

Article

Krill and Currents-Physical and Biological Interactions Influencing the Distribution of *Euphausia superba*

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Abstract : The distribution and abundance of Antarctic krill (*Euphausia superba*), particularly in the South Atlantic, has traditionally been viewed as primarily determined by the flow of the Antarctic Circumpolar Current. Krill are viewed as being particles on a conveyor belt that carries them around the Antarctic continent resulting in a single circumpolar population. The evidence to support this viewpoint is largely circumstantial and there is very little direct evidence available of krill being moved by the currents-krill flux. There is also considerable biological and physical evidence which suggests that other factors may play a dominant role in the life history and distribution of krill. This review examines the evidence for krill flux and also examines evidence that does not accord with this theory. The management implications of assuming krill flux are outlined and some lines for future research are suggested.

Key words : Antarctic krill, flux, transport, distribution, Antarctic Circumpolar Current

1. Introduction

Interpretation of the population dynamics of Antarctic krill (*Euphausia superba*) has been dominated by the concept of krill flux, or krill transport. In this concept, developed from the South Atlantic, krill are viewed as particles in the flow of the Antarctic Circumpolar Current (ACC) and thus their distribution and abundance is described in terms of the ebb and flow of the regions currents. This concept has a number of important implications both for interpreting regional population dynamics and also for the understanding the Antarctic marine ecosystem and how to manage it effectively. In this paper, I critically evaluate the concept of krill flux, inspect the evidence that has led to the development of the concept of flux, and evidence that may not accord with the concept of flux. Finally, I will look at alternative models that could explain krill distribution and abundance and examine their implications and predictions.

Krill flux

The concept of "krill flux" has been a dominant paradigm

in Antarctic ecology. The basic underlying theme is that of a "krill conveyor belt" which carries krill in the ACC along the Western Antarctic Peninsula past the South Orkneys and South Sandwich Islands to South Georgia (Hofmann *et al.* 1998). Krill are, to a large extent, viewed as passive drifters in the flow field, though regions with consistently high biomass within the general area, and are viewed as having extended residence times which are oceanographically determined (Murphy *et al.* 1998). These are sometimes referred to as retention zones. Although this conceptual model has been developed to explain observations in the South Atlantic, it is also generally applied to other areas of the Southern Ocean where Antarctic krill occur. This concept was first put forward in the Discovery reports (Marr 1962), but despite its venerable history there is surprisingly little unequivocal direct evidence that indicates that large-scale transport of krill actually occurs. Most often, the concept of krill flux is taken to be already demonstrated and studies have merely set out to investigate the rate of flux and how to explain observations in light of this conceptual model (Reid *et al.* 2002).

There are a number of observations that suggest that there is a transfer of a significant portion of the krill

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population from one region to another in relatively short timescales (<1 year):

1. There is a large population of Antarctic krill in the waters around South Georgia yet there is little evidence of successful reproduction occurring there.
2. The estimated biomass of krill at South Georgia is insufficient to account for the estimated consumption of krill by land-based predators at South Georgia.
3. The prevailing currents in the Scotia Arc are of sufficient magnitude that krill populations would be unable to resist the prevailing flow patterns and that krill from the Antarctic Peninsula would naturally arrive at South Georgia.
4. There is no evidence that the Antarctic krill population is subdivided into individual stocks.
5. The population dynamics of krill in relatively distant areas appears to be linked.
6. There is direct evidence of krill being transported by the currents.

I will examine these observations to determine how compelling the evidence is for large-scale krill transport.

2. Examination of physical and biological factors affecting krill distribution

There is a large population of Antarctic krill in the waters around South Georgia yet there is little evidence of successful reproduction occurring there

There has always been some uncertainty concerning the self-sustaining nature of the krill population at South Georgia (Mackintosh 1972; Marr 1962). Krill larvae have been found in this area (Marr 1962) but some studies do report their absence or rarity (Ward *et al.* 1990). This latter study (Ward *et al.* 1990) is a frequently cited reference to support the lack of reproduction at South Georgia, however, the sampling in this study took place in April, November-December and July-August, whereas the peak spawning period for Antarctic krill is January-February (Spirodonov 1995). Sampling any region of the Antarctic outside the summer period is likely to yield few krill eggs and early larvae, so the results in Ward *et al.* (1990) are not definitive evidence that Antarctic krill do not reproduce in the vicinity of South Georgia. Large reproductive females are sometimes found in high abundance in South Georgia waters (Marr 1962). Spent female krill are found in the region so they do spawn around South Georgia, but whether the eggs are retained in the locality or lost to the east through the prevailing water flow is unknown. The question of whether the South Georgia krill population is

self-sustaining comes down to whether the larvae from the eggs that are spawned nearby return to the adult population. Year one krill are found at South Georgia but their origin has always been assumed to be the product of spawning in some other area (Reid *et al.* 2002).

