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Learning about Antarctic krill from the fishery

SO KAWAGUCHI* and STEPHEN NICOL

Australian Antarctic Division, Department of the Environment and Water Resources, 203 Channel Highway, Kingston, TAS 7050, Australia
**So.Kawaguchi@aad.gov.au*

Abstract: Antarctic krill has been studied for many decades, but we are still long way from understanding their biology to be able to make reliable predictions about the reaction of their populations to environmental change. This is partly due to certain difficulties in relation to logistics, operations and survey design associated with scientific surveys that have been obstacles for us to better understand krill biology. The krill fishery is the largest fishery in the Southern Ocean, continuously operating since early 1970s. Recent studies revealed its potential to be used as a unique source for scientific discussions to understand krill biology. In this paper, after a brief overview of krill fishery operation and krill biology, we examine how current data collection through the fishery operation could contribute to a greater understanding of krill biology, and then suggest future priorities for fisheries-related research in relation to recent changes in the Southern Ocean environment.

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Introduction

Antarctic krill is one of the best studied species of pelagic animal, yet there are still considerable uncertainties about key elements of its biology (Nicol 2006). In the past, considerable efforts have been expended to understand the biology and ecology of krill through a number of scientific surveys and these efforts are likely to continue into the future (Nicol 2003, Ross & Quetin 2003). During the last thirty years, general concepts of krill biology and its life history have changed dramatically as more information is collected from the field and from laboratory experiments (e.g. Kawaguchi & Nicol 2003, Siegel 2005, Nicol 2006). Krill, once believed to live for only 2–3 years, are now thought to live for 5–7 years in their natural environment (Siegel & Nicol 2000). Interactions with elements of their natural environment including sea ice, ocean currents, and primary producers are better understood.

Worldwide, fishery information is regarded as one of the most important sources of biological information on the targeted species. The krill fishery should not be the exception, although little direct use has been made to date of the biological information arising from the commercial fishery which has been operating since the 1970s. The krill fishery, of course, does not operate for scientific purposes, but concentrates on providing a stable supply of catch with sufficient quantities and quality. Consequently, the method adopted for searching and catching krill has evolved in a totally different way from the scientific surveys. Krill trawlers (Fig. 1) operate throughout the year, fishing repeatedly for days and weeks on the same swarms, in a way that is impossible for scientific surveys. Additionally, at current harvesting levels, and at any one time, there may be up to a dozen krill trawlers operating in the fishing grounds in the South-west (SW) Atlantic and this activity dwarfs scientific efforts in the same area. Thus, the krill fishery has a considerable potential to contribute to understanding krill biology by providing information on krill on different spatial and temporal scales from standard scientific surveys.

There are many review papers and reports of Antarctic krill and its fishery (e.g. Miller & Hampton 1989, Nicol & Endo 1999, Ichii 2000), and therefore reviewing krill biology or the krill fishery is not our intention. In this paper, after a brief overview of the krill fishery operation and krill biology, we will examine how current data collection through the fishery operation could contribute to a greater understanding of krill biology, and then suggest future priorities for fisheries-related research in relation to recent changes in the Southern Ocean environment.

Overview of Antarctic krill fishery

History and distribution

An exploratory fishery targeting Antarctic krill first started in the 1962 fishing season, and full scale commercial operations were underway by the mid 1970s (Nicol & Endo 1999). The annual total catch peaked in early 1980s (over half million tonnes) and rapidly declined thereafter down to around 120 000 tones due to problems with krill processing and an increased interest in finfish (Kock & Shimazu 1994) (Fig. 2). The catch from the1986 to 1992 fishing season was between *c.* 300 000–400 000 tones. A marked drop in catch occurred in the 1993 fishing season after the USSR ceased fishing operations (Ichii 2000). Since the 1992/93 season the annual total catch remained close to 100 000 tones, although there appears to be a small but consistent recent increase in catches (CCAMLR 2006a).

Nations involved in Antarctic krill fishery have changed

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Fig. 1. A Japanese krill trawler, *Nitaka-Maru*. (Photograph by courtesy of B. Yoshitomi at Nippon Suisan Kaisha Ltd).

dramatically. Until 1992 fishing season, the major fishing nation was the USSR taking between 56% and 97%, but Japan had also been continuously operating from early 1980s. From 1993 fishing season onwards, Japan became the major nation taking more than 50% of the total catch of 100 000 tonnes. Other countries (Poland, Ukraine, Korea) were also regularly operating during this period. More recently, the USA (2000 fishing season onwards) and Vanuatu (2004 fishing season), entered the krill fishery taking 30 000 tonnes each, while Japan reduced its catch to only 25% of the of 120 000 tonnes caught in the 2004 fishing season (CCAMLR 2006a). This considerably changed the balance of national catches.

Krill catches have been reported from around the Antarctic continent (Fig. 3), however, the majority of catches have been from the SW Atlantic sector, and currently all the krill fisheries are operating in this area (CCAMLR 2006a). On a local scale, krill fisheries tend to be associated with the main island groups and are not spread throughout the area, with the bulk of the catches coming from either the continental shelf or close to the shelf break (Everson & Goss 1991). Historically, the main fishing season used to be the summer, but more recently, year round operations have became more common largely as a result of

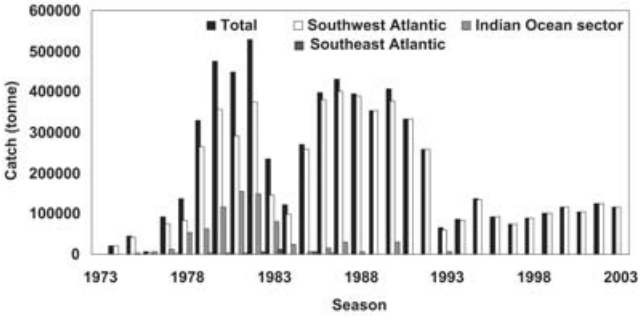


Fig. 2. Succession of annual catch of Antarctic krill in the Southern Ocean. Modified from CCAMLR Statistical Bulletin (CCAMLR 2006a).

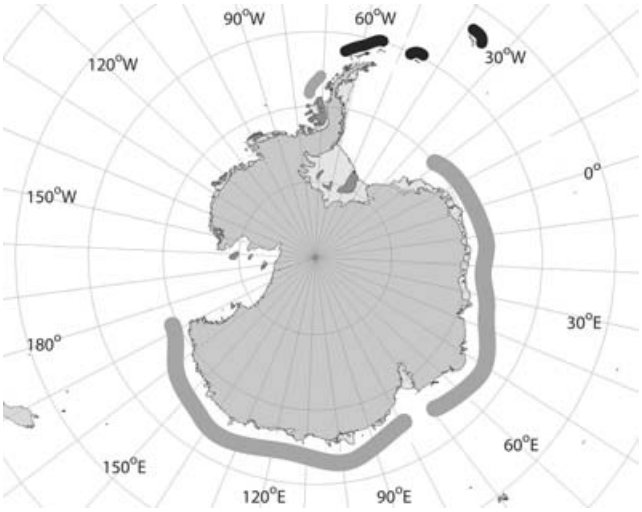


Fig. 3. Location of existing (black) and past (grey) Antarctic krill catches.

reduced ice cover in the Antarctic Peninsula region. Currently, there are three main fishing grounds; the South Shetland Islands, the South Orkney Islands, and South Georgia (CCAMLR 2006a).

