управлению ресурсами Южного океана и подчеркивается необходимость информации о промысловых и зависимых видах, их взаимодействиях и характере естественной изменчивости их популяций. Крупномасштабными взаимодействиями занимается Модель вылова криля (KY-модель). Рассмотрение взаимодействий более мелкого масштаба концентрируется на трех основных категориях: наличии криля, изменчивости демографических и жизненных показателей зависимых видов и перекрытии между коммерческим промыслом и ареалами кормления хищников. Программа АНТКОМа по мониторингу экосистемы (CEMP) дает хорошую основу для изучения наличия криля. Жизненные и демографические показатели могут изучаться как непосредственно, так и в рамках CEMP. Ведется мониторинг перекрытия промысла с ареалами кормления хищников. Обсуждается механизм совместного рассмотрения этих компонентов в рамках экосистемного подхода к управлению.

Resumen

Este documento describe los requisitos de un enfoque ecosistémico para la ordenación de los recursos del Océano Austral, y subraya la necesidad de información sobre las especies explotadas y dependientes, sus interacciones y la variación natural de sus poblaciones.

El modelo de rendimiento de kril (KYM) toma en cuenta las interacciones en gran escala. Las interacciones en escalas menores se agrupan en tres categorías principales: la disponibilidad de kril, la variación de las tasas vitales de las especies dependientes y el área de superposición entre la pesquería comercial y la búsqueda de alimentos por parte de los depredadores. El programa de seguimiento del ecosistema de la CCRVMA (CEMP) proporciona un marco adecuado para investigar la disponibilidad de kril. Las tasas vitales pueden estudiarse directamente y también mediante el programa CEMP. Se está estudiando el grado de la superposición entre las actividades de pesca y el radio de alimentación de los depredadores. Se discute un mecanismo para aunar estos elementos tan diversos en un enfoque ecosistémico para la ordenación.

Keywords: ecosystem approach, fisheries management, ecosystem monitoring program, harvested and dependent species, CCAMLR

INTRODUCTION

Consideration of the major issues relevant to ecosystem monitoring and management within CCAMLR is recognition of Article II of the Convention, which is partly reproduced below:

Article II, paragraph 3:

Any harvesting and associated activities in the area to which this Convention applies shall be conducted in accordance with the provisions of this Convention and with the following principles of conservation:

(a) prevention of decrease in the size of any harvested population to levels below those which ensure its stable recruitment. For this purpose its size should not be allowed to fall below a level close to that which ensures the greatest net annual increment;

(b) maintenance of the ecological relationships between harvested, dependent and related populations of Antarctic marine living resources and the restoration of depleted populations to the levels defined in subparagraph (a) above; and

(c) prevention of changes or minimisation of the risk of changes in the marine ecosystem which are not potentially reversible over two or three decades, taking into account the state of available knowledge of the direct and indirect impact of harvesting, the harvesting, the effect of the introduction of alien species, the effects of associated activities on the marine ecosystem and of the effects of environmental changes, with the aim of making possible the sustained conservation of Antarctic marine living resources.

The implementation of these requirements means that the management process must provide adequate safeguards for harvested species and that harvesting activities should not prejudice the long-term future of dependent species. This paper concentrates on the krill-centred system and

discusses the extent to which the ecosystem approach has been implemented by CCAMLR, with a view to examining how the present management regime might be improved.

TARGET SPECIES CONSIDERATIONS

The first subparagraph of Article II.3 is essentially a restatement of the traditional single-species approach to fisheries management, the main components of which have been elaborated many times. The Krill Yield Model (KYM) that was developed by Butterworth et al. (1991, 1994) and Constable and de la Mare (1996) is a development of this approach. It requires for its calculation information on standing stock, mortality, recruitment, growth, age and size at spawning, dependent species requirements and fishing pressure. The model assumes that the distribution of the target species is known and that sufficient information is available to indicate the extent of management units or stocks.

Antarctic krill (*Euphausia superba*), hereafter referred to as krill, is found throughout most of the Southern Ocean south of the Polar Front. Although widespread, its distribution is extremely patchy and is dependent on the Southern Ocean circulation. On the macro-scale, where the management unit encompasses a large part of the Southern Ocean, patchiness is of little consequence when implementing the KYM. At smaller scales, of the order of tens or hundreds of kilometres, the extremely contagious nature of the krill distribution needs to be taken into account. At scales other than the macro-scale, the movement of krill through a region may also be important. This has been taken into account through consideration of krill flux (SC-CAMLR, 1994).

Information on krill growth has recently been reviewed by Siegel and Nicol (2000). Although it is difficult to estimate age directly, experiments

on laboratory growth rates viewed in conjunction with estimates from length-frequency distributions almost certainly provide reasonable estimates of size-at-age.

Estimations of mortality and recruitment when used in age-based studies, require knowledge of the abundance of different year classes. In theory, this can come from an analysis of length-density distributions, although this is made difficult by the patchy nature of the krill distribution. If the length densities can be linked to standing stock, from large-scale surveys in successive seasons, then such estimates can be refined. The broad range of estimates of natural mortality has been reviewed recently by Siegel and Nicol (2000).

The problem of standardising recruitment to the standing stock was addressed by Hewitt (2000), who defined a proportional recruitment index that was derived by comparing year-class strengths within samples from within a season. The method is thought to be reasonably robust for most sources of variation but, since it assumes that sampling is representative of the population, it is dependent on sampling over a wide area. This might be tested through analysis of data from the recent CCAMLR 2000 Krill Synoptic Survey of Area 48 (CCAMLR-2000 Survey) (SC-CAMLR, 2000).

Regarding the incorporation of information on dependent species into the KYM, providing their foraging activities are widespread, or they are able to search over a wide area for krill, there is little difficulty in incorporating this impact into the model analysis. This topic is developed further in a later part of this paper.

The level of fishing can be monitored through reported catches; on the macroscale considered through the KYM this is adequately covered.

DEPENDENT SPECIES

Large-scale Interactions

The second part of Article II.3 sets out the basis of the ecosystem approach. If the dependent species are not constrained in their foraging range then a basic estimate of their food requirement is adequate for incorporation into the KYM. Examples of dependent species that fall into this category are some species of baleen whale and the crabeater seal (*Lobodon carcinophagus*). Although these dependent species are not uniformly or randomly distributed, it is assumed that they are able to cover large areas in search of food, should the need arise. In essence, their foraging

is assumed to be unconstrained geographically relative to krill distribution. Other dependent species may be constrained in their foraging activity. Land-breeding species, such as birds and fur seals, are restricted to foraging in areas local to their breeding site during the breeding season. Outside the breeding season their foraging activity is less constrained. A third category is species that are more or less constrained geographically throughout their life, such as the mackerel icefish (*Champsocephalus gunnari*), a species that is restricted to the shelf region.

In terms of the KYM, the total dependent species requirement can be calculated by summing over all known predators for incorporation into the model. An example of this is given by Thomson et al. (2000). The key input parameters for such a calculation are the predator population size, recruitment, mortality and a functional relationship between predator survival and krill availability.

On the large scale, the KYM can be used to estimate the impact of different levels of harvesting on dependent species. This would be adequate, provided that all the dependent species are not restricted in their foraging. However, since many dependent species are constrained in their foraging activity during the breeding season (birds and fur seals), or their distribution is restricted (mackerel icefish), local conservation measures may be needed to provide an added level of protection.

Smaller-scale Interactions Involving Harvested and Dependent Species

Developing models at smaller scales is difficult and requires knowledge of the key dependent species and their spatial and temporal foraging behaviour. Spatially we need to consider both horizontal (geographical) and vertical (location in the water column) planes. Temporally the most important scales are probably season and time of day although, depending on the topic of interest, months and longer-term trends are also important. These considerations were incorporated into the plan for an ecosystem assessment by WG-EMM (SC-CAMLR, 1995) and can be summarised as the following series of questions:

- (i) Is the availability of krill changing?
- (ii) Are populations of dependent species in decline?
- (iii) How much krill is required by the dependent species?

Table 1: Time and space scales of CEMP parameters for penguins, black-browed albatross and fur seal. Information summarised from SC-CAMLR, 1991.