Other organisms with planktonic larvae that populate the waters around South Georgia such as fish or copepods appear to have self-sustaining populations, or at least are assumed to have residence times which are significant in terms of their overall lifespans (Atkinson *et al.* 2001). Similarly, other island groups in the ACC also appear to have resident populations of organisms which are either planktonic or which have planktonic phases in their life cycles so the mere existence of a strong prevailing current is not sufficient to require the concept of flux to explain the existence of a persistent population around an island group. There is also evidence from other oceanic regions that distinct populations of pelagic organisms can arise, despite the homogenizing effect of ocean currents, e.g. various species of krill in the North Atlantic (Bucklin *et al.* 1997; Zane *et al.* 2000). Many oceanic, and even truly holoplanktonic organisms display genetic heterogeneity between populations (Aoyama *et al.* 1999), site fidelity (Swearer *et al.* 1999) and self-recruitment (Jones *et al.* 1999). Thus, the notion of a self-sustaining population of krill at South Georgia, where the adult population is recruited largely from offspring spawned locally, should not be dismissed without direct evidence.

Krill are spawning in the waters around South Georgia, so what happens to their larvae? Antarctic krill spawn in deep water off the continental shelf and at South Georgia, this would place them within the flow of the ACC. If the larvae were to develop and return to South Georgia, then they would have to enter a system that carried them southwards to the Weddell Sea where they would pass the winter under the ice before emerging the following spring in waters that would take them to South Georgia. Examination of gross current flows in the region suggest that such a trajectory is not impossible (Amos 1984).

The estimated biomass of krill at South Georgia is insufficient to account for the estimated consumption of krill by land-based predators at South Georgia

One of the key reasons that krill flux has had to be inferred is the mismatch between the demand for krill at South Georgia, estimated from predator diet analysis, and the biomass of krill in the waters around South Georgia, estimated by acoustics. At South Georgia, the average density of krill is generally amongst the highest measured

anywhere around the Antarctic (Brierley *et al.* 1999), although there are years when krill appear to be nearly absent (Heywood *et al.* 1985). Despite the extraordinarily high level of krill density, acoustic estimates have failed to approach the krill biomass required to feed the land-based predators in the South Georgia area (Croxall *et al.* 1985). It has been estimated that the population of krill at South Georgia would have to be replaced every month during the summer to account for the mortality inflicted by the land-based predators (Atkinson *et al.* 2001). A recent analysis, however, has suggested that the mismatch may not be as great as first envisaged and further, indicates that production by the local krill population was sufficiently high that there does not need to be either a fast turnover of krill, or an efficient concentration mechanism to meet the estimated predator demands (Atkinson *et al.* 2001). Additionally, a recent modeling study has indicated that the Western Antarctic Peninsula cannot provide enough production to supply the estimated consumption at South Georgia (Constable *et al.* 2003).

The perceived disparity between predator demand and estimated krill abundance, however, is not a problem unique to South Georgia. Recent global estimates of krill abundance using acoustic data from around the continent fall considerably short of that required to support the global requirements of land-based and pelagic predators of krill (Nicol *et al.* 2000a). There seems to be a general problem with matching availability of krill to calculated demand even in the closed system of the entire Southern Ocean, and this problem cannot be solved by implying immigration from external source areas. It is difficult to envisage an import-driven production system at South Georgia when the global population of krill is unable to provide the level of export required.

Part of the problem in matching supply and demand for krill in regions such as South Georgia may come from an underestimation of *in situ* production. Estimated production to biomass ratios for krill range from 0.8 to 5.0, the higher figure, including larvae of all developmental stages (Siegel 2000a). There is also evidence that there is no fixed P/B ratio for krill and that in certain areas it may be close to zero (Ross and Quetin 1988). Standing stock estimates at South Georgia of 1.5 million tons (Trathan *et al.* 1992) could thus generate production of between 1.2-7.5 million tons, depending on which estimate of P/B is used. Estimates based on measured growth and carbon assimilation rates have suggested that production by the krill population at South Georgia is probably of a similar order to the best estimates of predator removal during

their breeding period (Atkinson *et al.* 2001). Obviously, the degree to which flux must be implied to support consumption depends on the level of production, as well as on realistic estimates of abundance and distribution of krill, and consumption by predators. These two latter methodological aspects are known to be fraught with uncertainties (Watkins 2000a, b) but both are amenable to study and refinement.