Management of the harvest of all marine living resources (other than whales and seals) in Antarctic waters is regulated by the Convention on the Conservation of Antarctic Marine Living Resources (CCAMLR). The details of the management will be dealt with in a separate review (Reid 2007).

Commercial fishery operations

Commercial trawlers must operate in a cost-effective way to make a profit. The factories on krill trawlers produce krill products as the vessels operate. Optimum efficiency is attained if the factory is continuously operated at its maximum capacity. Krill needs to be processed immediately after being caught because it starts to degrade quickly. Therefore skippers try, as much as possible, to provide constant supplies of required types of krill to the factories through round the clock operations. Furthermore, it is vital that the operator adequately selects the fishing grounds which can fulfil this requirement (Kawaguchi *et al*. 2005a, 2005b).

Operations in Antarctic waters are primarily affected by ice condition; krill trawlers can only operate in ice free areas. In the SW Atlantic sector, South Georgia is ice free year round and could be subject to krill fishing at any time of the year, whereas the other two fishing grounds are only available during summer–autumn (Kawaguchi *et al.* 2006a). The seasonal succession of total catches generally suggests that the main fishing area is associated with the ice edge and follows its movements (Everson & Goss 1991). However, the recent analysis of fishing ground selection by nations

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revealed that fleets from individual nations tend to have their own preferences in choice of fishing areas (Kawaguchi *et al.* 2006a). Recent changes in the balance of catches between nations, the entry of new nations, and the adoption of new fishing technologies (e.g. the pumping method, see later paragraphs) into the krill fishery, may change existing fishing patterns (Kawaguchi *et al.* 2006a). Because the fishing operators are also concerned about product quality, including colour, size, bycatch etc (Butterworth 1988b, Kawaguchi *et al.* 1998, Ichii 2000), fishing vessels swiftly change fishing grounds and location to obtain better quality krill (Kawaguchi *et al.* 2005b).

Krill generally form aggregations extending from several hundred metres up to several kilometres (or even more) horizontally and tens of metres vertically (Watkins 2000). Fishing skippers must first identify the location and depth of fishable aggregations and krill trawlers are equipped with sonar (detectable ranges of 400 m extending up to 800 m around the vessel if conditions are good) and echo-sounders to search for and locate krill aggregations for this purpose (Ichii 1987). Once a target is located, the vessel is turned around and the depth of the net is set to the target. The krill fishery utilizes large mid-water trawls with mouth areas of 300–1000 m^2 and 13–15 mm mesh cod-ends (Kawaguchi *et al.* 1997). Towing time is important since long tows and/or large catches can reduce the quality due to crushing in the nets therefore the skipper regulates towing time to adjust the catch to supply an adequate amount for the factory, usually 10–15 tonnes. Towing time usually lasts 30–90 minutes (Kawaguchi *et al.* 2006a), but fishing vessels from the USSR often conducted tows that extended for several hours (Litvinov *et al.* 2004). The Catch per Unit Effort (CPUE) arising from short targeted tows reflects within aggregation density rather than regional krill density (Butterworth 1988b, Ichii 2000, Kawaguchi *et al.* 2005a), whereas longer tows are likely to reflect regional density (Litvinov *et al.* 2004). A new fishing method, which uses a fish pump to continuously pump krill from the cod-end of a midwater trawl without hauling the net onboard, has recently been employed in the fishery (CCAMLR 2004). The pumping method is thought to be a more gentle way of landing krill but a single haul can extend for weeks and this produces problems for conventional analyses of CPUE (Kawaguchi *et al.* 2006a).

Once the net is hauled onto the deck, krill are released from the cod-end directly down to the fishpond in the factory through an open hatch (Fig. 4). Size distribution, quality and bycatch are recorded following each haul, and product grade and processing details (frozen, boiled, peeled, meal etc) for every haul are recorded (B. Yoshitomi personal communication 2006). Generally, large gravid females are rated as high grade, and product with bycatch and/or green colouration due to intense phytoplankton feeding are rated low grade and are often unsuitable for frozen products but are still of value for producing krill meal (Butterworth 1988b). Krill are then sent to the relevant





Fig. 4. Landing krill catch onboard fishing vessel. **a.** Releasing catch from the cod-end through opened hatch. **b.** Krill held in a fish pond. These krill are then sent through into the onboard factory area by conveyer belts. (Photographs by courtesy of B. Yoshitomi at Nippon Suisan Kaisha Ltd).

Table I. A list of krill products.

Usage	Products
Feed and baits	frozen krill
	krill meal
	krill oil
	krill protein solubles
Human consumption	frozen krill tail meat
	krill protein concentrate
	krill hydrolysed solubles
	krill flavours
Chemicals	krill pharma oil
	astaxanthine
	dried krill shell
	chitin
	chitosan
	krill enzymes

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processing plant (e.g. freezing pans, peeler, meal plant etc) on the conveyer belt. Fresh krill start to degrade rapidly following death so the whole process must be quick. The entire processing must finish before the next krill catch is loaded in the fishpond (Kawaguchi *et al*. 2005a).

Products of the krill fishery and its trends

A wide variety of products have been produced from krill and these have been aimed at aquaculture, animal feed, human consumption and the production of pharmaceuticals and chemicals (Table I). A number of technical problems have arisen with using krill and many of these problems have provided information about some of the basic biological properties of the animal. The strength of krill enzymes first became apparent through the rapid deterioration of the catch (Bykowski 1986). These enzymes have subsequently been the subject of considerable research which has advanced basic knowledge of krill biochemistry and has prompted the development of new products manufactured from krill. The presence of fluoride in the shells of krill has initiated research into ways in which the concentration of this element can be reduced and this in turn has led to a better understanding of the role that fluoride may play in krill biology (Nicol *et al*. 2000).

Trends in patents registered provide a good indication of where the commercial interests in krill lie and the directions that research and development (R&D) are taking. The number of patents that have been filed have been dominated by those from Japanese firms and mostly relate to human consumption, but the relative proportion of Japanese patents declined in the 1990s (Nicol & Foster 2003). Most Japanese firms operating in the krill fishery were food suppliers so their R&D naturally concentrated on end products for human consumption. Krill did not prove as a popular food product as the operators anticipated partly because it was hard to indicate krill's superiority for human consumption compared to other available crustacean products and partly because it was difficult to produce economical krill products for human consumption (B. Yoshitomi personal communication 2006). As a result krill products became steadily directed to aquaculture feed and as bait for sports fishing. Recent trends in patents related to krill demonstrate this shift of the focus from products for human consumption to the development of a range of products with particular focus on aquaculture. This trend was mainly driven by countries other than Japan and Russia, which were the traditional krill fishing nations. The growing demand for marine oils and for aquaculture feed, and the decline in traditional supplies of fishmeal will mean that the Antarctic krill fishery will not continue to stagnate (Nicol & Foster 2003).

Comparison: scientific surveys vs the krill fishery

Scientific surveys are specifically designed in a standardized way to collect information and data on krill and to answer particular scientific questions. There is no doubt that such surveys will be the primary source driving further understanding of krill biology. However, there are certain difficulties in relation to logistics, operations and survey design associated with scientific surveys. In this section we will compare the types of information derived from scientific surveys and the fishery, describe their advantages and disadvantages, and discuss the possibilities of using krill fisheries as platforms for scientific surveys

Table II. Comparisons of the type of information available from scientific surveys with that available from the fishery.

