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Harvesting Krill: Ecological Impact, Assessment, Products and Markets

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Harvesting Krill

Ecological Impact, Assessment, Products & Markets

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DIRECTION'S INTRODUCTION

"Let them eat krill"

Tony J. Pitcher, Fisheries Centre, UBC.

Krill are defined here as the euphausiids, a relatively small (about 85 species world-wide) and uniform taxon of large (10-80 mm adults) pelagic shrimp-like filter-feeding crustaceans. Most species inhabit the upper 400m of the ocean and shed their eggs into the sea, but a few (e.g. *Nyctiphanes*) have evolved parental care of the eggs until hatching into nauplii. Many species exhibit diurnal migration, approaching the surface to feed at night. Krill biomass world-wide is thought to exceed 300 million tonnes and they are particularly abundant in North Atlantic, Antarctic and North Pacific oceans.

In the North Pacific, the large-eyed *Euphausia pacifica* occurs in sub-arctic waters less than 300m deep, is especially plentiful in the Sea of Japan, North Pacific drift and Californian current, and is the species that has been considered for commercial harvest in British Columbia.

Ecological Role of Krill
Krill, whose biomass often rivals that of copepods in the plankton community, comprise a critical link in oceanic food webs between their phytoplankton food and their fish predators, many of which are commercially important fishes. It follows that direct harvesting of such a pivotal component in the food web has an ecological impact that must be evaluated if large-scale fisheries for krill are contemplated.

Most krill species are herbivorous, and in high latitudes krill consume many diatoms, but many krill species can utilise zooplankton as well, and some (e.g. *Megayctiphanes*) are carnivorous. So for most krill species, through the 'cascade' effect, phytoplankton might be expected to increase when krill are harvested by man,

Organisms that feed on krill might decrease in abundance if krill are harvested. These include many species of fish that are themselves the subjects of substantial human fisheries. In the North Pacific, krill form an important component of the diet of herring, salmon, pollack, sardine, mackerel and capelin, all of which support important commercial fisheries. The role of krill as food of squid is thought to have been overestimated.

Hence there is a fear that excessive harvest of krill might lead to:

- algal blooms of unharvested phytoplankton
- negative impacts on krill-dependent predators
- subsequent lower abundance of commercial fish stocks

Krill consumption by fish has been estimated and modelled in the Antarctic and so this workshop would aim to set up analogous models for the BC coastal region. Using the models, the impact of various levels of krill harvest in this region may be forecast.

Assessment, Potential Yield and Management of Krill Fisheries
Abundance is the key input parameter for the evaluation of all harvest impacts and for fishery regulation. The assessment and measurement of krill abundance presents challenges to both existing sonar technology and to mathematical modelling.

Estimating the biomass of krill in the plankton cannot be done with standard fisheries acoustics technology, most of which has been designed for fish which are larger and have relatively high target strengths. Selection of equipment, selection of frequency, target identification, calibration of gear and measurement error are important topics in acoustic methodology for krill assessment.

Although krill growth appears to be well understood, modelling their population dynamics is subject to considerable uncertainty, especially in recruitment and the effect of social swarming behaviour. The design and analysis of surveys that can provide robust estimates of krill abundance is therefore critical to success.

Estimation of the potential yield of krill stocks leads to problems in demographics and in the estimation of recruitment. Assessment and potential yield evaluations may subsequently be used in developing suitable management measures for krill fisheries. In the Antarctic, CCAMLR researchers in particular have recently made some progress in these two areas.

Harvesting Technology for Krill
The Russian, Norwegian and Japanese have harvested Antarctic krill since the 1960s, trawling on the large social swarms that gather. Cost effective harvesting of krill in other waters appears not to have been extensively investigated, although recent innovations have been made in British Columbia.

Processing and Products from Krill
The processing of organisms high in oils and pigments presents both technical difficulties and economic opportunities to serve new and emerging markets.

Markets for Krill
Unconventional processing of krill products is developing unexpected new markets. For example, krill pigments that may be used in the aquaculture feed industry fetch much higher prices and profits than using krill for fishmeal or using krill tails for human consumption, as has been done in Russia and Japan.

The BC Krill Industry
The krill harvesting industry in BC has already invested a considerable amount of work in three areas:

- harvesting technology
- acoustic assessment technology
- product technology

The small krill harvest quotas currently allowed in BC have not been subjected to independent review. This workshop brings together the BC industry, government and independent fishery scientists to address this problem.

New Fishery Guidelines
Essential features of the development of a new fishery are summarized in Figure 1.

The Workshop
The workshop aims to provide a rational basis for krill exploitation by evaluating ecological parameters and impacts, assessment methodology, krill products and markets.

The workshop was held on 14-16 November, 1995. It brought together international experts on krill from South Africa, the United Kingdom, Australia, Chile, Japan, Germany and the USA together with concerned representatives from BC fishing industry, BC government, local researchers and scientific staff from the UBC Fisheries Centre. Clients for the workshop are BC fishing industry. The workshop was co-sponsored by Sustainable Oceans Resource

Society of B.C. and participating companies; B.C. Ministry of Agriculture, Fisheries and Food; and Spark Oceans Initiative, Science Council of B.C.

Apart from this FC research report, an important output is a multi-author book in the *Chapman & Hall Fish & Fisheries Series*, with the suggested title: *Harvesting Krill: ecological impacts, assessment, products and markets*, edited by I. Everson and T.J. Pitcher. It is hoped that the book will be published in 1997.