The prevailing currents in the Scotia Arc are of sufficient magnitude that krill populations would be unable to resist the prevailing flow patterns and krill at the Antarctic Peninsula would naturally arrive at South Georgia

The overall circulation pattern in the South Atlantic is well understood and is dominated by the flow of the ACC across and through the Scotia Arc (Fig. 1). Modeling studies have indicated that particles in this general flow field could be transported from the Western Antarctic Peninsula region to South Georgia in 140-160 days. This is of the same order of time that it takes a krill juvenile to develop from a newly released egg (Hofmann *et al.* 1998). Such modeling studies indicate what is possible given the constraints of the model, and the assumptions on which is predicated. In particular, the implications of these studies are that the krill population is mainly to be found in the eastward flow waters of the ACC. Studies off the Antarctic Peninsula indicate that this is not the case, most post-larval krill are to be found in the waters of the Antarctic Coastal Current (East Wind Drift), which flows in a southwesterly direction and the krill population exhibits a considerable distributional structure within the coastal water mass (Ichii and Naganobu 1996; Ichii *et al.* 1998). It is apparent that the distribution of krill is a product of both behavior and circulation patterns. Younger, non-

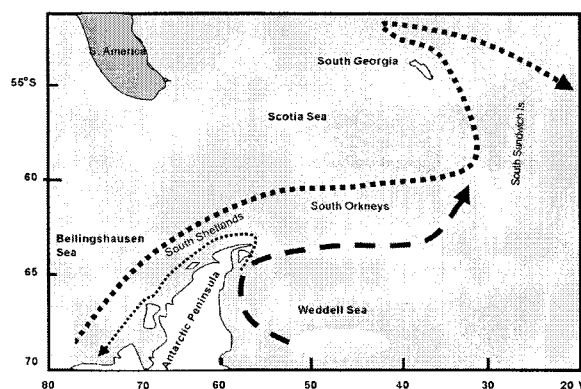


Fig. 1. Sketch map of the South Atlantic showing the major current systems.

reproductive krill are found on the shelf, whereas reproductive adults are generally found offshore of the shelf break in summer (Siegel 1988; Lascara *et al.* 1999; Nicol *et al.* 2000b). Krill appear to be concentrated in the inner shelf area in the Western Antarctic Peninsula region when compared to the outer shelf area in all seasons (Lascara *et al.* 1999). Further to the northwest of the South Shetlands, krill were of a magnitude more abundant in the inner shelf region (138 g m^{-2}) when compared to oceanic waters (8 g m^{-2}) (Ichii *et al.* 1998). In these locations, the observed geostrophic flows have been described as sluggish, and tend to have a south-westerly direction with limited exchange along the shelf either north or south (Ichii and Naganobu 1996; Smith *et al.* 1999) in contrast to the models of large-scale geostrophic flows in the region, which indicate a west-east flow towards South Georgia (Hofmann *et al.* 1998). Given these conditions, it is difficult to envisage a system that would allow gross movements of adult krill from the Antarctic Peninsula to South Georgia of the magnitude that has been suggested the entire population being replaced on a monthly basis (Atkinson *et al.* 2001).

Explaining the distribution of krill through the analogy of particles would require that the particles become randomly assorted along their journey so that the processes of concentration and retention would work. This is not the case and the general ontogenetic distributions of krill life history stages are found in all areas of the South Atlantic and elsewhere (Siegel and Harm 1996). Early studies pointed this out: "...the patchiness of the larvae that persists from their earliest deep appearance until the completion of their life-cycle in the surface, arises directly from their being assembled in a system of swarms in which the separate individuals in each instance are of the same or much the same age and, which, *from hatching onwards*, seems to keep them together until the end of their natural span." (Marr 1962). The spatial segregation of different age and size classes has been shown for most areas of the Antarctic that have been studied (Siegel 1998; Nicol *et al.* 2000b) and there is evidence from very detailed sampling programs around South Georgia that there can be considerable differences between adjacent swarms in terms of their maturity stage and sizes (Watkins 1986). In addition, the number and sizes of aggregations in an area can change over the course of a year, with fewer, but larger, aggregations being found in winter (Lascara *et al.* 1999). These changes are thought to be behaviorally induced with many small, widely dispersed, foraging aggregations in summer coalescing into the

smaller number of larger onshore wintering aggregations (Ross *et al.* 1996). This is very different from what might be expected if the distribution of krill were merely a product of the water movements.

Crucial to the concept of flux is the existence of source regions. In the South Atlantic, the two most often cited source regions are the Bellingshausen Sea and the Weddell Sea. Neither of these regions have been extensively surveyed for krill on a regular basis but the indications from those surveys that have been conducted are that these are not regions with consistently high densities of krill of the magnitude that would be required to fuel the production of the entire South Atlantic (Siegel and Harm 1996; Siegel 2000b; Murray *et al.* 1995). The concept of such source regions also begs the question of where the krill that stock the source regions themselves come from. The circumpolar currents of the Antarctic usually provide the answer and the argument rapidly becomes somewhat circular. If the South Atlantic is populated by imported krill, then there must be a site that exports krill in vast numbers. All evidence to date indicates that the abundance and biomass of krill is at its highest in the South Atlantic (Nicol *et al.* 2000a). It seems unlikely, therefore, that other areas contribute greatly to this biomass by exporting their lower level of production.