	Scientific survey	Fishery
Operation	Synoptic coverage of wide geographical areas, time series of surveys at fixed location, or process studies at a range of scales.	Long-term operations, often following a single aggregation. Several fishing vessels operating within and between different fishing grounds.
Coverage (season)	Mostly summer, but also in other sasons. Single vessels rarely operate for longer than 3 months.	Year round operation.
Coverage (geographical)	Can vary from large scale synoptic surveys to small scale process studies.	Located where krill are locally most abundant but may move between locations in response to changes in abundance, or seasonally.
Area of operation	Throughout Southern Ocean	On fishing grounds - currently only in SW Atlantic.
Sampling gear	Relatively small nets (< 8 m^2)	Large mid-water trawls (300–1000 m^2 mouth opening). Continuous pumping method.
Aggregate detection	2D. (under the ship, or from towed body) using scientific echo-sounders	3D. combination of echo-sounder and 360 sonar around the vessel, plus net monitor
Towing frequency	Mostly once at a location, usually small number of towing locations (< 100)	~10 tows a day throughout fishing season.
Towing depth	Usually 0–200 m	0–> 800 m - wherever fishable aggregations are detected.
Instrumentation	Wide range of ancillary information available from scientific instrumentation	Limited range of measurements possible.

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into the future.

Table II compares the type of information available from scientific surveys with that available from the fishery. In general, scientific surveys are designed for abundance estimation through randomized transect surveys using precision acoustic instruments. They also conduct demographic studies, onboard experimentation using freshly caught krill and collect samples for physiological measurements often from a wide geographical area. Scientific surveys are not only limited in scope but their effort is restricted when compared to the fisheries operations. For example, the CCAMLR 2000 survey of the SW Atlantic utilized four research vessels for a month and required many years of planning (Watkins *et al*. 2004); the krill fishery operation regularly involves up to a dozen vessels all year every year in the same area. Despite their specific design, there are a number of methodological problems with scientific net-based and acoustic surveys that have not yet been fully resolved (Miller & Hampton 1989, Nicol 2000). Some of these problems are related to the techniques themselves e.g. acoustic target strength or net selectivity, and some relate to the survey design. Additionally, analysis of krill populations through time requires that the same population is being sampled from one survey to another and because scientific surveys rarely stay in an area for a prolonged period, there is little certainty that the same population is being sampled repeatedly (Nicol 2000). The fishery, however, is not designed to be random, but concentrates in the area where krill density is high and repeatedly samples huge quantities of krill and often maintains itself in the same population for an extended period throughout the year (Kanda *et al*. 1982). The fishery also targets aggregations throughout the water column from the surface to several hundred metres, and occasionally towed layer deeper than 800 m according to records in the fishery logbooks (M. Naganobu personal communication 2006). These deep tows were based on the knowledge obtained through intensive experimental bottom trawling surveys (100 m, 300 m, 500 m, and 800 m) pursued by Japanese fishing vessels in the early 1980s (Takahashi & Iwami 1997). The stomachs of the demersal fish caught during these surveys were in many cases full of freshly ingested krill, which implied constant presence of bottom krill populations at certain amounts (Takahashi 1991).

Because the fishery takes samples from a krill population several times a day for extended periods it is an excellent platform for collecting data on biological parameters, physiology, particularly with regard to short term or seasonal changes. Observations from fishing vessels and of fishing behaviour can also provide information on krill behaviour and distribution at the population level throughout the water column and also seasonally. Commercial nets are much larger than scientific nets (Fig. 5). Using commercial nets also means there is likely far less net avoidance than is the case with scientific nets so krill density estimates from commercial size nets can provide additional information on *in situ* density within aggregations (Fig. 5).

Current practice of fishery data submission to CCAMLR, and collection of other information by commercial vessels

CCAMLR Secretariat holds and maintains fishery data which are central to the formulation of scientific advice on the management of fisheries and marine living resources within the CCAMLR Convention Area (see Reid 2007 for details of CCAMLR management).

Four types of data submissions are required from countries fishing within the CCAMLR convention Area (http://www.ccamlr.org/):

1. Real-time catch and effort reports aggregated into management subdivisions, for each monthly interval during fishing seasons,
2. Haul-by-haul catch and effort data,
3. Observer data and reports including biological data and technical information, and
4. Annual and monthly summaries of catch and effort (STATLANT) data aggregated into FAO statistical areas.

Types 1, 2, and 3 include details of time, date, and positions of start and finish of fishing, accompanied with general information of the vessel and conversion factors of the products (CCAMLR 2006b). These are subject to strict rules of access and use, and originators/owners of data retain control over the use of their unpublished data outside of CCAMLR. Type 4 is open to public through published statistical bulletin (CCAMLR 2006a).

As mentioned in the earlier section, fishery operators also generally archive data for their own records. These can be anecdotal and/or quantitative information such as operational strategies, behaviours, aggregation status, krill length frequency data, searching time, krill patch size etc depending on their interests and benefits (Kawaguchi *et al*. 2005a, 2005b). These data belong to companies, therefore they have been so far used for scientific analyses only when the data holders wish to or agree to such purpose (e.g. Kanda *et al*. 1982, Kawaguchi *et al*. 1997, 2005a). There have been several important findings published using this type of information as outlined in the following sections.

Can the fishery contribute to an understanding of Antarctic krill biology?

Scientific questions about Antarctic krill biology

Since the publication of the monograph on krill by Marr (1962), the biology of krill has been reviewed on a number

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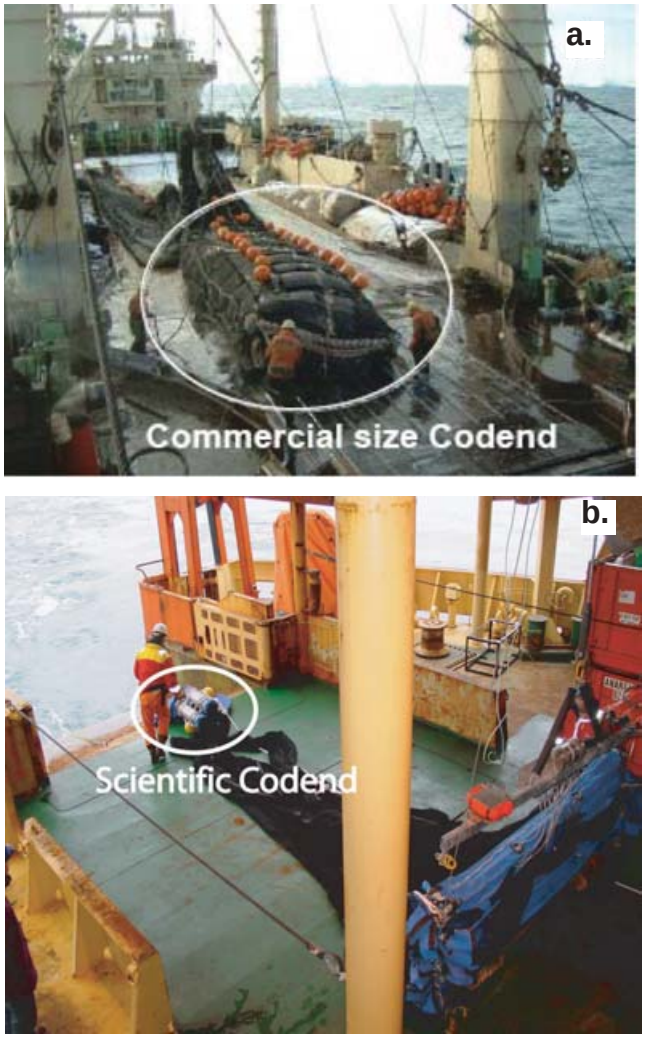


