# KELVIN WAVES

*See* **COASTAL TRAPPED WAVES.**

# KRILL

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## Introduction

Krill play a major role in the transfer of energy in marine food webs, being important consumers of phytoplankton and other zooplankton, and prey of many higher trophic level predators that are often commercially important. The importance of krill in the diet of marine predators is reflected in their name; 'krill' comes from the Norwegian whaler's description of the larger food of the great whales. Krill form an order within the Crustacea, the Euphausiacea, which comprises over 80 species in 10 genera. Detailed keys are available to identify individual species that have broadly similar body pattern (**Figure 1**). The euphausiids occur in a wide range of habitats – coastal, oceanic, and deep-ocean regions – and their distributions also extend into the ice-covered regions of the Arctic and the Antarctic. Krill are generally more abundant in higher latitudes and can occur in such large numbers near the surface that they discolor the water.

The phylogenetic relationships of many of the euphausiids are unknown, but for some of the key oceanic species their evolutionary development appears to have been associated with the formation of the major circulation patterns of the world's oceans. This link to large-scale ocean circulation patterns is also reflected in the population distributions and life histories of the euphausiids. Many of the oceanic krill species occur over broad regions in which the centers of the populations tend to be associated with restricted features of the ocean circulation. However, the patterns of flow often result in transport of krill out of their main breeding regions to areas where they do not breed successfully. This also appears to be crucial to their role in many food webs, providing energy input into regions remote from their own main areas of production. The observation that krill are often transported into regions where they do not reproduce also highlights the colonization potential of the group should any changes occur in patterns of ocean circulation.

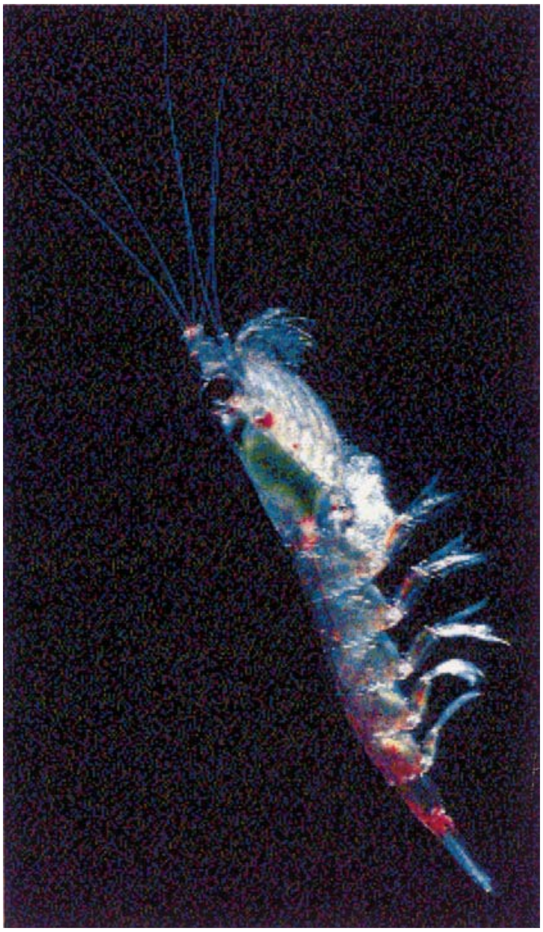
There are several features that mark the euphausiids as unusual plankton. A number of species are relatively large with a long life span compared with other zooplankton. The largest of the krill grow to over 60 mm and can live for more than 5 years. Another key feature is that in a number of the species the individuals form dense aggregations known as swarms. In some of the larger euphausiids these swarms might more appropriately be thought of as schools, similar to those formed by small fish, where members of the aggregation are aligned and show coherent patterns of behavior.

In the Antarctic the term 'krill' is often used to denote a single species: the Antarctic krill, *Euphausia superba* Dana (**Figure 1A**). This is, as its name suggests, the 'superb' krill that is large in size, occurs in vast numbers in the Southern Ocean, and is central to the Antarctic food web. It is the food of not only the now greatly depleted populations of whales but also many of the seals, penguins and other sea birds, and of fish and squid. It is the most studied species and much of the available information on euphausiids in general is based on knowledge of the Antarctic krill, so it is important to remember that this is something of an extreme representative of the group.