If there is a "river of krill" flowing from the Antarctic Peninsula to South Georgia then a gradient in density might be expected to compensate for the mortality that occurs along the journey. This is quite the opposite of what is observed; densities at South Georgia are consistently higher than those on the Peninsula (Siegel 2000b). This has been explained by the concepts of retention zones concentration areas and flow rates. However, purely mechanistic processes do not accord with the biological processes taking place simultaneously. Concentration and retention of "particles" requires either that more "particles" be added to a water mass, or that water is extracted from an existing concentration to increase "particle" density. Purely mechanistic factors cannot result in biologically realistic models of concentration without invoking a considerable degree of behavior on the part of the "particles".

There is no evidence that the Antarctic krill population is subdivided into individual stocks

From the earliest days of investigations into the biology of Antarctic krill, there has been recognition that some areas of the Southern Ocean have perennially larger populations of krill than others (Marr 1962). The post-larval population has been divided into stocks by some

authors (see Everson 1976): the Weddell stock, the Bouvet Island, the Enderby, the Kerguelen-Gaussberg, and the Bellingshausen stocks. Two smaller stocks in the Pacific have also been identified (Mackintosh 1973). These "stocks" may not be distinct biological entities and may in many instances be linked to physical features. For example, the Kerguelen-Gaussberg stock located between 85-100°E was recently surveyed and was shown to be related to the presence of an eddy in the Antarctic Coastal current (Nicol *et al.* 2000b).

Fisheries data have lent support to the concept that there are areas where krill are generally to be found aggregated (Ichii 1990). This is also becoming apparent from repeated acoustic surveys off the Antarctic Peninsula (Hewitt and Demer 1994) and South Georgia (Brierley *et al.* 1999). As these aggregations have not been targeted for concerted study, it is not possible to determine whether their presence in an area is a result of active processes undertaken by the krill, because of retention processes in the current system or because of interaction between the two. One of the few detailed analyses of the interaction between the dynamics of pelagic populations and physical processes (Huntley and Niiler 1995) concluded that mesoscale oceanographic processes influencing the resident time of zooplankton in an area play a crucial role in keeping zooplankton and krill in areas of high primary productivity. The results of that study indicate the great potential for movement from one region to another over the generation time (7-10 years) of a population but that individuals were likely to be retained within a region over the course of a season yielding high secondary production in areas of high primary production.

Populations of different krill species in the Southern Ocean are usually separated from one another. For example, *E. crystallophias* is usually found inshore of *E. superba* although the oceanographic environment that they inhabit is similar (Siegel and Harm 1996). Similarly, there are distinct pelagic communities that vary from inshore to oceanic waters, whose boundaries cannot be explained merely by physical features (Hosie 1994). These separations must be maintained by a combination of behavior, life cycle traits, and interactions with their physical environment. Currents alone cannot explain why they remain distinct.

There have been a limited number of studies that have examined the stock structure of Antarctic krill using genetic techniques. Early studies using allozyme data indicated that the circum-Antarctic krill population may be homogeneous; (Fevolden and Ayala 1981, Fevolden and Schneppenheim 1988, 1989; MacDonald *et al.* 1986).

However, a more recent study using mitochondrial DNA sequence analysis indicated significant differences between krill collected at different sites around the continent (Zane *et al.* 1998). This study indicated significant genetic differences between krill collected from the Weddell Sea and South Georgia, but revealed no differences between krill collected from the Ross Sea, South Georgia, or Bellingshausen Sea. The authors suggest that oceanographic barriers could be sufficiently strong and temporally stable to restrict gene flow between regions. Other genetic studies are proceeding and molecular techniques are being rapidly refined, so the ability of these studies to detect subtle differences between the stocks in different regions of the Antarctic is improving. The nature of these studies is such that a result indicating a homogeneous stock may merely reflect the relative insensitivity of the technique or the smallness of the sample size (Bucklin *et al.* 1997). A result indicating genetic differences, on the other hand, is more difficult to explain, other than through the existence of limited mixing between populations. The most recent results (Zane *et al.* 1998), therefore, should be examined in this light. A recent study on *Euphausia crystallophias* from around the coast of Antarctica revealed considerable genetic diversity within small areas (Jarman *et al.* 2002). The implications of this study are that a high-density sampling regime is required to genetically define the population of krill in an area (Jarman and Nicol 2002). The suggested sampling regime is 20 samples of at least 100 animals for each area of interest. None of the studies conducted on Antarctic krill so far have used a sampling regime of this nature. Therefore results that show either no differences (Fevolden and Schneppenheim 1988) or significant differences (Zane *et al.* 1998) have to be viewed with caution. The use of more sensitive techniques and more comprehensive sampling programs will permit more confidence in the analysis of the genetic basis of stock structure.