Species	CEMP Parameter	Integration Period of Observations	Integration Period of a Single Observation	Foraging Range/Area (km)
Penguins	A1 Adult arrival weight		6-7 months	100s
	A2 Duration of first incubation shift		7-8 months	25-150
	A3 Breeding population size		>1 year	100s
	A4 Age specific survival		1 year	100s
	A5 Foraging trip duration	2 months	1-2 days	25-50
	A6 Breeding success	2-3 months		100s
	A7 Chick fledging weight		2 months	25-50
	A8 Chick diet	2 months	1-2 days	25-50
Black-browed albatross	B1 Breeding population size		>1 year	
	B2 Breeding success		7 months	
	B3 Age specific survival		1 year	
Fur seal	C1 Foraging trip duration	2-3 months	Several days	20-100
	C2 Pup growth	2-3 months	2-3 months	30-150

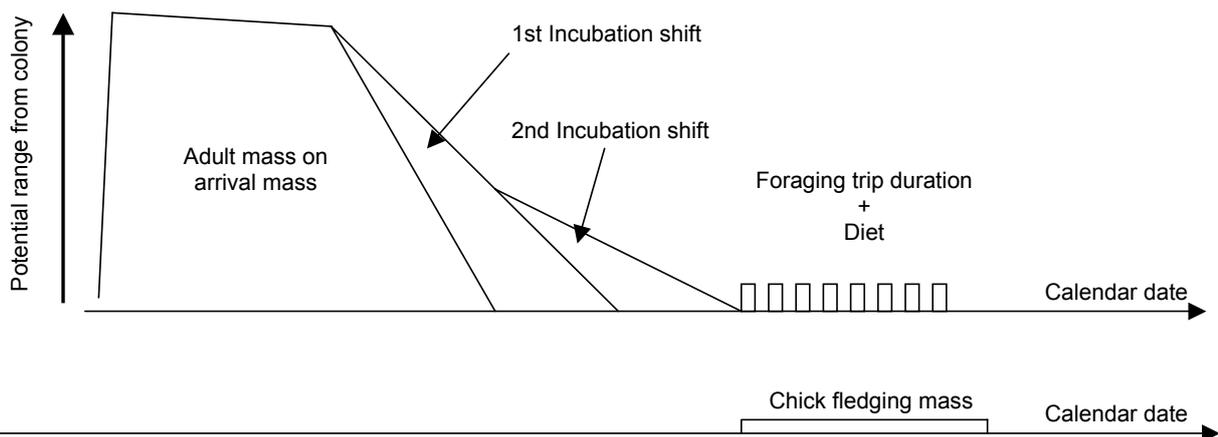


Figure 1: Temporal and spatial scales of the interaction between penguin foraging activity and krill availability.

- (iv) What is the extent of overlap between krill fishing and foraging by dependent species?

These questions are taken in turn (below) to develop a framework within which a management regime can be developed.

Is the Availability of Krill Changing?

This question was central to the development of the CCAMLR Ecosystem Monitoring Program (CEMP) (CCAMLR, 2000). Taking an essentially pragmatic approach, CEMP has set up regular monitoring of key parameters likely to be sensitive to variation in krill availability and that are associated with several krill-eating species. The dependent species that have been identified for CEMP are: Adélie (*Pygoscelis adeliae*), chinstrap (*P. antarctica*), gentoo (*P. papua*) and macaroni (*Eudyptes chrysolophus*) penguins, black-browed albatross (*Diomedea melanophrys*), Antarctic (*Thalassoica antarctica*) and Cape petrels (*Daption capensis*), fur (*Arctocephalus gazella*) and crabeater seals (*L. carcinophagus*). In addition, krill as a harvested species and major prey item and certain key environmental variables are also included.

The CEMP parameters for dependent species (A1 to A6, B1 to B3, C1 and C2), along with time and space scales of their dependence on krill are set out in Table 1. A full description of CCAMLR standard sampling protocols for each of these parameters is given in CCAMLR, 2000.

Most of the CEMP parameters have been monitored as part of the program since 1989 or 1990, although in some instances national programs were in place over a decade prior to that time. The CEMP database, augmented by national programs, consequently forms a very powerful archive with which to study ecosystem interactions.

From the outset, the importance of understanding the time and space scales of predator foraging activity was recognised (SC-CAMLR, 1991), and the relevant information is summarised in Table 1. Each of the CEMP parameters has different response characteristics to the availability of krill. At the one extreme, foraging trip duration reflects the local availability of krill immediately prior to the period of observation, whereas at the other extreme, adult mass on arrival reflects a time period of months and relates to a much greater area. Further complication is caused by the transient nature of krill concentrations, which affect krill availability through the formation and dispersion of concentrations on which predators

might feed and the movement or flux of such concentrations through an area (Watkins, 2000). Thus, the answer to the question 'Is the availability of krill changing?' will depend on which parameter is being considered, and the answer may not be the same for all parameters.

The CEMP parameters need to be considered independently in order to gain the maximum value from them. Furthermore, two key relationships need to be developed. Firstly, to determine the time and space scales over which CEMP parameters integrate krill availability (Table 1) and, secondly, to determine the response time and impact of changes in krill availability on each parameter. This requires an understanding of the functional relationship between the predator and its prey (i.e. krill).

In the case of penguins, as is shown in Figure 1, at the shortest time and smallest space scales are chick diet (parameter A8) and foraging trip duration (parameter A5). The latter is an index that uses the time taken for an adult penguin to obtain sufficient food for itself and its chick; the longer the trip, the lower the availability of krill. These indices are likely to have very short response times and provide spot indications of the availability of krill. They are not sufficient to provide integration over a period of anything other than, at the most, a few days and over an area local to the breeding colony.

Krill availability over periods of a few weeks to a few months can be tracked by consideration of, for example, the weight of adult birds on arrival at the breeding colony (parameter A1). This is integrated over a period of around four or five months prior to a set calendar date. At South Georgia, where the krill fishery is concentrated in the winter months, this may be the period of greatest predator–fishing overlap, a topic considered later. In the case of penguins, the duration of the first incubation shift (parameter A2) may be influenced not only by the arrival weight (parameter A1), but also by the availability of krill to the birds as they replenish reserves for their next incubation shift. On a longer time scale we have breeding success (parameter A6), monitored throughout the season, and fledging weight (parameter A7). Together these indicate how successful the adults have been in finding krill and bringing it to the colony to provision the chick over the same period.

This part of CEMP is therefore a very good mechanism to monitor changes in dependent species in response to the availability of krill, the first of the series of questions.

In terms of the aims of CEMP, the parameters are used to monitor activities when the species is thought likely to be most sensitive to krill availability, therefore it is not a disadvantage that there is very little monitoring of krill outside these times. Such a conclusion is not true for all dependent species. For example, the mackerel icefish at South Georgia is restricted to the shelf and is dependent on krill as a major component in its diet. Krill availability has been shown to influence the species' diet, condition and reproductive indices (Kock et al., 1994; Everson et al., 2000a; Everson and Kock, 2001). In this case, the dependent species is widespread on the shelf and is likely to be sensitive to variation in krill availability at any time of year.

Are Populations of Dependent Species in Decline?

This question, although apparently simple, is in reality very complicated. Taking as an example one species, chinstrap penguin, which is widespread in the Antarctic Peninsula region, and one parameter, A3, demonstrates the complexity of the issue.

When observed at sea feeding, it is not obvious which breeding site a particular bird or group of birds will use. If there is a high degree of mixing on the feeding grounds between individuals from different breeding colonies, then probably this will not matter. However if individuals from particular colonies tend to feed in the same locality, then a single colony is unlikely to be representative of all colonies. In reality, during the winter months there may well be a great deal of mixing, whereas during the breeding season feeding localities may be colony specific, as is indicated in Figure 2. So both approaches may be used to define the population! The easier of the two to monitor is the breeding colony, whereas the more important for management issues may be the group of colonies within a region.

At the root of all population studies is the definition of 'population'. In the case of fish, such definitions are based on the geographical distribution of a species and the biological characteristics of fish in one area compared to those from an adjacent locality. For icefish, which appears to be restricted to the shelf region, such a designation provides a reasonable descriptor. Within that region there is likely to be movement that may be related to feeding and spawning activity (Everson et al., 2001), although movement outside of that mesoscale region is thought to be minimal.

Penguin colonies are easily observed, and mechanisms are in place to provide counts of breeding pairs. What is less clear is the relationship between one colony and those adjacent to it because the availability of krill to them will almost certainly differ over the year. Thus, in terms of small-scale interactions, such as those associated with parameters A5 and A8, responses to krill availability may be colony specific, as is shown in Figure 2. On the other hand, for those parameters that integrate information over greater time and space scales, the colony may provide an indicator that is valid over a much wider region.