A number of the euphausiids have been exploited in fisheries. As krill are typically a low trophic level species there has been recognition of the potential impact this could have on the higher trophic levels of marine food webs. The pivotal role of krill in marine food webs has meant that, particularly in the Antarctic, an ecosystem approach to the management of krill fisheries is being developed that has relevance to the sustainable management of marine ecosystems globally.

## Species Separation and Geographical Distributions

Euphausiids are found throughout the oceans of the world, but their distributions highlight marked differences in habitat and life history amongst



(A)

(B)

**Figure 1** Two krill species: (A) the Antarctic krill, *Euphausia superba* and (B) a North Atlantic krill, *Meganyctiphanes norvegica.*

apparently similar species. There is a continuing debate about the exact number of species of euphausiids and the degree of separation of subgroups. There are indications from evolutionary studies of mitochondrial DNA that vicariant speciation (separation by formation of a natural barrier) has been important in the development of euphausiid species in the Antarctic. The generation of the Antarctic Polar Front about 25–22 Ma probably led to the separation of the 'Antarctic clade' (*E. superba* and *E. crystallorophias*) from the sister clade of *E. vallentini* and *E. frigida*) dated at about 20 Ma.

Although some euphausiid species occur in coastal and bathypelagic regions (1000–2500 m), most are found in oceanic epipelagic (0–200 m) and mesopelagic regions (200–1000 m). Although broad distributions have been described for many of the euphausiids, because these animals frequently occur in only relatively low numbers their local distributions are often not well defined. Generally, there is a trend of increasing abundance of krill at higher latitudes. However, there are variations in this pattern, with strong links between the ocean current systems and the regional distribution of krill species.

A feature of the euphausiids is that in Southern Ocean and Southern Hemisphere regions many of the key species occur across the full longitudinal range (**Figure 2**). In the Southern Ocean the ocean circulation is circumpolar, so the same basic pattern of species distribution is found throughout the connected ocean. The key species in the mainly ice-covered regions is *E. crystallorophias* which inhabits the Antarctic continental shelf, although on occasion it has been found transported northward by the major current flows. Further to the north in the seasonally ice-covered areas of the main flow regions of the Antarctic Circumpolar Current are *E. superba* and *E. frigida,* with *Thysanossa vicina* and *T. macrura* extending northwards to the Antarctic Polar Front. All of these species have heterogeneous distributions in the region. For *E. superba* there appear to be centers of population in which they can spawn and reproduce successfully, separated by and possibly connected through, regions that are not favorable to breeding but in which krill are found (**Figure 3**). *E. triacantha* overlaps the northern limit of *E. superba* in the south and in the north it overlaps the southern limit of the range of *E. vallentini* extending north to south of 40°S. Further north still are less abundant species such as *E. longirostris* and *E. lucens* that extend north of 40°S in areas encompassed by the eastward flows in the southern regions of the main ocean gyres of the Pacific, Atlantic, and Indian Oceans. To the north of this *E. similis* occurs in all three ocean basin