Small amounts of interchange between populations may be enough to maintain a genetically homogeneous population of krill over the medium to long-term timescale. In terms of the individuals or swarms, and in the context of krill flux, the question is not whether there is genetic interchange - there almost certainly is - but whether an individual or a swarm is transported from one area to another within its lifetime.

The population dynamics of krill in relatively distant areas appears to be linked

Considerable attention has recently focused on examining

the relatedness of krill life-history events across the whole South Atlantic sector of the Southern Ocean (Brierley *et al.* 2000). Data on krill density have indicated that changes co-occur at sites off Elephant Island and off South Georgia with no time lag and this has been thought to imply that krill density is being impacted by the same physical and biological factors across its range in this area.

Estimates of krill density in a region are critically dependent on the area being surveyed and comparisons between areas must include an assessment of the comparative nature of the surveys. The survey data from the Scotia Arc were obtained from a number of different survey designs and covered widely different areas, though no indication of the survey area was given. Additionally, some surveys were conducted on the shelf, some largely off the shelf, and some straddling the shelf (Brierley *et al.* 2000). Similarly, the Elephant Island surveys have covered widely different areas (17,338 km² to 43,474 km²) (Hewitt and Demer *et al.* 1994). The mean density obtained from a survey is very sensitive to the areas included in the averaging process (Pauly *et al.* 2000). Antarctic krill are known to concentrate close to the shelf front zone (Ichii *et al.* 1998; Lascara *et al.* 1999; Pauly *et al.* 2000) so the more tightly a survey focuses on this area, the higher the mean density is likely to be. Additionally, the latitudinal width of the band of krill rich waters can change considerably between regions (Nicol *et al.* 2000c), so average densities of krill can vary depending on the relative amounts of krill-rich and krill-poor waters are surveyed (Lascara *et al.* 1999). Thus, comparisons of krill densities between areas should be viewed with caution.

There has been considerable evidence provided that similar population processes could be taking place in krill populations observed at South Georgia and in areas of the Scotia Arc (Brierley *et al.* 2000). This is thought to indicate that krill from the Antarctic Peninsula carry their biological characteristics with them as they are transported to the north (Reid *et al.* 2002). What may be equally plausible is that large-scale oceanographic phenomena affect the ecosystems of South Georgia and the Peninsula and that these affect the population dynamics in similar ways in both areas.

The population dynamics of krill at fixed sites have been subject to a number of longterm studies. In areas off both the Western Antarctic Peninsula (Ross *et al.* 1996), and in waters off South Georgia (Reid *et al.* 2002), year classes of krill have been detected in local populations, which can be followed from year to year. These studies suggest that at least on the timescale of the studies (4-5

years), there may be definable resident populations in these areas, although this interpretation has not always been adopted (Reid *et al.* 2002). In the Western Antarctic Peninsula region, studies have also shown significant relationships between local reproduction and local recruitment. In both regions, however, the populations exhibit occasional years when there are considerable perturbations. These can be interpreted as large scale changes in the physical environment that affect the distribution of the krill populations (Priddle *et al.* 1988).

Krill at South Georgia are not an homogeneous population either in terms of the small scale or meso scale (Watkin 2000b). The population of krill from the northeast of the island has been shown to be distinct in its size structure from that at the west of the island (Watkins *et al.* 1999). There have been attempts to explain this disparity through differential rates of transport to the two areas from two distinct sources, differential retention times and through mixing of krill from different sources to produce new mixtures of sizes (Watkins *et al.* 1999). Again, there has been a limited examination of these two areas from the perspective of there being two regional populations of krill with very limited interchanges between them.

Model results have been used to reconcile the disparate size frequencies observed between the Antarctic Peninsula and South Georgia (Reid *et al.* 2002). By utilizing regional differences in growth and mortality rates, the model results indicated that the observed differences could have been the result of krill from the Antarctic Peninsula being transported to South Georgia. However, the model indicated that first year krill would have to be advected into both areas simultaneously. No modeling studies to date have examined whether observed size frequency distributions could be better predicted through in situ processes on a resident population or through changes occurring in a population being advected from one area to another.

Largescale water movements can be thought of in two ways. The more common view of water movements is advection - the river that carries krill from one area to another (Hofmann *et al.* 1998, Murphy *et al.* 1998). The second possibility is that of displacement, whereby whole habitats are moved by extremely largescale oceanographic or meteorological disturbances such as El Nino (Priddle *et al.* 1988, Nicol *et al.* 2000c). The tip of the Antarctic Peninsula and the South Georgia region are extremely susceptible to largescale displacements because in this region the series of frontal systems that defines many of the biological habitats of the region are compressed into a

very narrow strip, thereby amplifying any oceanic disturbances that are present .