In order to identify a decline in a population, a time series of observations is required. A direct census each year would provide a good estimator. This approach has been taken by Reid and Croxall (2001), who studied fur seal, macaroni and gentoo penguins and black-browed albatross. Their study showed a downward trend in the population size of all these species over the period from the mid-1980s to the present. This trend was thought to be related to krill availability as inferred by the size distribution of krill present in the predator diets.

The conceptual framework (Figure 1), whereby dependent species are viewed as central-place foragers, is subject to an additional complication caused by water circulation. Several scenarios are possible, two of which are indicated in Figure 3. The simplest, shown in Figure 3(a), has a strong long-shore current within which krill could be entrained, as found by Everson and Murphy (1987). In this situation krill are likely to be passing all the colonies and krill availability would be largely dependent on the predation impact of successive colonies. In the coastal region, circulation patterns are topographically driven such that adjacent colonies may be receiving water with different origins, as outlined in Figure 3(b). The extent of such variation may be large, as, for example, in the Atlantic sector where some island groups receive water with Bellingshausen and Weddell Sea influences. Whatever the circulation pattern that is encountered in the vicinity of a particular colony, it is important to note that the amount of krill carried in the current may have been affected by commercial fishing upstream sometime earlier. Recent developments in telemetry mean that a much clearer picture is emerging of foraging activity from specific sites (e.g. Boyd et al., 1997), thus adding greatly to our knowledge of foraging behaviour. Quantification of these effects is essential in developing an ecosystem approach to management.

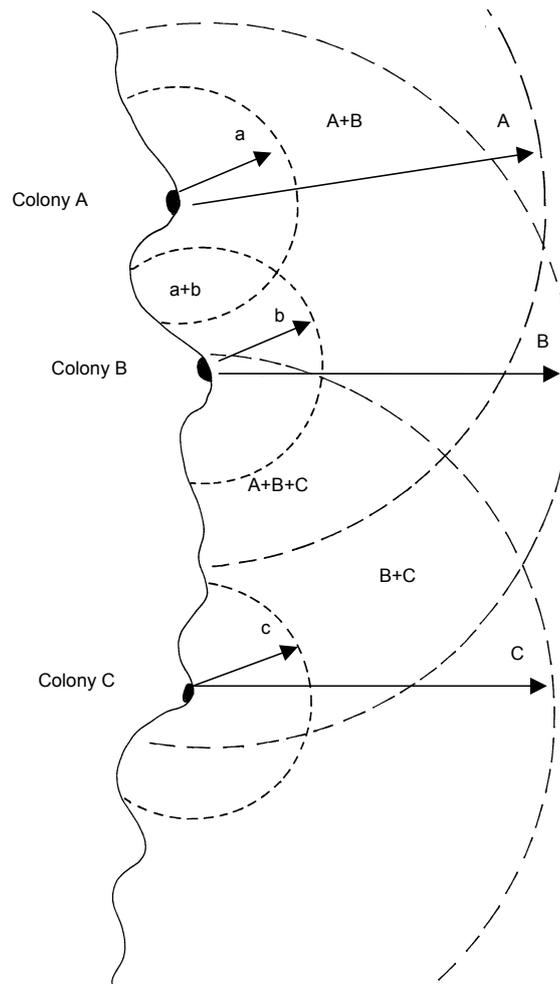


Figure 2: Foraging areas available to predators breeding at three colonies. Two spatial scales are indicated: lower-case letters (a, b, and c) relate to short time-scale local activities such as parameter A5, A7 and A8; upper-case letters (A, B, and C) relate to larger spatial scale foraging activity such as A2.

Looking in greater detail at the population size (parameter A3) and its relationship to demography (parameter A4), the number in a given year will come from the number present in the previous year, decreased by mortality and increased by recruitment, and with a factor to account for errors in the estimators. If the balance of recruitment over mortality is decreasing, then the population size will suffer a downward trend.

In the case of a penguin species, the first stage of the recruitment process can be considered as the number of chicks produced during a breeding season (parameter A6). Those chicks will be susceptible to mortality over the years leading up to the arrival of the survivors at a breeding colony. As a direct consequence, if there are no chicks produced in a particular season there can be no recruitment from that year class in the season

when it would have reached maturity. If the reproductive life span of the bird is short, then the loss of a single year class will have a major effect, whereas if it is quite extended, over perhaps decades, then the impact will be small. Allied to this, it can be seen from Figure 4 that for those species for which survivorship is lowest, breeding failures will cause greater fluctuation in population due to the dependence of breeding population on the recruiting year class. Statistically this could be investigated through the variance of the population size irrespective of whether or not a trend is present.

In theory, chick production should provide some indication of recruitment in subsequent years. The implications of this conclusion can be explored through the relationship between population size, recruitment and mortality. Assuming a normal

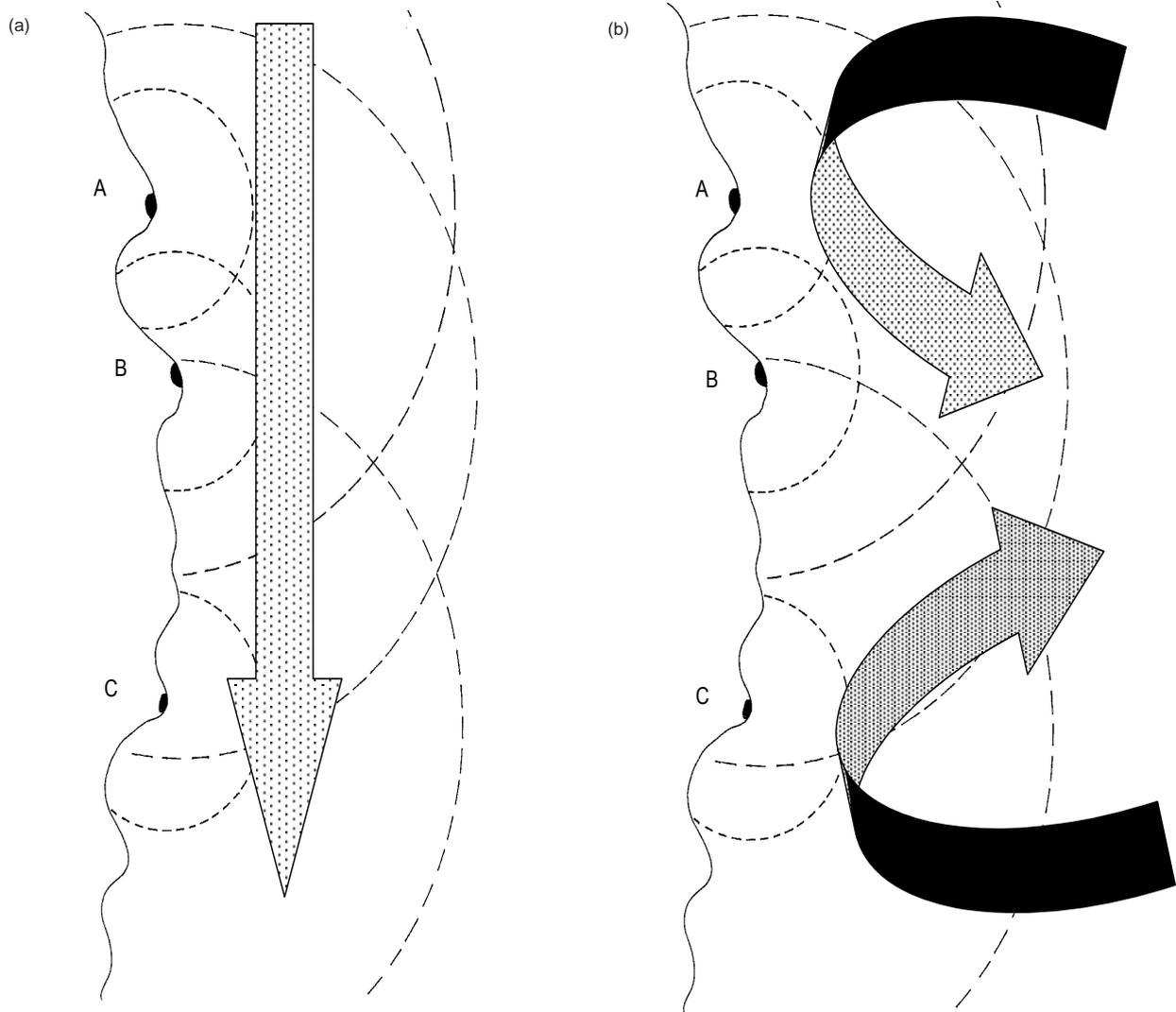


Figure 3: Schematic representation of circulation pattern carrying krill in the vicinity of colonies of land-breeding predators. (a) direct longshore movement of krill past a series of colonies, (b) topographically driven circulation bringing krill from different sources to colonies in fairly close proximity.