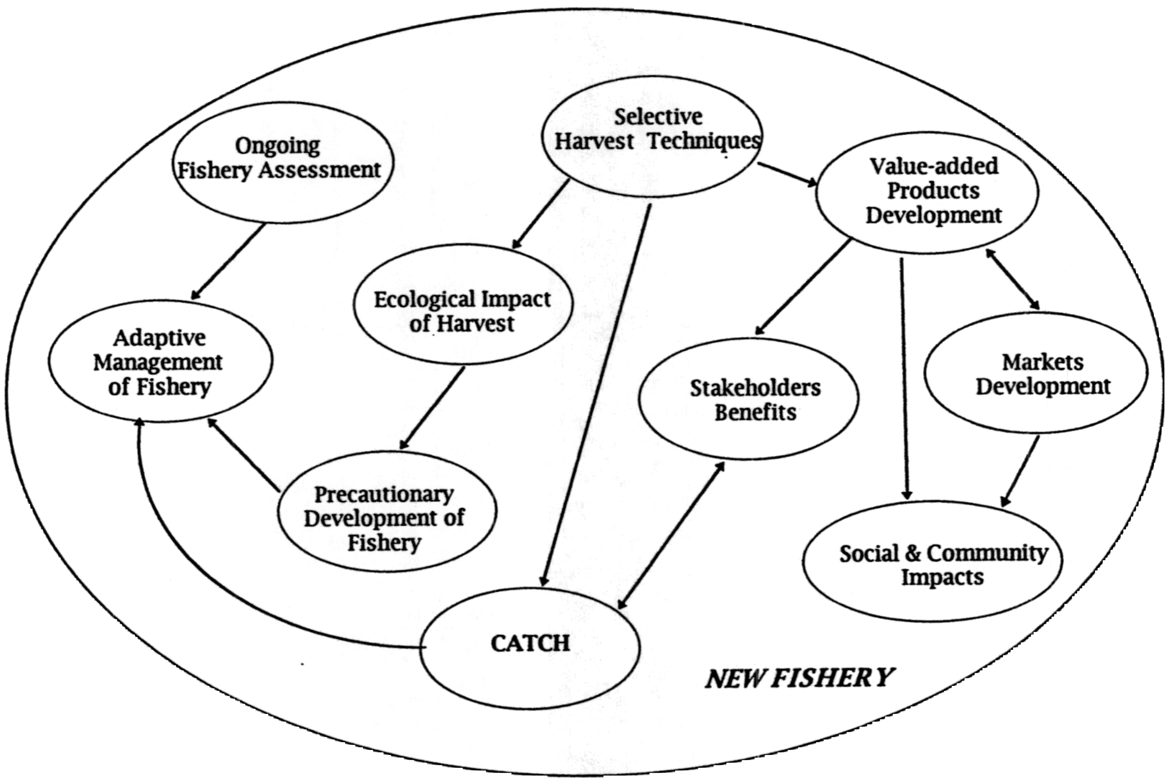

Figure 1. Diagram summarising essential features of the development of a new fishery.

MODELLING AND DATA REQUIREMENTS FOR MANAGEMENT OF THE ANTARCTIC KRILL-BASED ECOSYSTEM

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Scope

The development of CCAMLR's management of Antarctic krill (*Euphausia superba*), and the krill-based ecosystem has been described in some detail by Miller & Agnew, Everson and Nicol (a) in this volume. This paper explains some of the models used, and the data (see also Nicol (b) this volume) that CCAMLR has required to develop and implement these models.

Underlying philosophies: precautionary and ecosystem approaches and dealing with uncertainty

CCAMLR has considered two underlying philosophies in its approach to managing Antarctic resource exploitation, both of which arise from its Article II (see Everson and Miller & Agnew this volume). These are the precautionary approach and the ecosystem approach. The precautionary approach, which is essentially a set of guidelines for responsible exploitation includes, especially, a re-adjustment of the concept of the burden of proof. One of its central concepts is that fisheries should develop in a controlled fashion in concordance with the information available to manage them, and that the consequences of development should be demonstrated prior to that development. Although this approach has been the subject of much international discussion recently (in particular see the report of the FAO/Government of Sweden meeting in Lysekil and the FAO Code of Conduct) CCAMLR has been using these concepts in its management since the mid-1980s.

The ecosystem approach and strategies for dealing with uncertainty arise naturally out of this philosophy. Among the consequences which should be considered as fisheries develop is the effects these fisheries have on dependent and related species. This will depend on ecosystem complexity and interactions, and its consideration is termed the ecosystem approach. Similarly uncertainty must be taken into account in developing management advice within a precautionary approach.

Importantly these ideas should not be taken to imply that fisheries cannot start until all information to predict the dynamics of a system has been gathered, nor should it be taken to imply that lack of information is a reason to impose management systems which are independent of scientific advice. On the contrary, models for management should be constructed to incorporate all uncertainties, and efforts should always be made to decrease these uncertainties within the constraints (practical, economic, biological) of the system. Management advice developed using such models is truly precautionary, and in general will tend to be more conservative (in terms of the TAC and effects on the stock and dependent species) as uncertainty increases.

Conceptual Framework

CCAMLR has developed a conceptual framework of the Antarctic ecosystem within which it is developing a management system which takes the approaches outlined above into account (Figure 1: see SC-CAMLR 1995 for explanation). The components of this framework have been selected as the most important ecosystem components for management of the system. It is not an attempt to model the whole antarctic ecosystem, neither is it a framework for an ecopath approach (see Jarre-Teichmann this volume).

Within this framework several models of individual components and interactions have already been developed. CCAMLR's intention is to further develop these models and to integrate different models as required for specific management objectives.

Krill yield model

The krill yield model is the model that is being used currently to set precautionary limits for the krill fishery. It developed from the approaches developed by Beddington and Cooke (1983), and involves stochastic projections of a population which is subjected to a constant fishing yield. Uncertainty in any model parameters, such as selectivity, natural mortality, production and recruitment are taken into account in the modelling and stochastic process. The yield is expressed as a ratio of unexploited biomass determined from a survey, which itself can be associated with various levels of uncertainty, in the equation yield = g Bo, where Bo is the pre-exploitation biomass survey and g is the ratio calculated by the model.