Fig. 5. Comparison of sizes of the cod-ends used on **a.** commercial trawlers, and **b.** research vessels. (Photograph A by courtesy of B. Yoshitomi at Nippon Suisan Kaisha Ltd).

of occasions (e.g. Miller & Hampton 1989, Everson 2000, Mangel & Nicol 2000, Kawaguchi & Nicol 2003). Through these reviews, we can see how our understanding of Antarctic krill biology has changed over the last few decades (table 1 of Nicol 2006). The krill life cycle, once viewed as 2–3 years (Marr 1962), is now believed to be 5–7 years (Siegel 1987) - even longer if kept in captivity (Ikeda & Thomas 1987). However, age determination and growth of krill in the field is difficult to validate unless the same krill population is repeatedly sampled for an extended period. Krill undergo ontogenetic migrations with the reproductive population offshore and immature krill inshore during reproductive season (Siegel 1988). Generally, adult krill feed very little in winter and their metabolism is reduced (Quetin & Ross 1991) but there is also evidence that krill can migrate inshore and also feed on ice algae (Siegel 1989). The survival of young krill and reproductive success of mature krill has been linked to winter sea ice conditions; more ice leads to more food resulting in :

1) high survival of young krill demonstrated by subsequent high recruitment indices (Loeb *et al*. 1997),
2) higher energy accumulation in spring (Quetin & Ross 1991), and
3) later and reduced salp blooms which may compete with krill for food (Siegel & Loeb 1995).

This conceptual model has been developed for the Antarctic Peninsula region and probably cannot be generalized for the whole Southern Ocean (Constable *et al*. 2003). Krill are also found closer to the bottom during winter (Kawaguchi *et al*. 1986, Gutt & Siegel 1996), however, it is still uncertain how important a life cycle strategy this is. Certainly, the krill fishery in winter utilizes deeper aggregations of krill than it does in summer (Jackowski 2002, Taki *et al*. 2005).

Krill have been described as animals which exhibit complex social behaviour, they are schooling species and can demonstrate concerted escape responses from larger predators (Hamner & Hamner 2000), yet they are often portrayed as passive drifters in simulation models (Nicol 2003). Many of the outstanding questions related to krill biology result from the logistic problems of operating in the Southern Ocean; half of the season their habitat is covered by seasonal ice, and research time is expensive and often shared with other initiatives. The use of alternative platforms to collect information on krill that is difficult to obtain through standardized scientific surveys will contribute to answering many of the outstanding questions in krill biology. In the following section we will examine what these questions are and how they could be answered by using fishery-derived information.

Fishery information to understand krill biology

Seasonal distribution and abundance. Recent scientific studies of seasonal krill distributions have given the strong impression that this species is distributed in oceanic regions during spring and summer and moves towards the costal regions in autumn, which are covered by pack ice during winter. The krill fishery operates throughout the year every year so is able to provide information on seasonal distributions - although it obviously only operates where aggregations occur. The krill fishery needs dense aggregations to operate, and the SW Atlantic sector is regarded as the region with highest krill abundance, therefore, pelagic aggregations of krill during winter must be prevalent. The fishery may provide an excellent platform for examining such pelagic winter populations, however, it will not provide information on krill populations under the ice or in the epibenthic layer.

The majority of our knowledge on the krill biology is based on those from the pelagic area especially from the

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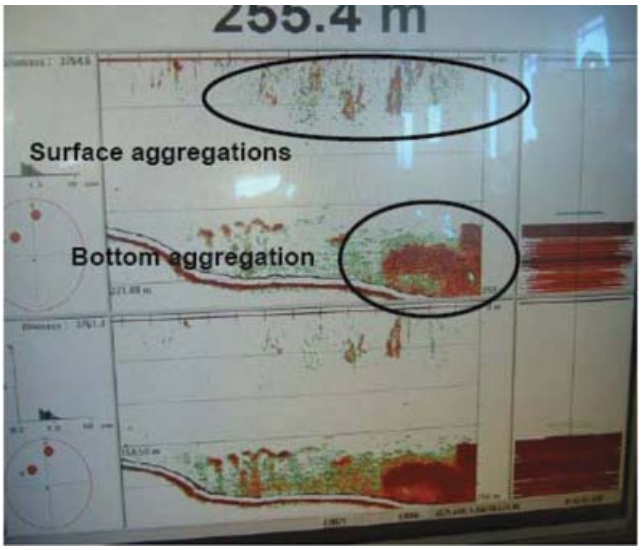


Fig. 6. An echogram from winter operation showing bottom krill aggregation. (Photograph by courtesy of B. Yoshitomi at Nippon Suisan Kaisha Ltd).

surface 200 m. The reason for this is because depth of krill distribution during summer when most of the Antarctic surveys are undertaken is generally restricted to the surface (top 200 m of the water column) (e.g. Siegel *et al*. 2004). Recently, there has been an increasing number of scientific surveys undertaken during winter, and revealing variations in their physiology and habitat including distributional depth. However, the information is still limited. An analysis of seasonal trends in fishing depth and catch rates revealed that commercial tows were deeper during winter but the depth range varied among different fishing grounds (South Shetland Islands: 90–110 m; South Orkney Islands:160–240 m; South Georgia: 120–160 m) compared to depth range of 40–70 m with during summer (Taki *et al*. 2005). More interestingly, echograms from the winter fishery show some dense krill aggregations deep near the seafloor which the commercial trawlers target (170–250 m) (M. Takahashi personal communication 2006), but at the same time some aggregations are also observed near the surface (Fig. 6). The existence of two types of winter aggregations raises questions about their composition and such questions could be answered by sampling fishery catches.

To date, many studies on the utility of CPUE for assessing krill abundance have been undertaken with mixed results (e.g. Kawaguchi *et al*. 1997, Siegel *et al*. 1998, Litvinov *et al*. 2004). Since krill distributions are extremely patchy and because different fishing fleets employ different towing strategies it has been difficult to develop a standardized CPUE index that provides consistent information (Butterworth 1988a). It is possible that CPUE may be able to provide a variety of information on krill aggregations if sufficient information is provided on the operation of the vessels. Butterworth (1988a), through simulation models, concluded that information from the krill fishery could not be used as indices of regional abundance unless detailed information on searching time plus other information on fishing strategies are available. However, this information is difficult to record because of the ambiguous nature of operational time budget. Generally, CPUEs from short tows may be able to indicate within-aggregation krill density, while those from long tows may be closer to average krill density within the fishing area (Kawaguchi *et al*. 2005a).

Recently, the CPUE data was statistically standardized using a Linear Mixed Model (LMM) and a significant correlation between scientific acoustic data and CPUE index was demonstrated (Kawaguchi *et al*. 2005a). However, the study also revealed the strong effects of operational complexity and the skipper's fishing strategies on CPUE. In order to be able to calibrate CPUE data, either an acoustic survey by a research vessel needs to be carried out at the same time and location as the fishing operation, or fishing vessels need to carry out randomized research tows rather than their normal targeted operations (Kawaguchi *et al*. 2005a). It is obvious, therefore, that there are no simple ways of using CPUE data as direct krill abundance index, however, there are ways that CPUE data could be used to address particular questions if they are accompanied with appropriate operational information. For example, since the krill fishery operates around season every year at similar locations together with length frequency distribution data, it is able to deliver seasonal and interannual time series of relative krill abundance index and its population structure, which can be interpolated into scattered data points obtained from scientific surveys at the nearby locations, or into time serial trends in area where scientific surveys are not often undertaken, and to supporting understanding of the regional population dynamics of krill (Kawaguchi *et al*. 1997).