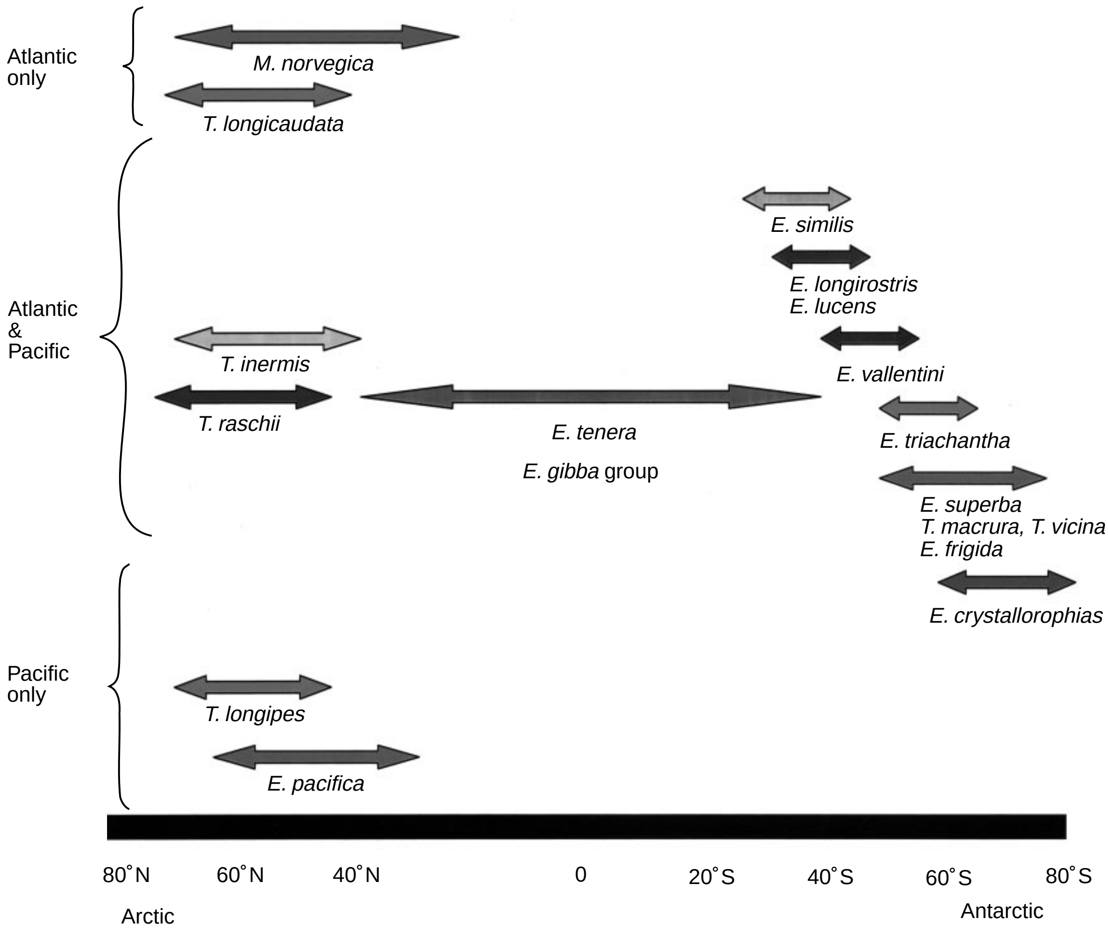



**Figure 2** The broad geographical distributions of some key euphausiid species.

regions, extending from about 50–60°S to 30°S, but the species is also present further north in the north-west region of the Indian Ocean to the north of Madagascar. Across the subtropical and tropical regions there is a wide range of species. One that occurs in all the ocean basins is *E. tenera*, where it has a wide distribution but is not very abundant in any region.

There are a number of other species found in both the Atlantic and Pacific Oceans. Some species, particularly in the central North Pacific and North Atlantic, are abundant but only found in one of the ocean basins. Key species that show this pattern are *E. pacifica* and *T. longipes*/*T. inspinata* that occur only in the northern North Pacific, while in the North Atlantic *Meganyctiphanes norvegica* and *T. longicaudata* are dominant (**Figure 2**).

In the northern North Atlantic and North Pacific there are species that occur in both oceans and through into the Arctic regions in the far north. In particular there are two important species, *T. raschii* and *T. inermis,* with distributions extending from about 45°N to about 80°N, although breeding is largely restricted to areas south of 70°N.

As well as geographical differences there are also marked differences in vertical distribution and many of the species show some form of vertical migration. For example, *E. pacifica* occurs mainly above 300 m during the day, moving nearer the surface (< 150 m) at night, while *M. norvegica* occurs between 100 and 500 m during the day and vertically migrates to shallower depths at night, and in the south *E. superba* occurs mainly above about 250 m and migrates nearer the surface at night.