The essential features of the model are that a range of g are chosen, a projection model with a number of stochastic parameters is run for 1000 simulations with catches equal to this yield, and statistics are calculated using the projected distributions of spawning stock biomass for the probability that the spawning stock biomass (Bsp) drops below a certain proportion (dcrit) of its unexploited median level (Ksp), and the median level of Bsp after a 20 year period of fishing.

A schematic diagram of the model is given in Figure 2 (see Butterworth et al 1994 and SC-CAMLR 1994 for a full description).

An appropriate long-term yield for the fishery may then be chosen by applying a number of clearly defined decision rules to the outputs of the model. In the CCAMLR system, the first decision rule has been to choose g1 such that the probability of spawning stock biomass dropping below 20% (dcrit) of its median level in the absence of fishing is 10%. This decision rule acts to safeguard the stock against overexploitation. The second decision rule has been to choose a g2 such that the median spawning stock biomass after 20 years is 75% of its median level in the absence of fishing. This second rule acts to protect predators against situations where their prey suffer unacceptable declines. The final decision rule has been to choose the most conservative of these two g as the final g that should be applied to an estimate of Bo to calculate a precautionary catch limit for krill.

Central to this model is variability in recruitment. In its first formulation (Butterworth et al 1994) the model used bounded variables for M (from U[.4,1.0]) and recruitment variance (from a log-normal distribution). However, later developments described by de la Mare (1994) and incorporated into the yield model by Agnew (1994) included the sampling of recruitment from distributions whose mean and variance were consistent with recruitement estimated from trawl survey data, and calculations of M which were also consistent with these data. These developments effectively reduced the uncertainty associated with estimation of recruitment and natural mortality by basing it upon empirical data, and demonstrate well the process of review and modification demanded of the precautionary approach.

Application of the yield model

Results for Antarctic krill have produced estimates of g1 and g2 of 0.149 and 0.116 respectively, although the model is currently subject to revision in some areas of the Antarctic. As an example of the use of these g values, for the southern indian ocean (Division 58.4.2) where Bo has been estimated as 3.9 Million tonnes, the calculated yield would be 450 000 tonnes.

The approach provides a framework for determining an estimate of yield that is calculated taking uncertainty in model parameters into account. Any number of parameters may be added to such a model, and uncertainty in any of them, to any degree, may be incorportated. The approach is ultimately extremely flexible, because the model itself may be modified, different parameters introduced, variances adjusted, and even autocorrelation and trends introduced as more information becomes available.

The decision rules are also subject to modification to suit local conditions. The incorporation of rules based on P/B ratios, for situations depending more heavily upon within-season production than the Antarctic system for which the present system was developed, is relatively simple. Similarly, adjustment of the "risk levels", that is the 10% probability of stock depletion or the limit of 75% depletion of the final stock, is also a matter for adjustment to suit individual situations. The choice of such levels is arbitrary, and depends on the individual comfort levels of managers confronted with various community concerns, but those values quoted above have been found to be acceptable in the Antarctic krill situation.

Most importantly, the approach offers a framework for the precautionary development of a fishery, because as uncertainty decreases so estimated yields increase. Under such a framework, a precautionary fishery could be allowed with a very conservative catch limit, based on a model with maximum uncertainty. As information from both the fishery and fishery-independent research becomes more comprehensive, uncertainty will decrease and, up to a point, catch limits will increase. The model should not be used as an excuse to do no research, but rather should be used in situations where there is little information so that some scientifically based management can be implemented immediately, while efforts to refine the model, and even to develop other, more responsive (feedback) approaches, proceed. Fisheries developing under such a regime should always be controlled by conservative catch limits and should avoid boom and bust situations which are dammaging to stocks, ecosystems and industry.

Other models

A number of other models have been developed under the conceptual model outlined in Figure 1. One of the earliest to be investigated was the overlap between predator foraging areas and the fishery, which has been the subject of much discussion in CCAMLR, because this overlap offers potential for competition between these two resource users. The krill fishery is generally concentrated in quite specific areas over the shelf break, and these areas may be within foraging distance (generally about100km) of penguin and seal colonies on the Antarctic mainland and offshore islands. These predators are dependent upon gathering large quantities of krill to feed offspring during the breeding period (January to March). Models developed by Agnew (1992), Ichii et al (1994) and Agnew & Phegan (1994) have explored the relationship between predator foraging areas and krill fishery distribution, and while the precise functional relationship which would define their interaction remains elusive, present evidence is that the overlap problem is decreasing.

Time and space does not allow a description of the other models, but full discussions may be found in the papers listed in the references section.

Data requirements

Data requirements for the modelling of krill yield are fairly minimal, and centre around an estimate of unexploited biomass, and estimate of recruitment proportion and variability, and krill growth - see Nicol (b) (this volume) for further infomation. Refinement of the yield model necessarily depends on a better understanding of the system or additional data. Other modelling demands more data, such as predator abundance, distribution, foraging characteristics, breeding biology and survivorship. Easily obtained fisheries data which have proved extremely valuable to CCAMLR are fine scale (at least 1/2o latitude by 1o longitude by 10 days periods) catch and effort data and representative length frequencies from the fishery.

One very important component, especially in a developing fishery, is the provision that scientific observers are on vessels for the accurate collection of basic biological and environmental data, and also to obtain data on bycatch of juvenile fish (see Moreno this volume) and other incidental mortality in the fishery.

Conclusion

CCAMLR has specified a framework within which it is developing a number of models of various parts of the Antarctic exploited ecosystem. The objective of all the modelling is towards rational management of Antarctic marine living resouces within the contexts of a precautionary approach and an ecosystem approach to management.

The first acceptance of such approaches was in 1991, when CCAMLR adopted a conservation measure setting a precautionary catch limit for krill which was calculated using the krill yield model outlined in this paper. The model incorporates uncertainty in a number of parameters, and decision rules are applied to its outputs which choose a level of fishing which both conserves the krill stock and protects predator requirements for krill. This approach has been accepted by CCAMLR, in its concensus decision making process, as an appropriate method for controlling the development of krill fisheries.