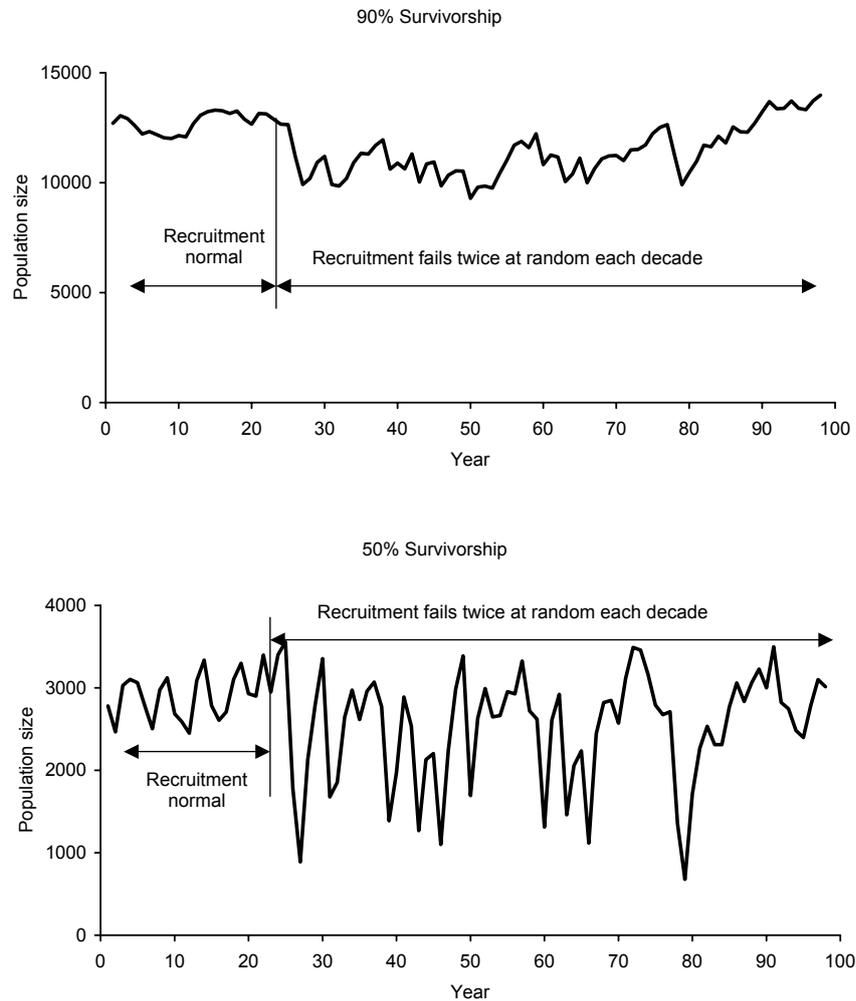


Figure 4: The effect of breeding failure and population size. During the first 20 years recruitment is randomly distributed between 1 000 and 2 000. From year 20 onwards for two randomly selected seasons in every 10 there is total breeding failure leading to recruitment failure of those year classes. The analysis has been run for two levels of survivorship and demonstrates the greater fluctuation of population size associated with low survivorship and a consequent dependence of population size on recruiting year class.

exponential decline in numbers with age due to mortality, we can estimate numbers-at-age from the basic equation:

$$N_t = N_0 e^{-Zt}$$

where N_0 is the number at time zero, N_t is the number at time t and Z is the coefficient of total mortality.

The breeding population (P_b) will be composed of animals within the age range from t_r , the age at first breeding, to t_{max} , the oldest animal likely to be present in the population, such that

$$P_b = \sum_{t_r}^{t_{max}} N_t$$

In a situation where the population size is not changing, the number of first-time breeders will equal the number dying during the preceding year. The number of first time breeders will depend on the number of chicks produced each season discounted by mortality up to age t_r .

The number of chicks produced in a season (N_0) can be derived from parameters A3 and A6 (Table 1), leading to an estimate of recruitment (N_r) given by:

$$N_r = N_0 e^{-Z \cdot t_r}$$

For the population size to be stable, the recruiting year class would need to balance the losses due to mortality, as indicated in Equation 1.

$$N_r = \sum_{t=r}^{t_{max}} N_t - N_{t+1} \quad (1)$$

An example of this analysis is given in Figure 5 and some other examples in Table 2. Note that the information is given as survivorship rather than mortality because that is the common form used in the literature on bird ecology. Estimates of survivorship by this method are the minimum consistent with population size remaining at the same level. It is known that not all penguins breed in a given year, therefore survivorship will need to be greater to accommodate this factor. The results in Table 2 indicate that for Adélie, chinstrap and gentoo penguins chick production is consistent with the estimates of survivorship. However, for macaroni penguin, the published survivorship is somewhat lower than that required to sustain the population, given the chick production. This

result, providing all the values are correctly estimated, indicates that the population would be in decline.

This approach uses very little information to estimate the population turnover needed to maintain a stable population size. If it is possible to identify first-time breeders, a further simplification can be made because their proportion in the breeding population can be used to estimate survivorship through the relationship:

$$\frac{N_r}{P_b} = (100 - S)\% \quad (2)$$

This approach is the direct analogue of that developed as the proportional recruitment index for krill (Hewitt, 2000).

It is also important to note the assumption that mortality is not varying with age. Williams (1995) indicates that mortality may be high during the first year of life but reduced thereafter; such variation could easily be incorporated into this form of analysis but has not been done here because the data are currently very sparse.

The above analysis has concentrated on recruitment as an indicator of survivorship in a stable population. Deviations from the mean values of chicks per adult or age at first breeding are thus providing indicators of population trends. The linkages with other components are less well defined. Adult survivorship can be estimated directly from mark-recapture experiments (e.g. Williams, 1995), although due account must be taken of emigration in order to provide a full interpretation of the results. A further extension of this work could be undertaken by looking at CEMP parameters in relation to these direct indicators. For example, the total mass on arrival at the breeding colony, a parameter assumed to be related to food availability, may also affect survival during the non-breeding period. The functional relationship between CEMP parameters and krill availability needs further study in order to provide better estimates of vital rates. Similar analyses are potentially feasible for other land-based dependent species, such as fur seal, using CEMP and related datasets.

The problems associated with determining vital parameters for fish are quite different to those for land-breeding predators. Population size is estimated by standard survey methods using trawl or acoustics. This varies from season to season due to a variety of factors, as discussed by Parkes (1993) and Everson et al. (1999). Mortality rates can

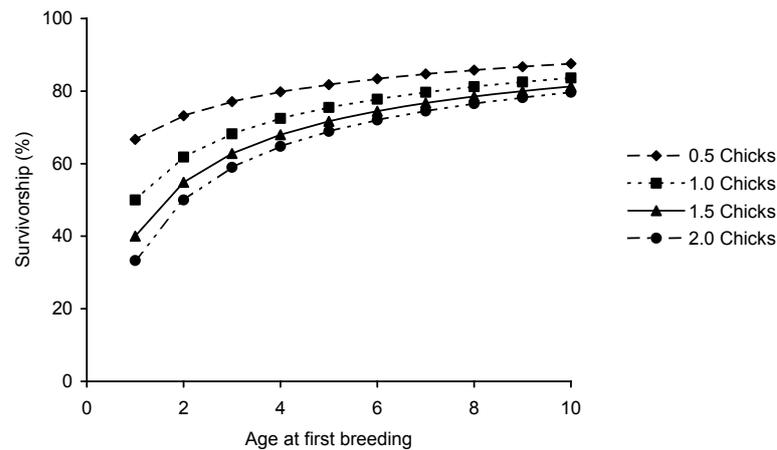


Figure 5: Estimated minimum survivorship necessary for a given age at first breeding to ensure a stable population size at four levels of chick production per breeding pair. The calculations have been made iteratively using Equation 1.

Table 2: Field observations of penguin survivorship compared with survivorship estimated from chick production and age at first breeding estimated using Equation 1.