3. There is direct evidence of krill being transported by the currents

There are very few studies that have provided direct evidence of krill actually moving across significant geographic distances. Kanda *et al.* (1982) provided evidence of cohesive krill swarms moving considerable distances (up to 185 km) against the set of currents at speeds up to 0.47 km per hour. These observations were made from fishing vessels, which were tracking the swarms and their notes were sufficiently detailed as to be considered reliable both in terms of observations and the conclusions they reach. There is also corroborating evidence on the changes in the biological state of the krill in the swarm, which appears to indicate that the same aggregation was being targeted for the whole fishing operation. Fishing data provided to CCAMLR by scientific observers from more recent years have also provided some indication of the movements of swarms but these observations have not appeared in the refereed literature.

A single study has reported an attempt to investigate the rate of flux (Everson and Murphy 1987). This study used repeated acoustic transects to derive an estimate of krill transport through an area and provided evidence of changes that could be interpreted as flux. Unfortunately, the timescale of observations was not long enough to unequivocally indicate whether they were seeing consistent movement of krill through an area.

The most convincing example of a krill swarm, which has been displaced over a considerable distance, is the Antarctic coastal krill *Euphausia crystallophias* (Brierley 1999). This is thought to be a neritic, cold water species yet was found in an oceanic environment some 1500 km from the Antarctic continent in a narrow jet of fast moving water. There are no such documented cases for *E. superba*, yet if the "conveyor belt" hypothesis is correct, observations of moving krill aggregations should be relatively commonplace, especially if the krill population at South Georgia needs to be replenished several times a year.

Although this is an unequivocal indication of krill being transported in a current jet, the rarity of such observations being reported seems to indicate that they are not a common phenomenon. Krill species tend to be found within their habitats and it is very rarely that *E. crystallophias* is found in waters that are the natural abode of *E. superba*

and vice versa. It is difficult to envisage a purely physical mechanism behind such species-level separations.

The distribution and abundance of krill off the Palmer Long Term Ecological research site has been subject to concerted study (Lascara *et al.* 1999). Examining the changes in krill distribution and abundance that were observed during four multi-disciplinary research cruises, the authors concluded that there is a seasonal shift in the preferred habitat of krill in this region. They concluded that advection is not the prime factor affecting seasonal changes in krill abundance and that krill behaviour, including active vertical and horizontal migration, may be responsible for a large part of the observed seasonal variability.

There appears to be little direct evidence to support the idea that adult Antarctic krill are transported in large quantities by the waters of the Antarctic Circumpolar Current. The situation for krill larvae is likely to be somewhat different. Krill larvae develop in deep water and are, without doubt, carried within the water mass where they are spawned. The question is whether krill larvae that are spawned by a population of adults in one area are carried around the continent to re-populate another area, or whether they are spawned in a region that favors the return of the larvae to the spawning area. Such migrations are thought to occur within other species of euphausiids, where the location of the spawning grounds, the current structure, and the behavior of the larvae as they develop result in the juveniles returning to join the adult stock (Siegel 2000b). The prevailing view of the Antarctic krill reproduction is that the adults spawn freely into the ocean and the larvae are then randomly distributed by the currents, developing into juveniles at a location that is a function of current speed and direction (Marr 1962). The juveniles then develop into adults, as they are swept along by the currents, and they then spawn at the location where they find themselves when mature. It is now well documented that Antarctic krill perform ontogenetic migrations (Siegel 1988; Lascara *et al.* 1999). In summer, spawning adults are found offshore in deep water, less mature adults are found in the shelf break region, and juveniles are found closest to shore. At some point during their life cycle, then, krill must sort themselves into this distributional pattern, and because it is evident in the juvenile stages, it must occur in the initial larval phase. It is difficult to envisage a purely physical mechanism for such segregation, and active migrations must play a significant role. Recent evidence also indicates that there may well be winter migrations in certain areas with the adults moving into

deeper coastal water in winter and the larvae utilizing the under-ice habitat further offshore.

When considering the distribution of krill, larvae and adults can be thought of as very different animals. Krill eggs are shed in deep water and sink to depths of at least 2000 m before hatching (Siegel 2000a). The larvae begin to swim upwards and reach the surface after 3-4 weeks. On the surface, they begin to feed and develop. During their development, they become increasingly more mobile; nauplii are weak swimmers, whereas calyptopis larvae (3-8 Weeks old) are stronger swimmers. There is no doubt that larvae shed into the deep waters of the ACC flow with the current. What is also becoming increasingly evident is that it is the larvae in winter that have an intimate association with ice. The larvae and the sea ice develop simultaneously and the larvae may colonize the underside of the ice as it expands and drifts, but retreat with it in the spring to populate the inshore waters once the ice has retreated. This may well provide the link that brings larval krill back to their source region. A conceptual model that incorporates physically induced and biologically mediated spatial movements has been proposed by Siegel (2000a).