## Growth, Development, Physiology

Krill species show a range of development strategies that vary between species, and also with the environmental conditions to which they are exposed. Studies of krill population dynamics and development are made difficult because of problems in determining the age of a number of the species. Traditional techniques involving the analysis of the

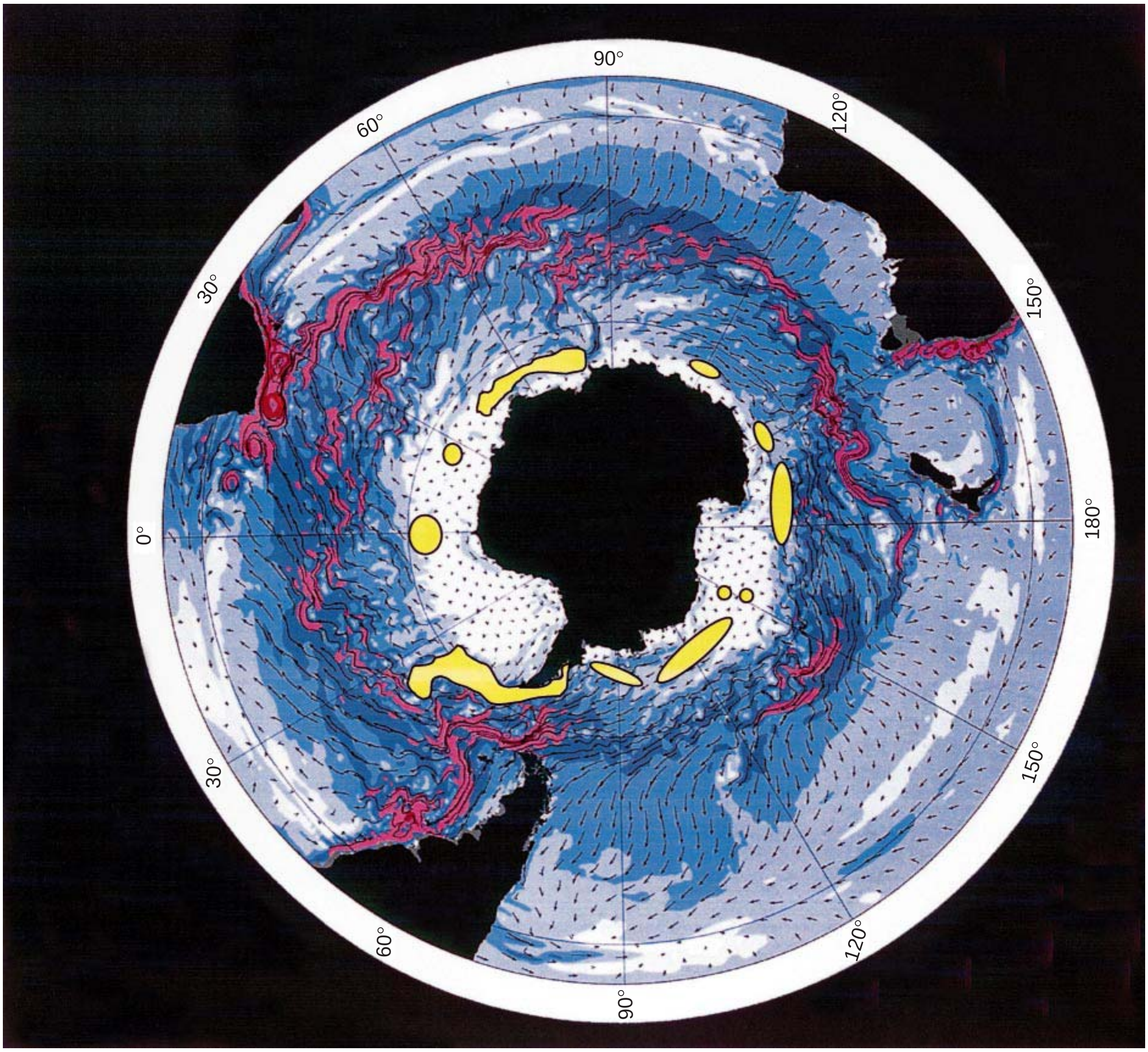



**Figure 3** The main regions of occurrence of Antarctic krill *E. superba* in the Southern Ocean and the pattern of surface circulation from the FRAM model (FRAM Group).