Penguin Species	Chicks/Pair (Williams, 1995)	Age at First Breeding (Williams, 1995)	Survivorship (%) (Williams, 1995)	Minimum Survivorship to sustain the Population (Equation 1, this paper)	Proportion of First-time Breeders to sustain the Population (Equation 2, this paper)
Macaroni	0.44±0.15	5♀ 6♂	78	83♀ 84♂	17♀ 16♂
Chinstrap	~1 (0.016–1.83)	(3?)	?	68	32
Adélie	~1 (0.68–1.89)	5♀ 6♂	81–97	76♀ 78♂	24♀ 22♂
Gentoo	0.85	3	75–85	70	30

Table 3: A comparison of the levels of survivorship required at different times in the early life history of the animals in order to maintain a 'steady state' population. Information on Adélie penguin from Table 2, and mackerel icefish from Kock, 1992 and Everson et al., 1999.

	Adélie Penguin	Mackerel Icefish
Egg production per breeding female	2	~15 000
Annual survivorship from egg to maturity to maintain population	~75%	~5%
Age at first maturity	5–6 years	2–3 years
Survivorship from juvenile to maturity	~75%	~70% (assuming M = 0.4)
Survivorship egg to juvenile	~50%	~0.3%

be estimated from year class strength in successive years, whilst recruitment is generally estimated by cohort analysis or some other age-based analysis after the event. These methods are well described in a number of standard texts, e.g. Saville (1977), Gulland (1983), Hilborn and Walters (1992).

Survey estimates of standing stock are subject to a large amount of variation. Part of this will be due to an error component in the estimation technique, something that is inherent in the system irrespective of whether the dependent species can be counted on dry land or has to be estimated from trawl catch rates. In addition, there will be variation due to the population structure. In the case of a short-lived species, this will be strongly dependent on the recruiting year-class strength. If the predator is limited to producing one or two offspring per season, as is the case for penguins and seals, this is likely to be indicated in the chick or pup production estimates. On the other hand, in the case of an icefish which might produce 15 000 eggs and have a natural mortality coefficient of around 0.4, most variation is likely to be caused by the proportion of the total number of eggs spawned that develop beyond the larval stage.

Taking penguins and fish as examples, it is clear that the situation with these two dependent species is quite different, as indicated in Table 3. In the case of penguins, recruitment is likely to be closely related to chick production and, therefore, breeding success. The level of recruitment for mackerel icefish will only be obvious as the fish approach spawning. Chick or pup production has the potential to provide an indication of recruitment several years before this would be seen in a fish population. On the other hand, because the age of an individual fish can be estimated by examining its otoliths, age-based population analyses are possible. Such analyses give greater insight into population dynamics than is possible for species for which direct age determination is currently impossible.

How much Krill is required by the Dependent Species?

In addressing this question we are faced with a quantitative problem that is dependent on time and space scales. The definitions associated with CEMP parameters provide good indicators of the time and space scales, these are refined by considering the foraging footprint (Trathan et al., 1998) of each dependent species. Determining the amount of krill required by each species requires knowledge of the total numbers of predators

feeding within the area and their energetic requirements. It is important to recognise that the population unit chosen needs to take account of the integration zone. If the consideration is restricted to a single breeding colony, then the effects are local, whereas if the chosen species is widely distributed, such as the crabeater seal, then the area may extend over much of the Southern Ocean.

A number of scientists have investigated in detail the energetic requirements of birds and seals (Boyd et al., 1997; Croxall and Lishman, 1987), and these have been incorporated into models to estimate food requirements (Croxall et al., 1984). In the case of icefish, there is good information on diet (Kock et al., 1994) that indicates reliance on krill. There have been no reported studies on the metabolic rate of mackerel icefish although there have been extensive studies on other members of the group (see review by Hemmingsen, 1991), which means realistic estimates of energy requirements are possible.

The adaptation of these energetics models and the refinement of parameter values following continued research into dependent species should provide a good basis upon which to estimate the krill requirements of dependent species. This is an important component in ecosystem studies that has two major elements: population size and the energy requirement. Population size has been considered in the second question above. Energy requirement is a complicated issue, a review of which goes beyond the scope of the present paper. Because it is used to scale components of an energy budget to tonnes of krill, it is the key point of contact between dependent species assessments and removals of krill due to commercial fishing. It is therefore very important that predator energy budgets are carefully researched and estimated.

What is the Extent of Overlap between Krill Fishing and Foraging by Dependent Species?

It is not a simple process to describe adequately predator–fisheries overlap so, in order to understand the process, we need to break it down into manageable components. For the sake of simplicity I consider the problem from two perspectives: qualitatively – in terms of time and space, and quantitatively – in terms of the amounts of krill taken by the fishery in relation to the requirements of dependent species.

Penguins during the breeding season provide a good example of a ‘central-place forager’ since they are constrained by the range to which they

can venture in search of food and return in good time to feed a chick. Thus, for any given colony, the foraging area can be described by the segment of a circle whose radius is the maximum foraging range. Foraging activity can be determined by direct observations from research vessels at sea leading to the identification of particular foraging localities. It is also possible, due to the miniaturisation of instrument packages, to monitor individual animals at sea. This has been done for fur seals and, to a lesser extent, due to the smaller size of the animals, for penguins. Outside the breeding season, it is assumed that the birds forage over a much greater area; this may not necessarily be true, but since they are then not constrained by the need to return to a breeding site, they are able to search for food in other localities.

The situation for fish is somewhat different. The mackerel icefish are known to be restricted to the continental shelf region. It is not known to what extent feeding migrations take place, so it has to be assumed that spatially the whole shelf region is a reasonable descriptor of their feeding range at all times of the year (Kock et al., 1994).

Several approaches to the problem of determining the relationship between predator foraging and commercial fishing have been considered by CCAMLR. These were defined in terms of the type of overlap.

Precautionary overlap, which considers the largest spatial scale, is intended to cover the whole distribution of krill and all krill predators. It is covered by the KYM described earlier, and also by the model developed by Butterworth and Thomson (1995).

Potential overlap, is on a very broad scale such that local overlaps or separations between predators and the fishery may be missed or misrepresented. This has been considered by CCAMLR as the Critical Period Distance (CPD). The index is currently calculated as the krill catch within 100 km of predator colonies during the period December to March. It is not a measure of competition between predators and the fishery, but is a simple expression of potential niche overlap. Ichii et al. (1994a, b) considered the spatial distribution of colonies and catches in the Antarctic Peninsula region. They showed that although a high proportion of the catch may be taken within the foraging distance of land-based colonies, those colonies containing the largest numbers of penguins were not adjacent to the main fishing grounds. In order to make further progress with this type of work, a more refined approach is needed.

Another approach that attempts to incorporate fishing impact was described by Agnew and Phegan (1995). For this index the whole area was divided into small units of 10 x 10 n miles and the proportion P of the total number of penguins that were likely to feed in each unit estimated. This is multiplied by the total krill requirement of the penguins to give a penguin-krill requirement for the location K_p . The other component is the krill catch K_c over the same period in the same area. The index is the product ($K_p \cdot K_c$) and increases where either predation pressure or fishing increases. Even so, this still does not answer the question of how much krill is available within the small units.

Realised overlap, in which fine-scale overlap is measured, but without taking account of any movement of krill through the region. To describe this, a simple standardised index, such as Schroeder's index, has been used (SC-CAMLR, 1997). This has the form:

$$I_t = 1 - 0.5 \sum |p_{i,t} - q_{i,t}|$$

where $p_{i,t}$ is the proportion of krill consumed by a predator in grid square i during time period t and $q_{i,t}$ is the proportion of krill taken by the fishery in grid square i during time period t . The index ranges from $I_t = 0$, indicating no spatial overlap during period t , to $I_t = 1$, indicating complete overlap. Currently this index is used by CCAMLR where the grid-square is defined as the fine-scale rectangles half a degree of latitude by a degree of longitude.

This approach has considerable merit in defining the localities and times during which the interaction is likely to be most significant. However, since the two proportions are determined independently and without reference to the other component, care needs to be exercised in interpreting the results. Thus, to take an extreme example, if the fishery were taking less than 1% by mass of the krill required by penguins and all those krill were caught from a high-index foraging locality, the index would have a high value and yet no problem might exist. Some mechanism is therefore needed to incorporate total available krill into the index.

The Schroeder index and the Agnew-Phegan model provide indices of overlap and predation pressure on krill. There is a third component which would assist in determining whether fishing is likely to be having an effect on krill locally. This can be defined as the Fishing to Predation Index (FPI), the ratio of the amount of krill taken by commercial

fishing (K_c) compared to the amount required by predators (K_p), the dependent species:

$$FPI = \frac{K_c}{K_p}$$

An increase in the FPI indicates that fishing is taking a larger proportion of the available krill and consequently fishing is more likely to be having an impact on the dependent species. It is important to note that this index does not necessarily indicate that any management action is required, but rather provides a warning that an effect might be noticeable in some of the predator demographic parameters.