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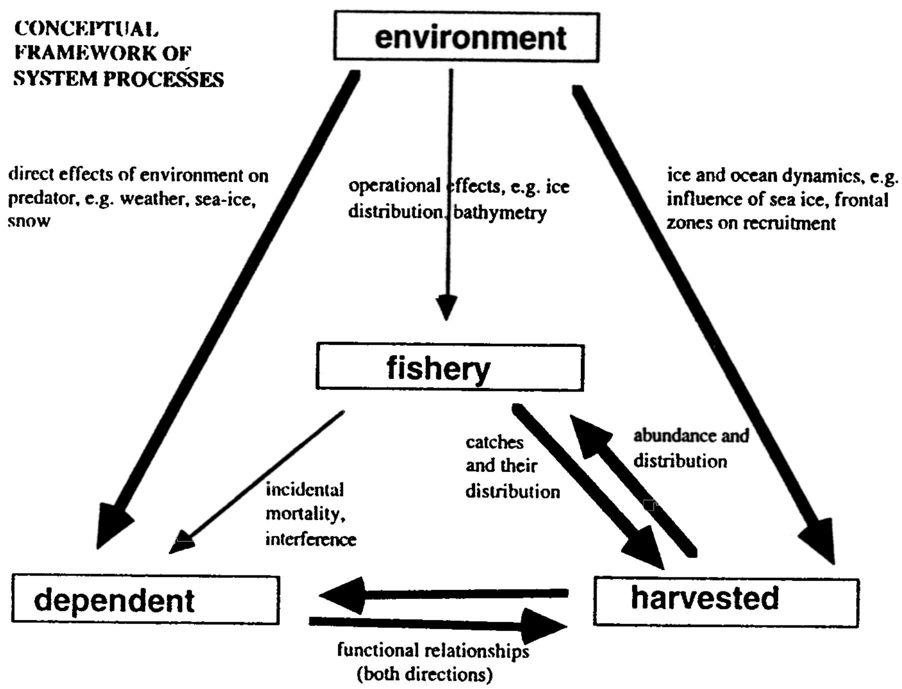

Figure 1 Conceptual framework of system processes

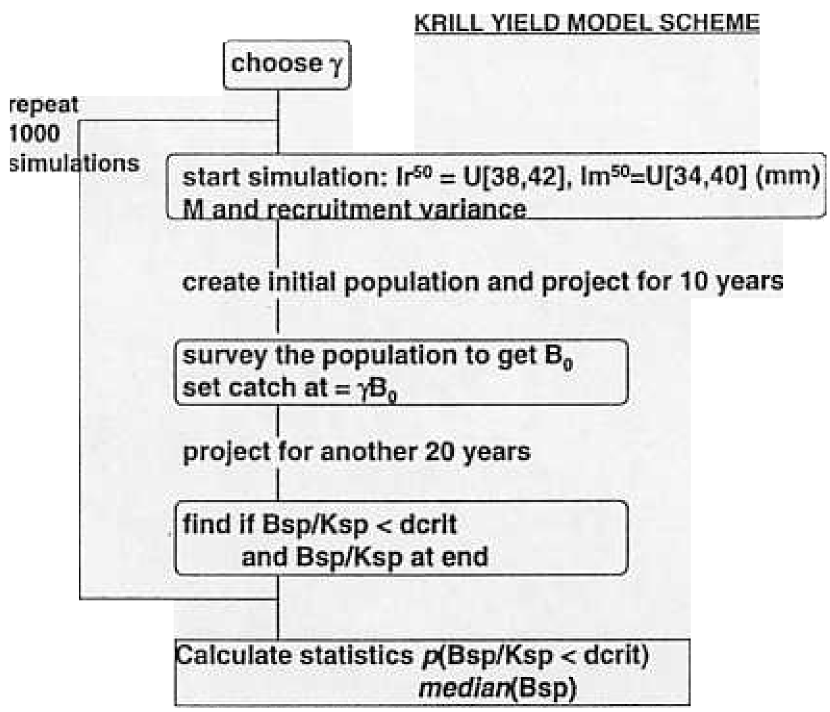

Figure 2. Krill yield model scheme

FISHERY BIOLOGY OF EUPHAUSIA PACIFICA IN THE JAPANESE WATERS

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The fishery on *Euphausia pacifica* or tsunonashi-okiami in Japanese vernacular name commenced in mid 1940s in the Sanriku waters, the sea area off northeastern Japan. The average annual catch is about 60,000 tons in the last 10 years. The fishing condition is highly dependent on the strength of the cold Oyashio Current. Attempts were made to predict the fishing conditions and the first fishing day of the year based on the southernmost latitude of the Oyashio Current in winter. There is some possibility that long-term trend in the fishing conditions can be predicted based on the wind field over the North Pacific Ocean upon which southward shift of the Oyashio Current seems to depend.

E. pacifica is considered as a key species in the Sanriku waters and many endemic and migrant predators including pelagic and demersal fishes, marine mammals, sea birds and possibly benthic organisms such as ophiuroids depend on the species as food.

Among demersal fishes, walleye pollack is most important in the Sanriku waters. A study examined the occurrence of *E. pacifica* in the stomachs of various size groups of walleye pollack, Pacific cod and Pacific herring and estimated the amount of krill consumed by these demersal fishes. The estimated values were 540,000, 8,500 and 1,300 tons for walleye pollack, Pacific cod and Pacific herring, respectively. A total of 550,000 tons of *E. pacifica* were consumed each year off Miyagi and Fukushima Prefectures. As about 52% of the demersal fish landings for the whole fishing grounds of krill is landed at the Ishinomaki Fish Market, about 1,000,000 tons of *E. pacifica* may be consumed by demersal fishes in the whole area.

Pelagic fishes such as sardines, Japanese chub mackerel and Japanese flying squid migrate in large numbers into the sea area in May-January. The quantitative estimates of krill consumed by these pelagic fishes are needed.