population age structure are still relied upon and a range of mathematical techniques have been employed to distinguish different cohorts in length–frequency size distributions. These are not always definitive and a range of other techniques has been explored such as using age pigment analyses, multiple-morphometric analyses, analyses of structures in the eye, and laboratory maintenance of live specimens. None of these techniques has so far provided a good and practical solution to determining the age of krill. However, there is general agreement about the broad characteristics of growth and development of many of the key species.

In the Southern Ocean, early studies of *E. superba* indicated a 2–3 year life cycle based mainly on samples from open-ocean regions. However, further detailed analyses of the size-structure and development of *E. superba* populations have led to a revision in the life-span up to $>5$ years with suggestions that in some areas 5–7 year classes can be identified. Laboratory experiments have maintained krill obtained from the sea for $>6$ years, indicating that a total age of 7–8 years is probably possible in the wild. The development and growth of the krill will depend on the conditions to which they are exposed. *E. superba* can reach a size of $>60$ mm with indications that growth may be very plastic, as in other euphausiid species, varying with the environmental conditions. Thus, krill in more northern and warmer regions may grow more rapidly and develop earlier than krill further south. In these more northern regions, such as around the

Island of South Georgia which lies at about 54°S, near the Antarctic Polar Front, the krill do not reproduce successfully, with few indications of any viable larvae being found in the area. The *E. superba* population in these regions is probably maintained by advection inputs from further south in the Southern Scotia Sea, Weddell Sea region, and from around the Antarctic Peninsula.

Such a plastic range of development is illustrated clearly in the northern species *T. inermis* and *T. raschii*. These species have a maximum age of 1 year at the south of their distribution (about 45°N), whereas further north they survive to over 2 years old, spawning in each year, although females may not mature until their second year. Continuing northward, the maximum age increases and maturation is delayed further with spawning delayed to year 3, and a maximum age of 3 years. In the high Arctic waters the krill still mature but do not spawn and it is the water circulation bringing krill from further south that maintains the species in these areas. Across this range *T. inermis* grows to over 20 mm, but the rates involved vary depending on the conditions, with slower growth and development occurring further north in their range.

*M. norvegica* is one of the most abundant North Atlantic krill and individuals can reach a maximum size of over 45 mm in some regions. This species shows less age variation across its range than the more northern *Thysanossa* species, but the variation is still significant. In the south of its range individuals live up to about 1 year and spawn only once, whereas further north they reach over 2 years of age, spawning more than once. Like *T. inermis*, this species does not spawn in the extreme northern part of its range, so advection in the current systems is again important in maintaining the distribution.

In the Pacific *E. pacifica* also shows this plastic character of changing maximum age with environmental variation. At the southern limit of its range individuals have a very short life span of only 6–8 months, whereas further north the maximum age is extended to about 15–21 months. In the most northern parts of the range the krill survive to over 2 years old and probably spawn twice. The maximum size across the range is about 20–22 mm, but growth is slower in the regions further north.

As well as these general changes in development and life span, there are also sex-related differences. For example, in the northern *Thysanossa* species the males mature at just over 1 year old while the females mature mainly at over 2 years of age. In *E. pacifica* both sexes mature and spawn at 1 year old, but females may continue to survive and spawn at over 2 years old. In *E. superba* the situation can be different, with females spawning and maturing earlier at 2 years old, while males may not mature until over 3 years old.

The euphausiids have the potential for rapid growth and development under suitable conditions, moulting as they increase in size. So, for example, *E. superba* has an energy input of perhaps 20% of body carbon per day or greater, sustained by a high and effective rate of filtration. This level of energy input can result in growth rates of $>0.1\,\mathrm{mm\,d^{-1}}$, particularly for the younger age groups. Krill have the capacity for a large and sustained reproductive output under good conditions, with continuous or multiple spawning occurring through the season in some species.