Behaviour. Very few direct observations of krill behaviour have been published (Hamner & Hamner 2000). The few observations published to date have used aquarium experiments (e.g. Hamner *et al*. 1983, Strand & Hamner 1990) together with extensive underwater observations through diving (e.g. Hamner *et al*. 1989), and revealed many important aspects of krill behaviour at the individual and at the school level and these observations are yet to be built into sampling strategies. Although there is compelling evidence of krill being a highly socialized animal and potentially active migratory species, they tend to be regarded as passive particles drifting in ocean currents when their population movements are dealt with at regional or local scales (Nicol 2000). Because of the cost of research vessel time, a single krill aggregation cannot be followed for sufficient time to definitively determine the causative factors behind its movement. The strategy of the krill fishery, on the other hand, is to do exactly that and individual fishing boats may remain with a single aggregation, sampling it regularly for weeks at a time.

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Kanda *et al*. (1982) successfully documented two cases of active migration of swarms of 560 m and 1089 m diameter from observations made from a fishing vessel which was actively harvesting the swarms. Both aggregations moved consistently southwards for more than two weeks with average velocities of 0.26–0.29 nautical miles (nm) per hour, and with a maximum speed of up to 2.09 nm hr^{-1} (~ 90 cm sec^{-1}). To date, this is the only scientifically documented information about long distance active movement of aggregations in the field. Krill aggregations which were passively drifting with ocean currents have been observed in vicinity of South Orkney Islands through the analysis of consecutive trawling positions of Soviet Union fishing vessels and such analyses indicate the utility of these observations (Sushin 1998). All fishing information is precisely recorded on the logbook of fishing vessels and recently most of those data are submitted to CCAMLR on a haul-by-haul basis. Using those historically accumulated data would be an excellent way of increasing information on aggregation behaviour and movement. However, it should be noted that ancillary information such as fishing strategies (i.e. how they traced the aggregations, sequential catch composition data, product information, etc.) are essential for a reasonable interpretation of the results of such analyses.

Length-frequency data and growth. A series of recruitment indices have been calculated using length frequency data collected through commercial vessel operation after appropriate stratification (Kawaguchi *et al*. 1997), and related to winter sea ice conditions (Kawaguchi & Satake 1994). These were in general agreement with the recruitment series obtained by scientific surveys in the same region (Siegel & Nicol 2000). Fishery operations concentrate in the local area where krill are highly concentrated consequently the information that they can collect on krill populations differs from scientific surveys which apply a more randomized sampling strategy. However, the general agreement of the fisheries-derived recruitment indices with the scientific data strongly suggests that if appropriate standardization of the fisheries-derived length frequency data is carried out, they can be used for scientific purposes. Since the fishery is operating throughout year, fisheries-derived recruitment information could be useful to fill in seasonal gaps of information that often hamper interpretation of the data originating from more sporadic scientific surveys.

Most krill growth estimates from scientific surveys use consecutive length frequency data from different seasons to estimate growth rates. This relies on the assumption that the same population is sampled each year. This assumption is problematic since krill is an open ocean species and there is still uncertainty over the longer term stability of local populations (Nicol 2000). Fishery operations would be useful in understanding natural population parameters such as growth since the fleet often fish on a same single swarm for weeks thus multiple daily samples from the same population become available for scientific study. Recently, a krill growth model and trajectory using data obtained through the instantaneous growth rate (IGR) technique combined with information on the intermoult period (IMP) was published (Atkinson *et al*. 2006, Candy & Kawaguchi 2006, Kawaguchi *et al*. 2006b, Tarling *et al*. 2006). Sequential samples of krill populations from the fishery could be used to determine intermoult period as well as a range of other parameters relating to growth and development.

Krill colour, feeding and species interaction. Salp bycatch and a strong green colouration of krill due to intensive feeding on phytoplankton are disliked by the fishing operators since they negatively affect the product grade (Butterworth 1988b). Therefore this information is recorded in detail in the vessel's logbook. Greenness of krill is directly related to the degree to which krill are feeding on phytoplankton. Combining fisheries indices of greenness with information on ambient phytoplankton size composition has allowed an analysis of seasonal feeding trends (Kawaguchi *et al*. 1999).

Fisheries results have been used to examine the degree of competition between krill and salps (Kawaguchi *et al*. 1998). Scientific survey results suggested that intensive phytoplankton grazing by salps during the spring phytoplankton bloom may deprive krill of food in summer, which would result in low krill fecundity (Siegel & Loeb 1995). Loeb *et al*. (1997) further linked this to sea ice conditions in winter. Seasons following low winter sea ice would be favourable for salp blooms resulting in an unsuccessful year for krill. By statistically analysing haul-by-haul salp bycatch data and records of krill greenness as feeding index, Kawaguchi *et al*. (1998) found no evidence of direct competition for food resources between krill and salps and concluded that salps and krill generally prefer different water masses, with salps residing in warmer oceanic water. This type of analysis was possible because the krill fishery continues to operate within the main krill habitat for such a long time, and maintains systematic records of appropriate ecological and operational factors throughout the year.

The fishery also makes observations that later require independent scientific examination. For example, fishing operators categorize krill products based on their redness: red, pink or white. Fisheries records suggest that colours of krill within the same aggregation are uniform, and on many occasions neighbouring aggregations show completely different colours. Krill caught near the bottom are generally white and firm (M. Takahashi personal communication 2006). The fishery also reports that winter krill are generally whiter than summer krill. Colour is used as a guide to product type, for example white krill (especially from

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winter) are firm and more suitable for bait for sports fishing (B. Yoshitomi personal communication 2006). This colour distinction must have a biological basis and this will require further scientific study.

Physiology. Many studies on biochemistry including enzyme activities (e.g. Anheller *et al*. 1989, Melrose *et al*. 1995) and lipid composition (e.g. Hagan *et al*. 1996, Falk-Petersen *et al*. 2000) have been undertaken on krill from scientific surveys, and the results have contributed to understanding krill life history and physiology. However, these studies suffer from the sporadic nature of such surveys in terms of their regional and seasonal coverage, and it is sometimes difficult to generalize results as a result. General information on elemental analysis of krill is of course available, and some of this has come from fisheries information (Suzuki 1981, Suzuki & Shibata 1990). However, there must be far more detailed information that has been collected by fishing operators but little is publicly available since they are the key measures to control the seasonal quality of the products, and may also include important information on the directions of the companies R&D which may be viewed as confidential.

Result presented by Yoshitomi (2005) demonstrating seasonal trends in enzyme activities are one of the few recent studies published using a fisheries platform. He showed a seasonal reduction in protease activity which significantly correlated with phytoplankton feeding index using digestive gland greenness ($P < 0.05$) but no correlations were observed with other variables such as maturity, body weight, or sex ratio of the samples. This implies that the food environment maybe one of the important determinants of the protease activity. However, it is still unclear whether or not krill at low protease activity instantaneously responds to a good food environment and increase regardless of season. This question relates to whether lowered metabolism is simply due to low food level or related to possible "hibernation" which is thought as one of their over-wintering strategy (Quetin & Ross 1991). This study has demonstrated the potential of fishery vessels as valuable platforms for year round krill sampling and also indicates some willingness by fishing companies to publish some of the results of their studies.