In early summer, sooty shearwater, slender-billed shearwater and pale-footed shearwater visit the Sanriku waters in large flocks during their northward migration. Slender-billed shearwater seems to be an important krill feeder because the species feed mainly on a euphausiid, Nyctiphanes australis in their breeding area of Tasmanian waters. In the fishing season of *E. pacifica*, a large number of auklets may feed on them, which seems to come to the sea area from the Okhotsk Sea to overwinter.

E. pacifica males with empty ejaculatory duct(s) are easily found in the commercial catch. Females with an attached spermatophore, however, are rare. Two possible reasons can be pointed out on the scarcity of females with an attached spermatophore. The first one is that copulated females leave the swarm and stay in the midwater deeper than 15 m in the daytime and therefore cannot be collected by bow mounted trawl. The second one is detachment of attached spermatophores from thelycum when molting, which was supported by the observation of successive occurrence of small number (15%) of females with an attached spermatophore but carapace not swollen in late March-early April, large number of females with an attached spermatophore and swollen carapace in early April, and finally females without spermatophore but swollen carapace in mid April off Ibaraki Prefecture.

Eggs and larvae of the species occur throughout the year but most of them occur in April-July. The life span of *E. pacifica* in the Sanriku waters is estimated to be one and a half years, which is similar to that in the Strait of Georgia, shorter than that in the Okhotsk Sea and off Kamchatka-south of Aleutians but longer than that off Oregon and southern California. Growth cessation in summer is not so long as reported in the Japan Sea.

In the coastal waters of Ibaraki Prefecture, the southernmost distributional range of the species, swarms descend to cooler mid water as the surface water temperature increases. Since this finding, mid water swarms as well as benthopelagic and surface swarms have been targeted. Surface swarms were formed in the years when cold water (5-7C) prevailed from the surface to the bottom, whereas benthopelagic swarms were formed when the water column was stratified with warm water>10C at the surface and thick cold water (6-9C) at the deeper layers. The benthopelagic population proved to occur throughout the year on the sea floor at 280m depth. Observations by submersibles showed that the dense bed of ophiuroids co-occurred with benthopelagic *E. pacifica* and ophiuroids were waving their arms as if they were trying to catch them. Distributional range, biomass, diurnal and seasonal migration of benthopelagic krill must be clarified to understand the structure of marine food webs of the Sanriku waters and management of krill fishery.

THE CCAMLR EXPERIENCE

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Increased pressure on conventional fishery resources during the 1960's caused several fishing nations to look further afield in their search for harvestable resources. As a direct result, the former Soviet Union sent exploratory fishing vessels to the Southern Ocean in search of krill and finish. Intensive fishing on Notothenia rossii around South Georgia for about three years around 1970 resulted in reported catches of over half a million tonnes with the result that the stock collapsed. At the same time that this fishery was active the technology to catch and process krill were being developed.

Experience in other parts of the world where major fisheries, such as the Peruvian Anchovy, had collapsed raised concerns amongst scientists concerned with Southern Ocean resources. The main reason for this concern was that, since krill is at the hub of the Southern Ocean food web, overfishing could have a major impact, not just on krill itself but also on dependent species such as whales, seals, birds, fish and squid. As a direct result the Scientific Committee for Antarctic Research (SCAR) set up a programme, Biological Investigations of Marine Antarctic Systems and Stocks (BIOMASS), focused on krill in the context of the structure and dynamic functioning of the Southern Ocean ecosystem. A major research initiative of BIOMASS was FIBEX, a large scale multiship survey of the standing stock of krill in part of the Southwest Atlantic and Indian Ocean sectors.

The same concerns which were behind the BIOMASS programme were also raised within the Antarctic Treaty system. After lengthy discussions between the Treaty parties agreement was reached on the Convention for the Conservation of Antarctic Marine Living Resources which came into force in 1982 as the Commission for the Conservation of Antarctic Marine Living Resources (CCAMLR). CCAMLR is unique among regulatory bodies since the Convention requires it to take an ecosystem approach to management. This means that the effects of exploitation of a given stock or species are considered not in isolation, but also in relation to the system as a whole, and in particular to species dependent on that stock. These critical and innovative features are enshrined in Article II of the Convention. The scientific advice comes CCAMLR from the Scientific Committee for the Conservation of Antarctic Marine Living Resources (SC-CAMLR).

Bearing in mind the agreed aims of the Convention, there are two primary considerations which need to be taken into account when assessing the impact of krill harvesting. The first one is the traditional single species approach whereby the resource is managed so as to ensure it remains healthy in perpetuity. The second is to ensure that harvesting on krill does not adversely affect dependent species, the so called ecosystem approach.

In order to develop advice for management of the krill fishery SC-CAMLR requires ecological data on distribution and annual production. Information on the large scale distribution of krill indicates that it is likely to be found anywhere south of the Antarctic Polar Frontal Zone (APFZ). However within this range its distribution is extremely patchy. Combining this patchy distribution with the enormous area, 36 million square kilometres, of the Southern Ocean, much of it covered by sea ice, means that standing stock is difficult to determine. Indeed the problems are so huge that there has never been a Southern Ocean survey to estimate standing stock, the nearest was the FIBEX survey which covered about a quarter of the area. Estimation of potential yield has therefore been undertaken only for these limited areas covered by FIBEX and not for the Southern Ocean as a whole. Fortunately the FIBEX survey covered the area in which over 90% of the krill catch has been taken.

Standing stock (B0) can be used to estimate potential yield using the equation Y= lambda M B SUB 0 where B0 lambda is a discount factor, typically less than 0.5, and M is the coefficient of natural mortality. This basic equation was modified to take account of the requirements of predators and in addition stochastic components incorporated to allow for variability in standing stock, recruitment, mortality and predator demand. All these have been incorporated into a single factor, gamma, which is computed such that the median standing stock should not fall below 75% of its pre-exploitation level and also that there should be less than a 10% probability that the standing stock should fall below 20% of its pre-exploitation level in any one season. This approach has been used as the basis for setting precautionary catch limits in Area 48 (Atlantic Sector) and 58.4.1. (*** Indian Ocean sector).