A key question for many of the species is how they survive during winter when food appears scarce, particularly in the extremely seasonal environments of the polar oceans. Studies of polar species show that the krill utilize stored lipids as a major energy source, but the dynamics of storage and utilization vary greatly between species. The lipids are accumulated primarily for winter survival or reproduction, but they may also provide a small degree of buoyancy that may help reduce the costs of swimming.

In the Southern Ocean, the diet of *E. superba* varies with age. Phytoplankton sources are important for the early stages while older groups utilize more animal-based food sources or detritus. Lipids are utilized in winter, but a strong seasonal bloom of production is necessary for reproduction. For *E. superba* the suggestion is that winter survival is dependent not only on reduced metabolic rate, a potential reduction in size, and use of lipids, but also on the use of alternative food sources. Antarctic krill have been observed to get smaller during poor feeding conditions in the laboratory, but it is unclear how much this occurs in the ocean. Larval *E. superba* are dependent on sea ice as a habitat and the observation of krill grazing algae associated with the ice indicates that they can utilize this as an alternative food source. It remains unclear how important sea ice algae are for maintaining adult *E. superba* and this is likely to be a variable contribution to the diet depending on opportunity of access to the right feeding conditions. *E. superba* are also known to graze other components of the plankton, including copepods, so that a range of possible feeding strategies is likely to be open to them, depending on opportunity.

*E. crystallorophias* occupies the area further south in the Antarctic where the spawning appears to occur before the main bloom, suggesting that lipid stores are used for survival and for reproduction. *T. macrura* has a similar distribution to *E. superba* but spawns earlier so it again is dependent on lipid stores for reproduction, but may also utilize other food sources to get through the winter. In northern regions *T. inermis* converts phytoplankton rapidly into lipids to cope with the seasonal environment, but also utilizes other available organic material such as detritus. *M. norvegica* also builds up high lipid stores but is more carnivorous, utilizing lipid-rich copepods.

Overall, there appears to be a pattern from high to lower latitudes in the strategies of feeding and energy storage. Truly polar species such as *E. crystallorophias* and *T. inermis* rely totally on the seasonal phytoplankton bloom and lipid stores, whereas species such as *E. superba, T. raschii* and *T. macrura* survive winter utilizing alternative food sources and require the bloom to reproduce. Further away from the polar regions, species such as *T. longicaudata* and *M. norvegica* are more carnivorous, utilizing copepods as their main food source.

## Spatial Distribution

At large scales there are heterogeneities in the distributions of euphausiids that extend for tens or hundreds of kilometers. Within these broad aggregations there are also more dense regions where krill form patches, swarms, or schools (**Figure 4**) forming a distribution generated by a very dynamic system, with aggregation and dispersal over a wide range of scales. These patches can be very dense and compact and it has been suggested that it is likely that on occasion all species of euphausiids aggregate to some extent. This ability to form such dense aggregations is certainly found in a number of species, particularly *E. superba*, but also *M. norvegica*, *Nyctyphanes australis*, *E. pacifica* and *E. lucens*.

The generation of such patchy distributions is the result of interactions between biological and physical processes over a range of scales. Over small scales and in very dense aggregations, behavior probably dominates. Swimming speeds can be high – $\sim 20\,\mathrm{cm\,s^{-1}}$ in short bursts in Antarctic krill – so individuals have a marked ability to undertake directed movement at least over relatively short spatial scales. The formation of these smaller aggregations, along with diurnal vertical migration, is considered to be mainly a predator avoidance effect. However, it will also lead to changes in the dynamics of the interaction of krill with their food and may generate complex outcomes in the dynamics of planktonic systems.