4. Discussion

One of the complications of the flux concept is that it can be used as a catch-all to account for a range of diverse observations. If population changes are observed at a single location, then what is being observed can be interpreted as the drift of animals from different regions into the area or alternatively as mixing of populations from different sources. If similar population processes are observed in different areas, then this can also be accounted for by the flux of individuals from one area to the next. Systematic changes in local populations can be interpreted as being indicative of widespread changes that affect the regional population rather than processes that occur in a static population.

Investigating the transport of krill is a difficult matter because of the nature of the problem, the biology of the animals, and because of the limitations in the techniques available. If it were possible to track aggregations of krill over a significant portion of a year, it might be possible to determine directly whether the aggregation was able to sustain itself in favourable locations or whether it was at the mercy of the currents. Unfortunately, tracking krill swarms has not generally proved possible - swarms can change shape and even entirely disappear, and rarely retain a configuration that allows for their unequivocal identification.

Although the technology exists to track the water in which krill swarms occur, it has not proved possible to ensure that the krill themselves are being monitored over biologically significant time periods.

Looking at the krill flux theory from the point of view of the reproductive and life history strategy, it seems to be unlikely for a number of reasons. For a large invertebrate, krill produce rather few eggs ~5,000 per spawning episode and they maybe spawn 10 times in their life cycle (Siegel 2000a). Although they are obviously not a *k* selected species, they are also far from being a classical *r* selected species. The implications of their reproductive output are that they cannot be entirely cavalier with their offspring. We know that female krill position themselves in deep water before spawning; do they also position themselves in locations that enhance the probability of their larvae returning to the same areas that the adults found favorable for reproduction? What is the evolutionary advantage of broadcasting one's reproductive output into currents that will take the larvae into far distant waters with uncertain food supplies?

Krill are most often referred to as zooplankton (Murphy *et al.* 1998) which are viewed as having "some powers of independent movement, but they cannot perform any effective horizontal migrations against the set of tides and currents." (Raymont 1976) It is not surprising, therefore that it has been assumed that they can be treated as particles when it comes to describing the forces that determine their distribution and abundance. Recent studies into pelagic organisms reveal that they appear to have developed mechanisms that allow individuals or populations to remain in, or return to, favourable areas despite the dispersive action of current systems (Palumbi 1999). The development of molecular techniques has allowed for the examinations of retention and the return of pelagic animals (Swearer *et al.* 1999; Jones *et al.* 1999; Barber *et al.* 2000) the re-examination of largescale migrations (Aoyama 1999) and population genetic studies on pelagic animals reveal considerable heterogeneity (Ayala and Valentine 1979; Bucklin and Wiebe; 1986; Bucklin *et al.* 1996; Zane *et al.* 2000). It is becoming increasingly obvious that adult krill are able to affect their location and that the life history of krill is too finely tuned to be entirely a product of the chance movements of currents. Krill have to move through the water; they cannot merely be transported in a packet of water.

Management implications of krill flux

Currently, it is assumed that land-based krill predators

are supplied with krill which is produced "upstream" from their breeding sites. This implies that any depletion of krill supplies offshore from these sites will be replenished. The more rapid the flux is, the quicker the replenishment will be (Miller and Agnew 2000). Furthermore, on a larger scale, it could be argued that depletion of krill in an entire subarea, such as South Georgia, would only be a temporary problem because of the rapid turnover that requires the biomass there to be replaced once a month anyway. Fishing at South Georgia would occur on a stock that is at the end of the "conveyor belt" and thus would need far less restriction than one that occurred "upstream". On a regional scale, depletion of krill within the Scotia Sea would be compensated for in the short term through the natural and rapid rate of immigration of krill from the "source" regions of the Bellingshausen Sea and the Weddell Sea. Under this scenario, krill fishing pressure throughout the region need not be too great a cause for concern because the entire population can be replaced quite rapidly.

In contrast, a management scheme that viewed each concentration of krill as a static local population on which the local population of land-based predators was dependent would need to be far more precautionary because local depletion would require far more time for recovery as it would occur through biological production, not through advection.

Given the lack of direct evidence for large scale krill transport, it is difficult to determine why CCAMLR has adopted a model which incorporates flux, over one which views the populations of krill as local "stocks" (Miller and Agnew 2000). This latter approach would be far more precautionary in both the short term and the long term. In the absence of certainty over the existence of krill transport, it would be erring on the side of caution for CCAMLR to assume that no flux between regions occurs.