While the precautionary approach outlined above is adequate for considerations on a large scale, it fails to take account of the differing spatial and temporal scales on which the krill and the dependent species function. The extent of this particular difficulty can be seen by considering the situation in the case of land-based predators such as penguins. During the breeding season, adult birds which are feeding chicks are restricted to an area perhaps within 100 kilometres range of their breeding site and also require to provision their chicks on a daily basis. The available area might only be, in the case of the Atlantic sector, less than one per cent of the total area. Conservation measures therefore need to minimise the chance that all commercial fishing will take place in that same area at the critical period of the breeding season. This particular problem, although foreseen several years ago, is one now being actively addressed by CCAMLR.

In order to understand these interactions and develop advice for management, it is necessary to obtain information on the distribution of predators, their diet, food requirements and the spatial and temporal scales over which these operate. These considerations were behind the establishment of the CCAMLR Ecosystem Monitoring Programme (CEMP). In considering the potential impacts of harvesting on dependent species CCAMLR took a pragmatic approach to the problem by concentrating on a small number of species and clearly identified parameters. With nearly a decade of information available for some of these CEMP parameters SC-CAMLR is now looking to incorporate this information into its advice to the Commission for management of the krill fishery.

During the course of little more than a decade, CCAMLR has taken the most advanced conservation management convention forward and developed precautionary conservation measures for the krill fishery in advance of the large scale development of the fishery. The management approaches have taken into account uncertainty in the data in developing a precautionary approach to management. These facts are even more remarkable since they have taken place in a forum operating by consensus in which members primarily interested in harvesting krill are in a minority. The atmosphere within CCAMLR is positive and constructive and it is to be hoped that this will continue so that current approaches can be refined and sustainable management for krill be sustained and initiated for other fisheries which might develop in the Southern Ocean.

PUTTING KRILL INTO ECOSYSTEM MODELS

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Abstract

More than two decades of intensive ecological research in the Antarctic have refined the over- simplistic view of "the Antarctic ecosystem" towards identification and investigation of a number of different subsystems. Within the pack-ice zone of the Weddell Sea (Atlantic sector of the Antarctic Ocean), a summer pelagic system breaks up into ice-bound and deep-living systems in winter. Furthermore, an export system at the borders of the Weddell gyre can be distinguished from a retention system at its center in summer. Continued studies allow for simple energy-flow budgets to be constructed of some of these subsystems, in which the varying role of krill can be analyzed. Such a model is presented for the ecosystem on the eastern Weddell Sea shelf. Although the benthic components dominate this ecosystem by biomass, the major part of the flows takes place in the pelagic, and these flows are analysed with focus on krill. The results are subsequently compared with a preliminary trophic flow model of a temperate shelf ecosystem off the southern coast of British Columbia. Krill appear to be generally well- used, being of more importance as food for homoiotherms in the Antarctic, and to fish off British Columbia. In view of efforts towards changing the exploitation of krill in any of these ecosystems, the role of krill in the food web needs to be quantified better than to date.

Introduction

Intensive ecological research in Antarctica under the umbrella of the Scientific Committee of Antarctic Research have substantially increased our knowledge on structure and processes in the Antarctic Ocean (see, e.g., Laws 1985 for an overview). Community studies of phyto- and zooplankton (Hart 1942, Voronina 1966, 1971) allowed to distinguish three zones, the ice-free zone, the seasonal pack-ice zone, and the quasi-permanent pack-ice zone, each with their own characteristic food-web (Hempel 1985). The simple food chain "diatoms-krill-consumers" was shown to be oversimplistic both from the lower and form the upper trophic levels (e.g., Hewes et al. 1985, Clarke 1985). Within the pack-ice zone of the Weddell Sea (Atlantic sector of the Antarctic Ocean), a summer pelagic system breaks up into ice-bound and deep-living systems in winter. Furthermore, an export system at the borders of the Weddell gyre can be distinguished from a retention system at its center in summer (Schalk et al. 1993). While sharing their importance with copepods and gelatinous zooplankton in the retention system, krill are a key element in the pelagic export system during summer, and a part of the ice-bound system winter. Increased knowledge of the various components of these ecosystems has allowed to assemble energy flow budgets of some subsystems, e.g., of the eastern Weddell Sea shelf as part of the summer export system(Jarre-Teichmann et al. in press).

After a brief introduction to the modeling approach used, the role of krill in this high Antarctic ecosystem will be compared to its importance in a temperate shelf ecosystem, based on a preliminary trophic flow budget of the shelf off British Columbia.

An approach for constructing ecosystem models

Among the many approaches used for assessing interactions between species in an ecosystem, trophic flow budgets have proved useful as they allow to combine a major part of the knowledge, i.e., that on population dynamics and trophic interactions, of the many components of an ecosystem into a single, coherent whole. Being straightforward to construct, they are useful to identify major flows in an ecosystem and/or identify gaps in one's understanding of species interactions (Silvert 1981). Furthermore, they can serve as an illustrative tool during the construction process of dynamic models (e.g., Jarre-Teichmann 1992). Assuming average ("steady-state") conditions over an appropriate period of time, trophic interactions between the components of an ecosystem (species or species groups) can be described by a set of linear equations, wherein the production of each component equals its predation by other components in the system (predation mortality), its export from the system (fishing mortality and/or other exports, e.g., emigration), and other losses (baseline mortality), i.e.,

Production by (i) = All predation on (i) + nonpredatory biomass losses of (i) + fishery catches of (i) + other exports of (i)....... (1)

The terms in this equation may be replaced by

Production by (i) = Bi * P/Bi
Predatory losses of (i) = M2
= *j (Bj *Q/Bj * DCj,i)
Other losses of (i) = (1 - EEi) * Bi * P/Bi

and this leads, for any component in the system, to

Bi* P/Bi * EEi - *j (Bj * Q/Bj * DCj,i) - Ex i = 0 (2)

where

- i — indicates a component (stock, species, species group) of the model
- j — any of its predators,
- Bi — its biomass,
- P/Bi — the production of a component per unit biomass (= total mortality under steady- state conditions),
- Q/Bi — the consumption of a component per unit biomass,
- DCj,i — the average fraction of i in the diet of j (in terms of weight),
- EEi — its ecotrophic efficiency (the fraction of the total production consumed by predators or exported from the system),
- Exi — its export from the system (e.g., by emigration, or advection, or fishery catch).