The way forward in collecting data from the krill fishery

We have examined how the krill fishery can contribute to a better understanding of krill biology, and it is evident that there are two kinds of contribution that the fishery can make. Firstly, the fishery can offer sophisticated standardized sampling of krill populations, resulting in a large variety and number of biological samples. Secondly, through the precise documentation of operational information, such as fishing strategies, the fishery can provide information that allows us to interpret data arising from krill fishing. However, at the same time some of the information may relate to commercially sensitive techniques and information so the operators may want to keep them confidential. This is quite understandable since the fishery is a commercial activity and will not release information that they perceive may put them at a disadvantage. However, the development of a dialogue with the fisheries operators (CCAMLR 2004) may assist in a mutually beneficial exchange of data and information.

Effective use of CCAMLR International Observer Scheme

Catch and effort data have been voluntarily submitted to the CCAMLR Data Centre and this includes fishery catch and effort data, data collected by scientific observers and research survey data at various scales of resolution from haul-by-haul to monthly 30 nm by 30 nm areas (http://www.ccamlr.org). CCAMLR's initiative to move towards smaller scale unit management for the krill fishery (see Reid 2007), will require information on detailed fishing positions, consequently all fishing nations are now submitting catch and effort data at haul-by-haul basis. CCAMLR operates a Scheme of International Scientific Observation. The Scheme is designed to gather and validate scientific information essential for assessing the population status of selected species and the impact of fishing on such populations, as well as those of related and dependent species. Currently, the krill fishery is the only fishery in the CCAMLR Area exempted from the mandatory deployment of scientific observers. Scientific observation is voluntarily undertaken by some nations. However, there is a lack of consistency of data collection amongst the fishing fleets and throughout the fishing season. A mandatory scientific observer scheme would mean that biological samples could be collected systematically and this would allow specific scientific questions to be answered. Additionally, scientific observers could collect the sort of operational information which is thought to be necessary to scientifically interpret the catch and effort data (e.g. searching time, fishing strategy).

The rationale behind the arguments for retaining the current scheme of voluntary scientific observation for krill is that current catches are small in relation to the precautionary catch limits, there has been no stated intention to increase krill catches dramatically in the near future, the catch is managed at an areal or subareal scale, and the krill fishery has a negligible bycatch. This reasoning is no longer valid because a number of nations are now showing renewed interest in the krill fishery and the catch is increasing. New fishing technologies, such as the pumping method which has higher operating efficiency, have also been introduced and without systematic observations it is difficult to assess the impact of these changes. Additionally, changes in the environment on the krill fishing grounds have been detected, and these affect the seasonal and

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temporal operation of the fishery, yet the spatial and temporal coverage of submitted observer data remains limited (CCAMLR 2005). The importance of collecting data from the krill fishery using scientific observers is growing, and it is anomalous that CCAMLR is yet to adopt a mandatory scheme of scientific observation for the largest fishery under its jurisdiction. Although there are obvious operational and financial implications involved in mandatory observer coverage, these obstacles have been overcome in other fisheries, including all other fisheries in the CCAMLR Area. It is a matter of urgency that the Commission reaches consensus on the mandatory deployment of scientific observers on all fishing vessels so that it can manage all fisheries in the Convention Area using the best scientific advice available (CCAMLR 2005).

Revisiting historical data

Although it is not a substitute for collecting scientific observations from current krill fisheries, gathering historical information that was not available for scientific purposes in the past would be an excellent way forward. Large amount of valuable information should have been accumulated by operators and national observers (e.g. haul-by-haul catch and effort, LFD, searching time, fishing strategies), but these data have not been made available in the past due to commercial confidentiality at the time. Several studies have been published using historical information which has not previously been available for scientific use (Litvinov *et al*. 2003, Kawaguchi *et al*. 2005a, 2006a), is an encouraging development. However, a comprehensive analysis using all available data has still never been undertaken. Such an assessment would allow an effective use of historical fishery information and would also allow an assessment of the utility of collecting certain types of information for long-term stock assessment purpose into the future. Since the circumstances surrounding the krill fishery has significantly changed, and because there is an increasing awareness of the importance of understanding the fishery operation for better management, it would be timely now to pursue a comprehensive analysis of the historical data. The sole example of krill migration, detected by accessing accumulated logbook data, the ship's diary and fish-finder records (Kanda *et al*. 1982) alone is evidence of the enormous scientific potential to be gained by re-examining available fishery information and through the reanalysis of this information.

International Polar Year (IPY) as a driving force

IPY (2007–2008) is of an international programme of coordinated, interdisciplinary scientific research and observations in the earth's polar region. Its objectives are to "…..utilise the vantage point of the polar region to carry out an intensive and internationally coordinated burst of high quality, important research activities and observations that would not otherwise occur. ….. Link researchers across different fields to address questions and issues lying beyond the scope of individual disciplines ……. Optimise exploitation of available polar observing systems, logistical assets and infrastructure ……. Develop and embrace new technological and logistical capabilities (http://www.ipy.org/)". The concept of using the krill fishery as a research platform would fit these objectives well and would be an important and excellent way to contribute to this campaign. A good correlation between the spatial distributions in abundance, size, and maturity of krill caught in the commercial fishery around South Shetland Islands area at the time of the CCAMLR 2000 synoptic survey and the US AMLR survey and the corresponding distributions observed during those surveys (Jones & Ramm 2004) underlines the usefulness of the fishery as an additional research platform. By deployment of scientific observers on fishing vessels as well as co-ordinating commercial krill fishery operations with scientific acoustic surveys, net tows and onboard experiments using research vessels, many outstanding questions on the ecology of krill could be answered.

Conclusions

Although the biology of Antarctic krill has been studied for many decades, and several conceptual models of krill life history have been proposed, we are still a long way from understanding their biology to the point where we may be able to make reliable predictions about the reaction of krill populations to environmental change. This uncertainty results from the poor spatial and temporal coverage of scientific surveys and the small amount of research effort that can be expended at any one time. Through an examination of the fisheries operation, we conclude that krill fishery has the potential to be an excellent source of information for widening and deepening our understanding of krill biology. This is partly because the properties of information and data related to krill that are accessible from the fishery are often different from those obtained through scientific surveys but also because of the scale of fisheries operations compared to scientific research (Table II). In the past, fishery information has been regarded as confidential and inaccessible, but the circumstances surrounding the krill fishery are changing (in terms of the management regime, the nations involved, the product trends, and general awareness to the environment and global warming issues affecting Antarctic ecosystem), and we believe it is time to give serious thought to the use of krill fishing vessels as research platforms. Such an approach will give us new insights into krill biology and could drive the breakthrough in further understanding their interactions with their oceanic environment as well as contributing significantly to the

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management of the Antarctic marine ecosystem through CCAMLR's ecosystem management regime.

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References

ANHELLER, J.E., HELLGREN, L., KARLSTAM, B. & VINCENT, J. 1989. Biochemical and biological profile of a new enzyme preparation from Antarctic krill *Euphausia superba* Dana suitable for debridemet of ulcerative lesions. *Archives of Dermatological Research*, **281**, 105–110.

ATKINSON, A., SHREEVE, R.S., HIRST, A.G., ROTHERY, P., TARLING, G.A., POND, D.W., KORB, R.E., MURPHY, E.J. & WATKINS, J.L. 2006. Natural growth rates in Antarctic krill (*Euphausia superba*): II. Predictive models based on food, temperature, body length, sex, and maturity stage. *Limnology and Oceanography*, **51**, 973–987.