Dynamic overlap, whereby the interaction would be described by the functional link between predators and the fishery, would take account of fine-scale vertical and horizontal distributions of predators and the fishery and the availability of prey to both resource users. Undoubtedly this is the most difficult and complicated scenario, however it does provide the greatest insight into the functioning of the system. An example of a model that makes comparisons of penguin reproductive success and adult survival in the absence or presence of a krill fishery was developed by Mangel and Switzer (1998). Even though the extent of work in this field is currently rather limited, there is sufficient evidence to indicate that progress will be made in the foreseeable future.

Each of these indices has merits in determining the extent of overlap between the foraging activity of dependent species and commercial fishing. In terms of providing advice on the potential impact of fishing on dependent species, the FPI provides the best direct comparison. The extent of commercial fishing can be estimated adequately from haul-by-haul data. The other component is dependent on population size and the energy requirements of the predators. This places a great deal of reliance on the outcome of studies on the amount of krill required by dependent species.

An Ecosystem Approach to Krill Management

Having addressed the four questions associated with developing an ecosystem assessment, we are now in a position to see how these might be incorporated into a management regime. The problem of krill management in an ecosystem context can be reduced to two key questions. The over-riding and first question is: 'Taking account

of the requirements of dependent species, is the krill fishery sustainable in the long term?' This question is adequately addressed using the KYM for which, for a given large-scale area, the key input parameters are standing stock, growth, mortality, age and size at first spawning and the predator feeding requirement. This approach assumes that the dependent species are not unduly constrained in their foraging range. Although the basic approach is that of a single-species fishery, due regard is given to dependent species. The KYM can therefore be considered as providing a maximum limit for the krill fishery, whilst at the same time incorporating the total requirements of dependent species but not taking account of any spatial foraging characteristics that may constrain their activities.

If this approach is applied in isolation, it does not necessarily follow that all the requirements of Article II will be met. This is for two reasons. Firstly, errors in estimating the various parameter values may lead to erroneous results; this is true particularly for estimating the krill requirement of dependent species. Secondly, there may be local effects of krill fishing which have a disproportionately large effect. This is true particularly for the land-based dependent species and is a key consideration of CEMP.

Incorporation of this idea into the management regime raises further questions such as: 'Are dependent species being adversely affected by krill fishing?'

This in turn breaks down into a series of interrelated questions and action points for which the primary consideration is to determine whether there is any evidence of a decline in the populations of dependent species. If there is evidence of a decline, then a second question needs to be asked: 'Is that decline likely to be due to fishing?'

In the case of penguins, a comparison of the results from direct census methods and those from studies of chick production, survivorship and age at first breeding would provide guidance as to the likely cause. If the problem appeared to be a reduction in chick production, then the cause may lie with local krill availability during the chick growth period. However if the problem appeared to be associated with adult survival, then the cause may lie with reduced food availability outside the breeding season. A further possibility is that reduced chick production may be due to the adult birds being underweight or in otherwise poor condition, a result that may be due to poor winter feeding conditions.

Recognition of the possible causes of the decline in a dependent species population leads to consideration of the overlap between foraging activity and commercial fishing. The Schroeder and the FPI indices provide a good indication of whether demographic changes in dependent species are attributable to fishing activity. Ultimately this will lead to models of dynamic overlap, such as that developed by Mangel and Switzer (1998).

Armed with this information, it is possible to indicate the localities and seasons during which protection would need to be given to dependent species; this is an option that translates directly into conservation measures which define closed seasons or areas and local catch limits. The relatively simple approach outlined above needs to be extended to take account of krill that are subject to commercial fishing upstream of the observed dependent species–krill interaction; this emphasises the need for good studies on physical oceanography of the region. An important consequence of this approach is that smaller-scale management areas are designated on ecological grounds. These may equate to statistical subareas, but equally well they might be set as ranges from coastlines where land-based species breed.

The same reasoning can be applied to other dependent species that are monitored under CEMP, although the time and space scales of the interactions will obviously differ. Albatross and seal species, like penguins, are limited in their production of offspring to one or less chick or pup each season. This means that juvenile production in relation to mortality of breeding individuals provides a useful starting point.

This approach cannot be used in the case of fish generally and icefish in particular due to the poor relationship between recruitment and spawning stock size (Parkes, 1993). In the case of icefish, because it is also a harvested species, direct 'single-species' assessments are likely to be made in the first instance. If there is thought to be an indirect effect on icefish due to krill fishing, then a balance may need to be struck taking into account the economic factors underlying the two fisheries in the manner envisaged by Everson et al. (2000b).

The decision processes envisaged above, and shown as a conceptual framework in Figure 6, provide a structure within which a science plan can be formulated. This could be used to provide advice for the management of krill fisheries in an ecosystem context – the main requirement of

Article II. Further refinements are clearly possible, but establishing these links would be a major step in fisheries management.

ACKNOWLEDGEMENTS

The ideas presented in this paper have come about as a result of observations that have arisen from discussions with many colleagues at British Antarctic Survey (BAS) and also within WG-EMM. Their contribution, in whatever form that has been made, is gratefully acknowledged. I know that they may not agree with everything I have written but, hopefully, they will see this paper as an opportunity to continue to develop the debate on this most fascinating subject.

REFERENCES

- Agnew, D.J. and G. Phegan. 1995. A fine-scale model of the overlap between penguin foraging demands and the krill fishery in the South Shetland Island and Antarctic Peninsula. *CCAMLR Science*, 2: 99–110.
- Boyd I.L., D.J. McCafferty and T.R. Walker. 1997. Variation in foraging effort by lactating Antarctic fur seals: response to simulated increased foraging costs. *Behav. Ecol. Sociobiol.*, 40: 135–144.
- Butterworth, D.S. and R.B. Thomson. 1995. Possible effects of different levels of krill fishing on predators – some initial modelling attempts. *CCAMLR Science*, 2: 79–97.
- Butterworth, D.S., A.E. Punt and M. Basson. 1991. A simple approach for calculating the potential yield of krill from biomass survey results. In: *Selected Scientific Papers, 1991 (SC-CAMLR-SSP/8)*. CCAMLR, Hobart, Australia: 207–217.
- Butterworth, D.S., G.R. Gluckman, R.B. Thomson, S. Chalis, K. Hiramatsu and D. Agnew. 1994. Further computations of the consequences of setting the annual krill catch limit to a fixed fraction of the estimate of krill biomass from a survey. *CCAMLR Science*, 1: 81–106.
- CCAMLR. 2000. *CCAMLR Ecosystem Monitoring Program: Standard Methods for Monitoring Studies*. CCAMLR, Hobart, Australia.
- Constable, A.J. and W.K. de la Mare. 1996. A generalised model for evaluating yield and the long-term status of fish stocks under conditions of uncertainty. *CCAMLR Science*, 3: 31–54.