The energy balance of each component is given by

Consumption = Production + Respiration + Non-assimilated food (3)

where the total consumption is composed of consumption within the system and consumption of imports (i.e., feeding "outside the system"), and the production is either consumed by predators, exported from the system, or accounted as a contribution to detritus. This structure defines the necessary parameters for the model. These are, for each component, an estimate of its

- biomass,
- production per unit biomass,
- total food consumption per unit biomass,
- assimilation efficiency,
- diet composition,
- exports from the system,

ecotrophic efficiency.

For each component, one of above parameters B, P/B, Q/B, or EE may be unknown. It is estimated when solving the system, along with the respiration of that component. If an acceptable result for each of the unknowns is achieved from the inputs, the model is regarded as balanced and may further be analyzed. The ECOPATH II software (Christensen & Pauly 1992) was used for balancing and for the analysis of the models.

A model of an Antarctic ecosystem: the eastern Weddell Sea shelf

A 20 box trophic flow model was constructed which summarizes much of the available information on the eastern Weddell Sea shelf (Jarre-Teichmann et al. in press) (Fig. 1).

Euphausia crystallorophias is the most important species on the Weddell Sea shelf. Benthopelagic aggregations of the Antarctic krill *E. superba* have been observed on the deeper shelf of the eastern Weddell Sea, but this species is of more importance in the oceanic area (Boysen-Ennen et al. 1991, Gutt and Siegel 1994). In accordance with Siegel (1987), the total mortality of krill on the eastern Weddell Sea shelf was estimated at 1.0 year-1, although the mortality of *E. crystallorophias* may be higher as it is smaller. Clarke and Morris (1983) estimated daily ration of adult male krill at 5.1% body mass, which led to a gross efficieny of 5.4%. The diet composition of krill was assumed to consist of 85% phytoplankton, 5% zooplankton, and 10% detritus.

Although the various benthic groups dominated the biomass in the system, the planktonic groups were more important with respect to production: the planktonic groups accounted for only about 15% of the biomass, but for about 95% of the prodution. Euphausiids alone contributed some 4 % to the total system throughput. The predation on euphausiids by whales was not further detailed by Jarre-Teichmann et al. (in press), but Miller et al (1985) scrutinized the predation mortality of krill. In their study, whales contributed about 53% to total krill mortality, seals 32%, squid and fish 8%, penguins 4% and flying birds 3%. The potential demand of predators was about twice as high as the production of krill based on the biomass given in Miller et al. (1985) and the productivity estimated by Siegel (1987,1992), indicating that krill are well-used as a food resource in the Anarctic ecosystem.

A preliminary model of the shelf ecosystem off southern British Columbia

During a workshop at UBC's Fisheries Centre immediately preceeding the present one, two preliminary trophic flow models were constructed, one representing the central region of the Alaska Gyre, and the other one the shelf off British Columbia (Pauly and Christensen, in prep.). For the shelf model, 39 groups were selected by the participants (Table 1). The model has to date only been very roughly balanced. Improvements of the set of input parameters are presently ongoing. The structure of the food web on the shelf off British Columbia differs from that on the Weddell Sea shelf - beyond a higher thoughput which is to be expected based on the temperature and primary productivity - in that the boxes appear to be better interconnected, and the feeding interactions are more widely spread among the trophic levels. One remarkable aspect of the modeling proces was the appreciation of the important role of krill (Thysanoessa spinifera and Euphausia pacifica) in the food web. The high demand from krill predators (Table 2) could, however, not be met by the available estimates of krill biomass (between 1.1 g wet mass m-2 (Romaine et al. this Workshop), and 3.8 g wet mass m-2 (R. Brodeur, pers. comm.)) and its productivity, i.e., 1.6 to 3.7 year-1 (R. Tanasichuk, this Workshop). If krill constitute about 50% of the diet of herring (R. Tanasichuk pers. comm., minimum estimate) they are the dominant predators of krill, followed by hake. All other predator groups are relatively unimportant, contributing not more than 1% to the total predation on krill. If krill is important to top predators such as whales and birds, as in the Antarctic, the interactions will be indirect to a much larger extent. On the other hand, their importance in the diet of hake, herring and ocean perch suggests that changes in the availability of krill, such as, e.g., those caused by an intensive fishery, are likely to affect these fish groups.

It is not quite clear yet which misconception led to the imbalance - by more than one order of magnitude - between krill production and herring and hake food demand on the shelf off southern British Columbia. Consequently, there is not point in further analysis of the flow network at this point in time. It can, however, be inferred that the krill resource appears to befully used within the ecosystem, leaving little scope for an extended fishery. Even without aiming at a complete understanding of the functioning of the food web, it appears crucial to analyze, probably on a seasonal basis, whether krill represent a bottleneck for the development of some life stages of these species, and, in turn, which may be the (direct and indirect) consequences of lower abundance of krill to even higher trophic levels in the food web, such as birds and whales.