BUTTERWORTH, D.S. 1988a. A simulation study of krill fishing by an individual Japanese trawler. *CCAMLR Scientific Committee Selected Scientific Papers*, **5**, 1–108.

BUTTERWORTH, D.S. 1988b. Some aspects of the relation between Antarctic krill abundance and CPUE measures in the Japanese krill fishery. *CCAMLR Scientific Committee Selected Scientific Papers*, **5**, 109–125.

BYKOWSKI, P.J. 1986. Possibilities of utilizing Antarctic krill. *Marketing Digest*, **6/86**, 11–13.

CANDY, S.G. & KAWAGUCHI, S. 2006. Modelling growth of Antarctic krill. II. Novel approach to describing the growth trajectory. *Marine Ecology Progress Series*, **306**, 17–30.

CCAMLR. 2004. *Report of the Twenty-third Meeting of the Scientific Committee*. (SC-CAMLR-XXIII). Hobart: CCAMLR, 680 pp.

CCAMLR. 2005. *Report of the Twenty-fourth Meeting of the Scientific Committee*. (SC-CAMLR-XXIV). Hobart: CCAMLR, 647 pp.

CCAMLR. 2006a. *CCAMLR Statistical Bulletin Vol. 18*. Hobart: CCAMLR, 239 pp.

CCAMLR. 2006b. *CCAMLR Data Form C1v2006*. Hobart: CCAMLR.

CONSTABLE, A.J., NICOL, S. & STRUTTON, P.G. 2003. Southern Ocean productivity in relation to spatial and temporal variation in the physical environment. *Journal of Geophysical Research*, **108**, art. 8079.

EVERSON, I., *ed.* 2000. *Krill biology, ecology and fisheries*. Oxford: Blackwell Science, 372 pp.

EVERSON, I. & GOSS, C. 1991. Krill fishing activity in the southwest Atlantic. *Antarctic Science*, **3**, 351–358.

FALK-PETERSEN, S., HAGEN, W., KATTENER, G., CLARKE, A. & SARGENT, J. 2000. Lipids, trophic relationships, and biodiversity in Arctic and Antarctic krill. *Canadian Journal of Fisheries and Aquatic Science*, **57** (Supp 3), 178–191.

GUTT, J. & SIEGEL, V. 1996. Benthopelagic aggregations of krill (*Euphausia superba*) on the deeper shelf of the Weddell Sea (Antarctica). *Deep-Sea Research I*, **41**, 169–178.

HAGEN, W., VAN VLEET, E.S. & KATTNER, G. 1996. Seasonal lipid storage as overwintering strategy of Antarctic krill. *Marine Ecology Progress Series*, **134**, 85–89.

HAMNER, W.M. & HAMNER, P.P. 2000. Behavior of Antarctic krill (*Euphausia superba*): schooling, foraging, and antipredatory behavior. *Canadian Journal of Fisheries and Aquatic Science*, **57**, 192–202.

HAMNER, W.M., HAMNER, P.P. & OBST, B.S. 1989. Field observations on the ontogeny of schooling of *Euphausia superba furciliae* and its relationship to ice in Antarctic waters. *Limnology and Oceanography*, **34**, 451–456.

HAMNER, W.M., HAMNER, P.P., STRAND, S.W. & GILMER, R.W. 1983. Behavior of Antarctic krill, *Euphausia superba*: chemoreception, feeding, schooling and molting. *Science*, **220**, 433–435.

ICHII, T. 1987. Observations of fishing operations on a krill trawler and distributional behaviour of krill off Wilkes Land during the 1985/86 season. *CCAMLR Scientific Committee Selected Scientific Papers*, **4**, 335–368.

ICHII, T. 2000. Krill harvesting. *In* EVERSON, I., *ed*. *Krill biology, ecology and fisheries*. Oxford: Blackwell Science, 228–261.

IKEDA, T. & THOMAS, P.G. 1987. Longevity of the Antarctic krill (*Euphausia superba*) based on a laboratory experiment. *Proceedings of the National Institute of Polar Research Symposium on Polar Biology*, **1**, 56–62.

JACBOWSKI, E. 2002. Distribution and size of Antarctic krill (*Euphausia superba* Dana) in Polish commercial catches taken in the Atlantic sector of the Southern Ocean from 1997–1999. *CCAMLR Science*, **9**, 83–105.

JONES, C.D. & RAMM, D.C. 2004. The commercial harvest of krill in the southwest Atlantic before and during the CCAMLR 2000 Survey. *Deep-Sea Research II*, **51**, 1421–1434.

KANDA, K., TAKAGI, K. & SEKI, Y. 1982. Movement of the larger swarms of Antarctic krill *Euphausia superba* off Enderby Land during 1976–1977 season. *Journal of the Tokyo University of Fisheries*, **68**, 25–42.

KAWAGUCHI, K., ISHIKAWA, S. & MATSUDA, O. 1986. The over wintering of Antarctic krill *Euphausia superba* Dana under the coastal fast ice off the Ongul Islands in Lutzow–Holm Bay, Antarctica. *Memoirs of National Institute of Polar Research*, **44**, 67–85.

KAWAGUCHI, S. & NICOL, S., *eds*. 2003. Proceedings of the International Workshop on understanding living krill for improved management and stock assessment. *Marine and Freshwater Behavior and Physiology*, **36**, 1–307.

KAWAGUCHI, S. & SATAKE, M. 1994. Relationship between recruitment of the Antarctic krill and the degree of ice cover near the South Shetland Islands. *Fisheries Science*, **60**, 123–124.

KAWAGUCHI, S., ICHII, T. & NAGANOBU, M. 1997. Catch per unit effort and proportional recruitment indices from Japanese krill fishery data in Subarea 48.1. *CCAMLR Science*, **4**, 47–63.

KAWAGUCHI, S., ICHII, T. & NAGANOBU, M. 1999. Green krill, the indicator of micro- and nano-size phytoplankton availability to krill. *Polar Biology*, **22**, 133–136.

KAWAGUCHI, S., CANDY, S., NICOL, S., TAKI, K. & NAGANOBU, M. 2005a. Analysis of trends in Japanese krill fishery CPUE data, and its possible use as a krill abundance index. *CCAMLR Science*, **12**, 1–28.

KAWAGUCHI, S., ICHII, T., NAGANOBU, M. & DE LA MARE, W.K. 1998. Do krill and salps compete? Contrary evidence from krill fishery. *CCAMLR Science*, **5**, 205–216.

KAWAGUCHI, S., NICOL, S., TAKI, K. & NAGANOBU, M. 2005b. A conceptual model of Japanese krill fishery. *SC-CCAMLR-WG-EMM05.30*.

KAWAGUCHI, S., NICOL, S., TAKI, K. & NAGANOBU, M. 2006a. Fishing ground selection in krill fishery: trends in its patterns across years, seasons, and nations. *CCAMLR Science*, **13**, 117–141.

KAWAGUCHI, S., CANDY, S.G., KING, R., NAGANOBU, M. & NICOL, S. 2006b. Modelling growth of Antarctic krill. I. Growth trends with sex, length, season and region. *Marine Ecology Progress Series*, **306**, 1–15.

https://doi.org/10.1017/S0954102007000296 Published online by Cambridge University Press

KOCK, K.-H. & SHIMAZU, Y. 1994. Trophic relationships and trends in population size and reproductive parameters in Antarctic high-level predators. *In* EL-SAYED, S., *ed. Southern Ocean ecology: the BIOMASS Perspective*. Cambridge: Cambridge University Press, 165–184.