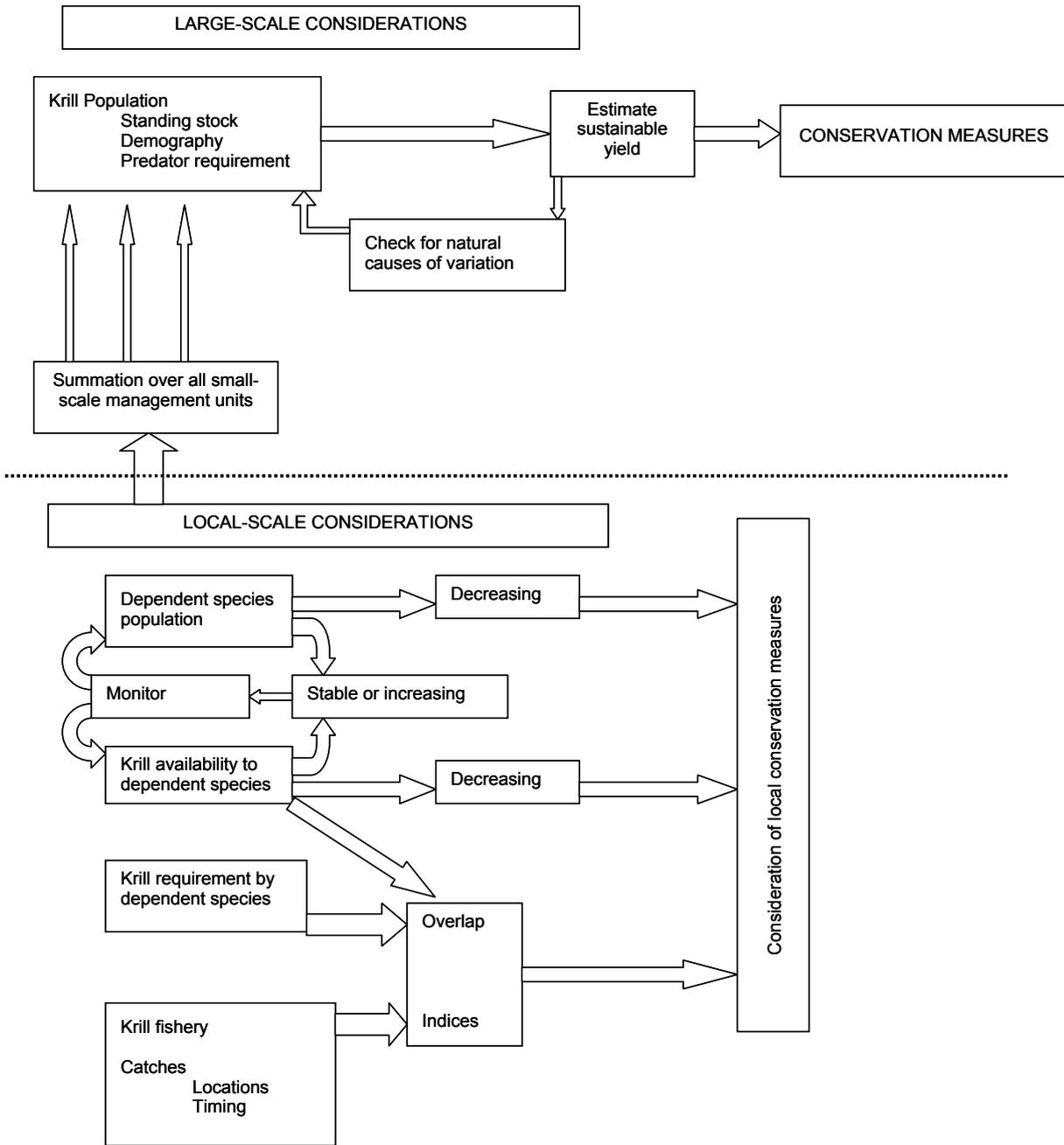


Figure 6: Key scientific information required to implement a management regime on a large scale, equivalent to a statistical area, and on a local scale.

- Croxall, J.P. and G. Lishman. 1987. The food and feeding ecology of penguins. In: J.P. Croxall (Ed.). *Seabirds: Feeding Ecology and Role in Marine Ecosystems*. Cambridge University Press, Cambridge: 101–131.
- Croxall, J.P., C. Ricketts and P.A. Prince. 1984. The impact of seabirds on marine resources, especially krill, of South Georgia waters. In: Whittow, C.G. and H. Rahn (Eds). *Seabird Energetics*. Plenum, New York: 285–317.
- Everson, I. and E. Murphy. 1987. Mesoscale variability in the distribution of krill *Euphausia superba*. *Mar. Ecol. Prog. Ser.*, 40 (1–2): 53–60.
- Everson, I. and K.-H. Kock. 2001. Variations in condition indices of mackerel icefish at South Georgia from 1972 to 1997. *CCAMLR Science*, 8: 119–132.
- Everson, I., G. Parkes, K.-H. Kock and I. Boyd. 1999. Variations in standing stock of the mackerel icefish *Champsocephalus gunnari* at South Georgia. *J. Appl. Ecol.*, 36: 591–603.
- Everson, I., K.-H. Kock and J. Ellison. 2000a. Interannual variation in the gonad cycle of the mackerel icefish. *J. Fish Biol.*, 57 (A): 103–111.
- Everson, I., D.J. Agnew and D. Miller. 2000b. Krill fisheries and the future. In: Everson, I. (Ed.). *Krill: Biology, Ecology and Fisheries. Fish and Aquatic Resources, Series 6*. Blackwell Science, Oxford: 345–348.
- Everson, I., A.W. North, A. Paul, R. Cooper and N.C. MacWilliam. 2001. Spawning locations of mackerel icefish at South Georgia. *CCAMLR Science*, 8: 107–118.
- Gulland, J.A. 1983. Fish stock assessment: a manual of basic methods. *FAO/Wiley Series on Food and Agriculture, Vol. 1*. J. Wiley and Sons, Chichester: 223 pp.
- Hemmingsen, E.A. 1991. Respiratory and cardiovascular adaptations in haemoglobin-free fish: resolved and unresolved problems. In: di Prisco, G., B. Maresca and B. Tota (Eds). *Biology of Antarctic Fish*. Springer-Verlag, Berlin Heidelberg: 191–203.
- Hewitt, R. 2000. An index of per capita recruitment. *CCAMLR Science*, 7: 179–106.
- Hilborn, R. and C.J. Walters. 1992. *Quantitative Fisheries Stock Assessment: Choice, Dynamics and Uncertainty*. Chapman and Hall Inc., London: 570 pp.
- Ichii, T., M. Naganobu and T. Ogishima. 1994a. An assessment of the impact of krill fishery on penguins in the South Shetlands. *CCAMLR Science*, 1: 107–128.
- Ichii, T., M. Naganobu and T. Ogishima. 1994b. A revised assessment of the impact of krill fishery on penguins in the South Shetland Islands. Document *WG-Joint-94/17*. CCAMLR, Hobart, Australia: 20 pp.
- Kock, K.-H. 1992. *Antarctic Fish and Fisheries*. Cambridge University Press, Cambridge: 359 pp.
- Kock, K.-H., S. Wilhelms, I. Everson and J. Gröger. 1994. Variations in the diet composition and feeding intensity of mackerel icefish (*Champsocephalus gunnari*) at South Georgia (Antarctica). *Mar. Ecol. Prog. Ser.*, 108 (1–2): 43–57.
- Mangel, M. and P.V. Switzer. 1998. A model at the level of the foraging trip for the indirect effects of krill (*Euphausia superba*) fisheries on krill predators. *Ecol. Modelling*, 105 (2–3): 235–256.
- Parkes, G.B. 1993. *The Fishery for Antarctic Icefish, Champsocephalus gunnari, around South Georgia*. Unpublished PhD thesis. Imperial College of Science, Technology and Medicine, London University: 465 pp.
- Reid, K. and J.P. Croxall. 2001. Environmental response of upper trophic-level predators reveals a system change in an Antarctic marine ecosystem. *Proc. Roy. Soc. Lon.*, B 268: 377–384.
- Saville, A. 1977. Survey methods of appraising fishery resources. *FAO Fish. Tech. Pap.*, 171: 76 pp.
- SC-CAMLR. 1991. Temporal and spatial scales for monitoring CEMP predator parameters (WG-CEMP). In: *Report of the Tenth Meeting of the Scientific Committee (SC-CAMLR-X)*, Annex 7, Appendix E. CCAMLR, Hobart, Australia: 413–418.
- SC-CAMLR. 1994. Report of the Workshop on Evaluating Krill Flux Factors. In: *Report of the Thirteenth Meeting of the Scientific Committee (SC-CAMLR-XIII)*, Annex 5, Appendix D. CCAMLR, Hobart, Australia: 267–289.

- SC-CAMLR. 1995. Report of the Working Group on Ecosystem Monitoring and Management. In: *Report of the Fourteenth Meeting of the Scientific Committee (SC-CAMLR-XIV)*, Annex 4. CCAMLR, Hobart, Australia: 105–253.
- SC-CAMLR. 1997. Report of the Subgroup on Statistics. In: *Report of the Sixteenth Meeting of the Scientific Committee (SC-CAMLR-XVI)*, Annex 4, Appendix D. CCAMLR, Hobart, Australia: 209–233.
- SC-CAMLR. 2000. Report of the B₀ Workshop. In: *Report of the Nineteenth Meeting of the Scientific Committee (SC-CAMLR-XIX)*, Annex 4, Appendix G. CCAMLR, Hobart, Australia: 209–273.
- Siegel, V. and S. Nicol. 2000. Population parameters. In: Everson, I. (Ed.). *Krill: Biology, Ecology and Fisheries. Fish and Aquatic Resources, Series 6*. Blackwell Science, Oxford: 103–149.
- Thomson, R.B., D.S. Butterworth, and I.L. Boyd and J.P. Croxall. 2000. Modelling the consequences of Antarctic krill harvesting on Antarctic fur seals. *Ecol. Appl.*, 10 (6): 1806–1819.
- Trathan, P.N., E.J. Murphy, J. Croxall and I. Everson. 1998. Use of at-sea distribution data to derive potential foraging ranges of macaroni penguins during the breeding season. *Mar. Ecol. Prog. Ser.*, 169: 263–275.
- Watkins, J.L. 2000. Aggregation and vertical migration. In: Everson, I. (Ed.). *Krill: Biology, Ecology and Fisheries. Fish and Aquatic Resources, Series 6*. Blackwell Science, Oxford: 80–102.
- Williams, A.D. 1995. *The Penguins Spheniscidae. Bird Families of the World*. Oxford University Press, Oxford.