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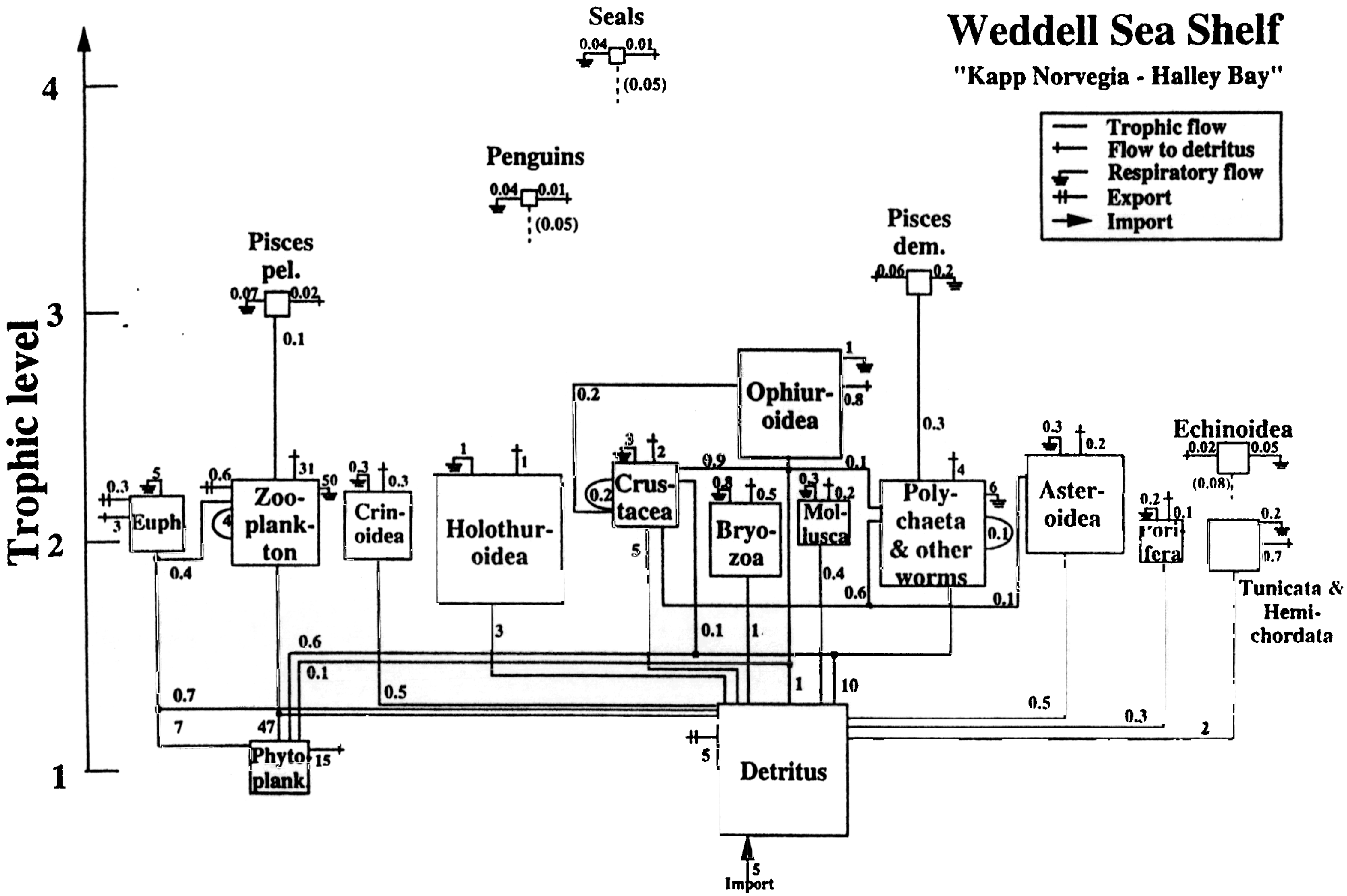

Figure 1. Diagram of carbon flows of the eastern Weddell Sea shelf (Jarre- Teichmann et al. in press). The components of the model are arranged along the vertical axis according to their trophic level. The size of the boxes is proportional to the biomass of the components in the system if they are imagined as cubes instead of squares. Respiratory flows, backflows to detritus, as well as exprots from the system are indicated. Flows enter boxes on the lower half, and leave them on the upper half. Flows of 1 g C m-2 year-1 or more are rounded to integers, flows between 0.1 and 1 g C m-2 year-1 are rounded to one digit. Trophic flows of less than 0.1 g C m-2 year-1 were omitted for clarity.

Table 1 List of the 39 boxes used for a trophic model of the shelf off southern British Columbia by the participants of the workshop on "Mass-balance model of trophic fluxes in the North Pacific", held November 6-10, 1995, at the Fisheries Centre, UBC, Vancouver.

Biological group	Boxes in trophic flow model
Planktonic invertebrates	Phytoplankton Velella, Bacteria Microzooplankton Small herbivorous zooplankton Carnivorous zooplankton Krill, Jellyfish , Salps, Squids
Benthic invertebrates	Polychaetes, Bivalves Benth. Amphipods Shrimps, Crabs Sea stars, Sea urchins Brittle stars, Other benthos
Pelagic fish	Herring, Smelts Sandlance, Resident salmon Transient salmon, Misc. pelagics
Semi-demersal and demersal fish	Rockfishes, Ocean perch Hake, Cod, Sablefish Sharks, Halibut, Misc. demersals
Homoiotherms	Toothed whales, Transient orcas Baleen whales, Pinnipeds, Marine birds
Detritus	One detritus box only, combining dissolved organic matter, particulate organic matter, and carcasses.

Table 2 Preliminary assessment of role of krill Thysanoessa spinifera and Euphausia pacifica in the food web on the shelf off southern British Columbia, Canada.

Fraction of krill in total diet (%)	Group	Fraction of total predation on krill[1] (%)
51-100	Hake	11
26-50	Herring	88
	Ocean perch	<0.1
0-25	Sablefish	0.2
	Sharks	0.2
	Marine birds	<0.1
	Baleen whales	<0.1

[1] Initial estimates only, model not balanced to date.