LITVINOV, F.F., SUSHIN, V.A., CHERNEGA, G.A. & BEREZHINSKY, O.A. 2003. The Soviet krill fishery in the Atlantic Sector of the Antarctic from 1977 to 1991: fishing effort distribution and interannual patterns. *CCAMLR Science*, **10**, 1–13.

LITVINOV, F.F., SUNDAKOV, A.Z. & ARKHIPOV, V.I. 2004. CPUE indices used in Soviet krill fishery statistics from 1977 to 1992 and their possible utility for evaluation of relative changes in krill biomass. *CCAMLR Science*, **11**, 165–177.

LOEB, V., SIEGEL, V., HOLM-HANSEN, O., HEWITT, R., FRASER, W., TRIVELPIECE, W. & TRIVELPIECE, S. 1997. Effects of sea-ice extent and krill or salp dominance on the Antarctic food web. *Nature*, **387**, 897–900.

MANGEL, M. & NICOL, S. 2000. Proceedings of the Second International Krill Symposium, Santa Cruz, California, August 1999. *Canadian Journal of Fisheries and Aquatic Sciences*, **57**, 1–202.

MARR, J.W.S. 1962. The natural history and geography of the Antarctic krill (*Euphausia superba* Dana). *Discovery Reports*, **32**, 33–464.

MELROSE, J., HALL, A., MACPHERSON, C., BELLENGER, C.R. & GHOSH, P. 1995. Evaluation of digestive proteinase from the Antarctic krill *Euphausia superba* as potential chemonucleolytic agents. *In vitro* and *in vivo* studies. *Archives of Orthopaedic and Trauma Surgery*, **114**, 145–152.

MILLER, D.G. & HAMPTON, I. 1989. Biology and ecology of the Antarctic krill (*Euphausia superba* Dana): a review. *BIOMASS Scientific Series*, **9**, 1–166.

NICOL, S. 2000. Understanding krill growth and aging: the contribution of experimental studies. *Canadian Journal of Fisheries and Aquatic Science*, **57**, 168–177.

NICOL, S. 2003. Krill and currents - physical and biological interactions influencing the distribution of *Euphausia superba*. *Ocean Polar Research*, **25**, 633–644.

NICOL, S. 2006. Krill, currents and sea ice: *Euphausia superba* and its changing environment. *BioScience*, **56**, 111–120.

NICOL, S. & ENDO, Y. 1999. Krill fisheries: development, management and ecosystem implications. *Aquatic Living Resources*, **12**, 1–17.

NICOL, S. & FOSTER, J. 2003. Perspective-recent trends in the fishery for Antarctic krill. *Aquatic Living Resources*, **16**, 42–45.

NICOL, S., FORSTER, I. & SPENCE, J. 2000. Products derived from krill. *In* EVERSON, I., *ed. Krill biology, ecology and fisheries*. Oxford: Blackwell Science, 262–283.

QUETIN, L.B. & ROSS, R.M. 1991. Behavioral and physiological characteristics of the Antarctic krill, *Euphausia superba*. *American Zoology*, **31**, 49–63.

REID, K. 2007. Monitoring and management in the Antarctic-making the link between science and policy. *Antarctic Science*, **19**.

ROSS, R.M. & QUETIN, L.B. 2003. Working with living krill – the people and the places. *Marine and Freshwater Behavior and Physiology*, **36**, 1–307.

SIEGEL, V. 1987. Age and growth of Antarctic Euphausiacea (Crustacea) under natural conditions. *Marine Biology*, **96**, 483–495.

SIEGEL, V. 1988. A concept of seasonal variation of krill (*Euphausia superba*) distribution and abundance west of the Antarctic Peninsula. *In* SAHRHAGE, D., *ed. Antarctic Ocean and resources variability*. Berlin: Springer, 219–230.

SIEGEL, V. 1989. Winter and spring distribution and status of the krill stock in Antarctic Peninsula waters. *Archive für FischereiWissenschaft*, **39**, 45–72.

SIEGEL, V. 2005. Distribution and population dynamics of *Euphausia superba*: summary of recent findings. *Polar Biology*, **29**, 1–22.

SIEGEL, V. & LOEB, V. 1995. Recruitment of Antarctic krill *Euphausia superba* and possible causes for its variability. *Marine Ecology Progress Series*, **123**, 45–56.

SIEGEL, V. & NICOL, S. 2000. Population parameters. *In* EVERSON, I., *ed. Krill biology, ecology and fisheries*. Oxford: Blackwell Science, 103–149.

SIEGEL, V., DAMM, U. & SUSHIN, V.A. 1998. Catch per unit effort (CPUE) data from the early years of commercial krill fishing operations in the Atlantic sector of the Antarctic. *CCAMLR Science*, **5**, 31–50.

SIEGEL, V., KAWAGUCHI, S., WARD, P., LITVINOV, F., SUSHIN, V., LOEB, V. & WATKINS, J. 2004. Krill demography and large-scale distribution in the southwest Atlantic during January/February 2000. *Deep-Sea Research II*, **51**, 1253–1273.

STRAND, S.W. & HAMNER, W.M. 1990. Schooling behaviour of Antarctic krill (*Euphausia superba*) in laboratory aquaria: reactions to chemical and visual stimuli. *Marine Biology*, **106**, 355–359.

SUSHIN, V.A. 1998. Distribution of the Soviet krill fishing fleet in the South Orkneys area (Subarea 48.2) during 1989/1990. *CCAMLR Science*, **5**, 51–62.

SUZUKI, T. 1981. *Fish and krill protein: processing technology*. London: Allied Science Publishers, 193–251.

SUZUKI, T. & SHIBATA, N. 1990. The utilization of Antarctic krill for human food. *Food Reviews International*, **6**, 119–147.

TAKAHASHI, M. 1991. *Trophic ecology of demersal fish community in the waters of north of the Antarctic Peninsula, with note on the ecological role of the krill*. PhD thesis, Tohoku University, 110 pp. [Unpublished, in Japanese].

TAKAHASHI, M. & IWAMI, T. 1997. The summer diet of demersal fish at the South Shetland Islands. *Antarctic Science*, **9**, 407–413.

TAKI, K., HAYASHI, T. & NAGANOBU, M. 2005. Characteristics of seasonal variation in diurnal vertical migration and aggregation of Antarctic krill (*Euphauia superba*) in the Scotia Sea, using Japanese fishery data. *CCAMLR Science*, **12**, 163–172

TARLING, G.A., SHREEVE, R.S., HIRST, A.G., ATKINSON, A., POND, D.W., MURPHY, E.J. & WATKINS, J.L. 2006. Natural growth rates in Antarctic krill (*Euphausia superba*): I. Improving methodology and predicting intermolt period. *Limnology and Oceanography*, **51**, 959–972.

WATKINS, J.L. 2000. Aggregation and vertical migration. *In* EVERSON, I., *ed. Krill biology, ecology and fisheries*. Oxford: Blackwell Science, 80–102.

WATKINS, J.L., HEWITT, R., NAGANOBU, M. & SUSHIN, V. 2004. The CCAMLR 2000 Survey: a multi-ship biological oceanography survey of the Atlantic sector of the Southern Ocean. *Deep-Sea Research II*, **51**, 1205–1456.

YOSHITOMI, B. 2005. Seasonal variation of crude digestive protease activity in Antarctic krill *Euphausia superba*. *Fishery Scienc*e, **71**, 12–19.

https://doi.org/10.1017/S0954102007000296 Published online by Cambridge University Press