Liste des tableaux

- Tableau 1: Échelles spatio-temporelles des paramètres du CEMP relatifs aux manchots, aux albatros à sourcils noirs et aux otaries. Récapitulation d'informations provenant de SC-CAMLR, 1991.
- Tableau 2: Observations sur le terrain de la survie des manchots comparée à la survie estimée à partir de la production de jeunes et de l'âge à la première reproduction au moyen de l'équation 1.
- Tableau 3: Comparaison des taux de survie nécessaires à différents moments des stades précoces du cycle vital des animaux pour conserver une population en état d'équilibre. Les informations sur le manchot Adélie proviennent du tableau 2, et celles sur le poisson des glaces de Kock, 1992 et Everson et al., 1999.

Liste des figures

- Figure 1: Échelles spatio-temporelles des interactions des activités d'alimentation des manchots et la quantité disponible du krill.
- Figure 2: Secteurs d'alimentation disponibles pour les prédateurs se reproduisant à trois colonies. Deux échelles spatiales sont indiquées : les lettres minuscules (a, b et c) représentent les activités locales à petite échelle temporelle telles que les paramètres A5, A7 et A8; les lettres majuscules (A, B, et C) représentent les activités d'alimentation à plus grande échelle telles qu'A2.
- Figure 3: Représentation schématique de la circulation des eaux porteuses de krill aux alentours des colonies de prédateurs se reproduisant à terre : a) mouvement direct du krill le long de la côte devant une série de colonies, b) circulation provoquée par la topographie amenant le krill de sources différentes à des colonies relativement proches.
- Figure 4: Effet de l'échec de la reproduction et taille de la population. Au cours des 20 premières années le recrutement est distribué au hasard entre 1 000 et 2 000. À partir de la vingtième année, pour deux saisons sélectionnées au hasard tous les dix ans, il y a un échec total de reproduction entraînant un échec du recrutement de ces classes d'âge. Cette analyse a été effectuée pour deux taux de survie; elle met en évidence une fluctuation plus importante de la taille de la population lorsque le taux de survie réduit, d'où il découle que la taille de la population dépend de la classe d'âge en cours de recrutement.

Figure 5: Estimation du taux de survie minimum nécessaire, pour une valeur donnée de l'âge à la première reproduction, pour assurer une taille de la population stable à quatre niveaux de production par couple reproducteur. Les calculs ont été effectués de façon itérative au moyen de l'équation 1.

Figure 6: Informations scientifiques clés nécessaires pour la mise en œuvre d'un régime de gestion à grande échelle, c.-à-d. à l'échelle d'une zone statistique, et à une échelle locale.

Список таблиц

Табл. 1: Временные и пространственные масштабы параметров СЕМР для пингвинов, чернобровых альбатросов и морских котиков. Обобщена информация НК-АНТКОМ, 1991 г.

Табл. 2: Полевые наблюдения выживаемости пингвинов по сравнению с выживаемостью, оцененной по рождению птенцов и возрасту при первом размножении (оценка по Уравнению 1).

Табл. 3: Сравнение уровней выживаемости, необходимых на ранних стадиях жизненного цикла животных для сохранения устойчивой популяции. Информация о пингвинах Адели взята из табл. 2, а о ледяной рыбе – из публикаций К.-Г. Кока (Cock, 1992) и И. Эверсона (Everson et al., 1999).

Список рисунков

Рис. 1: Временные и пространственные масштабы взаимодействия между наличием криля и поиском пищи пингвинами.

Рис. 2: Доступные хищникам ареалы поиска пищи – три участка размножения. Показаны 2 пространственных масштаба: строчные буквы (a, b и c) относятся к локальной деятельности с коротким временным масштабом (например, параметры A5, A7 и A8); заглавные буквы (A, B и C) относятся к добыче корма в большем пространственном масштабе (например, параметр A2).

Рис. 3: Схематическое представление характера циркуляции, переносящей криль в районе колоний размножающихся на суше хищников: (a) перенос криля вдоль берега, вдоль нескольких колоний, (b) топографически обусловленная циркуляция, переносящая криль из различных источников к соседним колониям.

Рис. 4: Влияние неудачного размножения и размер популяции. В течение первых 20 лет пополнение случайным образом распределено между 1000 и 2000. Начиная с 20 года, в 2 сезонах, выбранных случайным образом из каждых 10 сезонов, наблюдается абсолютная неудача размножения, приводящая к неудачному пополнению для этих годовых классов. Анализ для двух уровней выживаемости показывает, что большие колебания размера популяции связаны с низкой выживаемостью и, следовательно, большей зависимостью размера популяции от пополняющего годового класса.

Рис. 5: Оценочная минимальная выживаемость, необходимая при заданном возрасте при первом воспроизводстве, чтобы обеспечить стабильный размер популяции, – 4 уровня продуктивности (птенцов на размножающуюся пару). Итеративные расчеты по Уравнению 1.

Рис. 6: Ключевая научная информация, требуемая для реализации режима управления в крупном (равном статистическому району) и местном масштабах.

Lista de las tablas

Tabla 1: Escalas temporales y espaciales de los parámetros del CEMP correspondientes a los pingüinos, al albatros de ceja negra y al lobo fino antártico. Resumen de la información de CC-CRVMA, 1991.

Tabla 2: Observaciones en terreno de la supervivencia de los pingüinos en comparación con la supervivencia estimada a partir de la producción de polluelos y de la edad de la primera reproducción estimada mediante la ecuación 1.

Tabla 3: Comparación del nivel de supervivencia requerido en diversas etapas iniciales del ciclo de vida de los animales para mantener la población en un 'estado estable'. Los datos sobre el pingüino adelia provienen de la tabla 2, y los del draco rayado de Kock, 1992 y Everson et al., 1999.

Lista de las figuras

- Figura 1: Escalas temporales y espaciales de la interacción entre los pingüinos en búsqueda de alimento y la disponibilidad de kril.
- Figura 2: Zonas de alimentación disponibles para los depredadores que se reproducen en tres colonias. Se indican dos escalas espaciales: las letras en minúscula (a, b, y c) se refieren a las actividades localizadas realizadas en un corto periodo de tiempo tales como las descritas por los parámetros A5, A7 y A8; las letras en mayúscula (A, B, y C) se refieren a las actividades de búsqueda de alimento más prolongadas tal como las describe el parámetro A2.
- Figura 3: Ilustración esquemática de modelos de circulación oceánica del kril en los alrededores de las colonias de reproducción de los depredadores: (a) movimiento directo de la deriva litoral de kril, que abarca una serie de colonias. (b) circulación determinada por la topografía, trayendo el kril de diversas fuentes a las colonias situadas en estrecha proximidad.
- Figura 4: Consecuencias de una mala reproducción en el tamaño de la población. Durante los primeros 20 años el reclutamiento está distribuido aleatoriamente entre 1 000 y 2 000. A partir del veinteavo año, se produce el fracaso total de la reproducción en dos temporadas seleccionadas aleatoriamente de cada 10, con el fracaso consiguiente del reclutamiento de esas clases anuales. Se ha efectuado el análisis para dos niveles de supervivencia, demostrándose una mayor fluctuación en el tamaño de la población cuando la supervivencia es baja, y una consiguiente dependencia del tamaño de la población en la clase anual reclutada.
- Figura 5: Estimación de la supervivencia mínima requerida para que una edad dada de primera reproducción asegure un tamaño estable de la población a cuatro niveles de producción de polluelos por pareja reproductora. Los cálculos se han hecho iterativamente mediante la ecuación 1.
- Figura 6: Información científica clave necesaria para aplicar un régimen de ordenación en gran escala, equivalente a un área estadística, y en una escala local.