How can the issue of krill transport be studied effectively?

To definitively measure bulk krill transport, a swarm or series of swarms of krill would have to be followed over a considerable period of time, and this would have to be repeated in a consistent fashion to demonstrate that it is a common feature. The only study of this sort that has been reported has actually indicated that krill swarms and currents are moving differentially (Kanda *et al.* 1982). Identifying individual patches of krill and following them over extended periods is a difficult and costly process. Krill swarms can be remarkably ephemeral; they can

change shape rapidly, can disperse, and can undergo vertical migration such that they become undetectable at night. Detecting relative movement between krill swarms and the water mass they inhabit is possible on a very short time scale, but becomes extremely difficult beyond a period of a few days - a period too short to be able to produce meaningful results that relate to large-scale krill flux.

One of the explanations for the phenomenon of vertical migration has been that it allows pelagic organisms the ability to affect their horizontal position through the use of differential current velocities at different depths. Thus, net velocity of a swarm of vertically migrating krill will be the result of the sum of the horizontal displacement over a full diurnal cycle - a single measurement at one location will not be enough.

Using static, or quasi-static, maps of flow fields with associated krill distributions allows the establishment for an hypotheses on what might happen to krill if they merely behaved like particles - they do not provide evidence that krill do, indeed behave like particles.

The solution to the problem will require experiments using both Eulerian and Lagrangian approaches - neither alone will provide a complete solution. Perhaps the best source of Lagrangian information may come from observers on fishing boats as these vessels are required to remain over krill concentrations for extended periods and are constantly sampling the krill so are also obtaining long-term information on the population structure. Because the fishery concentrates on areas where krill is persistently aggregated, such studies may, however, be based entirely in retention zones where krill transport is sluggish or interrupted. Moored arrays can provide Eulerian information on the passage of krill past a point and on the currents at that point, but provide no information on the fate of the krill once it has moved on.

Because most studies have begun from the premise that krill transport is not only a reality but that it is one of the dominant forces in krill population dynamics in the Scotia Sea, there has been no attempt to examine alternative hypotheses. Futures modeling studies will need to examine whether it is possible to explain the observed population changes at South Georgia, and on the Antarctic Peninsula, simply on the basis of processes that are occurring *in situ*.

Future research

Examining the relationship between krill and currents is an extremely difficult task that has to be studied through a number of scales simultaneously. The use of acoustic data

on krill abundance collected at the same time as current data from underway current profilers can help to provide snapshots of instantaneous relationships between the vertical and horizontal distribution of krill and currents. Similarly, moored systems can provide information on the movement of krill relative to currents at a single location. Neither approach alone will provide unequivocal answers. Development of new imaging systems that can provide 3D information on krill swarm shapes will permit the accurate tracking of krill aggregations and will allow the examination of fine-scale krill movements. Larger-scale movements of krill will require different, more elaborate approaches. One source of information may be the fishery, which has provided some tantalizing information on krill swarm movements in the past (Kanda *et al.* 1982). Examination of the intimate movements of krill fishing vessels over an extended time period together with biological information from the harvested krill may provide an additional source of data. Further, more detailed and better co-ordinated research into krill population genetics will also be of assistance in the examination of a wider range of plausible scenarios in modeling studies. No one approach alone will be able to solve this complex problem.

5. Conclusions

Krill are large pelagic crustaceans that live in dense aggregations. They are known to move through the water rapidly and in a concerted fashion. They are also known to have certain habitat preferences and are capable of both horizontal and vertical migrations. Their distribution is uneven on almost every scale within their distributional range. Because they develop through such a wide size range through their life cycle, the physical and biological forces that determine the distribution and abundance of the eggs and larvae are almost certainly not identical to those that determine the distribution and abundance of the adults. It is likely that for an animal, that is as numerically abundant that the determinants of biological success are not entirely left to chance, that these animals have evolved mechanisms to cope with their environment rather and are not merely passive participants in the pelagic ecosystem. Knowledge of krill ecology and the behaviour of krill has advanced over the last two decades and krill are no longer thought of as helpless particles (Nicol 2003). The current concept of krill flux by treating krill adults and larvae similarly and by viewing both as particles, does not take into account the complexities of either the physical environment or of the biology of the animal itself. Krill flux, krill

transport, and the "krill conveyor belt" are expressions of a hypothesis that has been proposed to account for a number of observations of krill distribution and biology. This hypothesis has not yet been adequately tested, nor have any other possible hypotheses to account for these observations been examined in any depth. Further research is required into the behaviour of krill and into the relationship between krill populations and their physical environment before any firm conclusions can be reached on the ultimate determinants of their distribution and abundance.

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