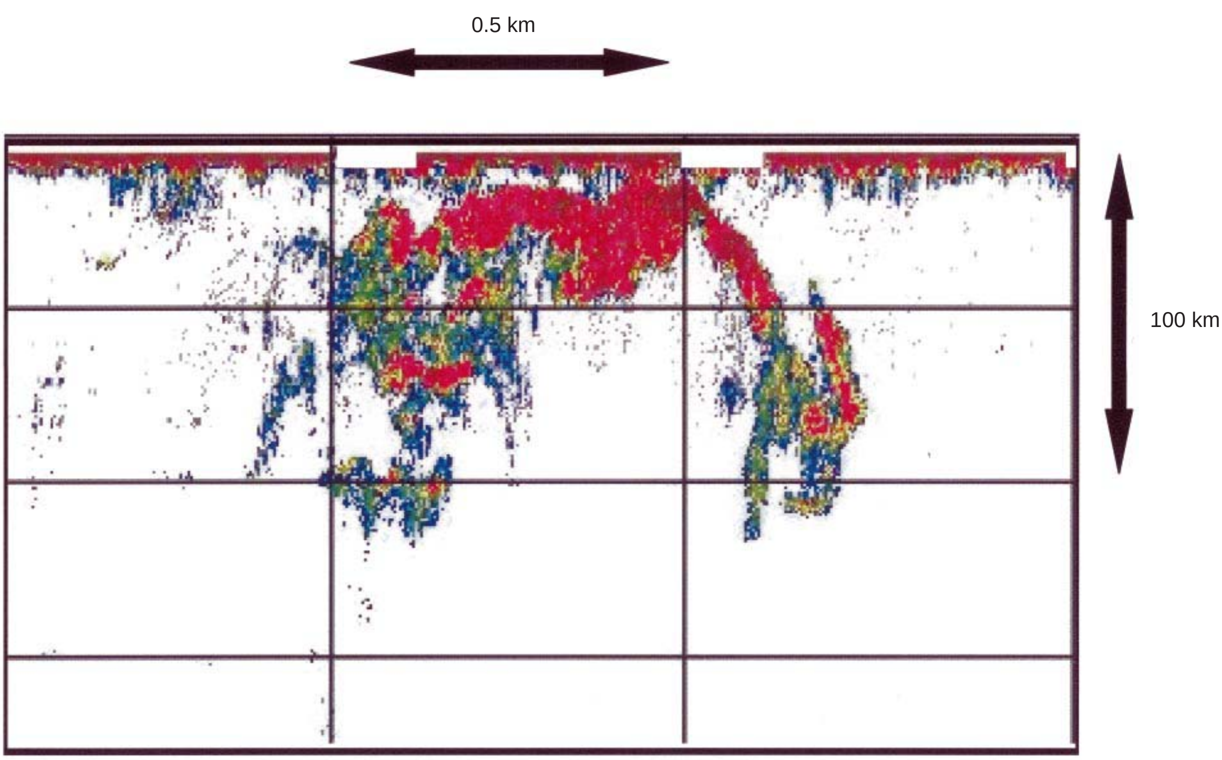



**Figure 4** A hydroacoustic trace of an aggregation of Antarctic krill, *E. superba.*

At larger scales physical processes probably dominate so that aggregations are dependent on physical concentration mechanisms in areas of shelf-breaks, around islands, in ice edge regions or associated with eddies. This larger-scale aggregation may be a precondition for behavioral effects to dominate at smaller scales. Krill within aggregations appear to share more similar characteristics in size and maturity compared with those in other aggregations in the same area. The densities of krill within these aggregations can be well in excess of $10\,000\,m^{-3}$; over $50\,000\,m^{-3}$ has been estimated for *E. superba* and *E. pacifica* and over $500\,000\,m^{-3}$ recorded for *N. australis*, *E. lucens* and *M. norvegica*.

Some of the aggregations are extremely large and can account for a considerable proportion of the total biomass in an area. So for example, in one survey of Antarctic krill $>10\%$ of the regional biomass was recorded in just one aggregation that extended about 1 km horizontally. This large aggregation was observed in the vicinity of a large number of whales, suggesting that some of the very large, dense aggregations may be the result of intense predator–prey interaction and emphasizes the dynamic nature of the spatial distribution of krill. This makes the design of krill distribution surveys using nets or hydroacoustic techniques challenging and the survey data require careful interpretation and analysis.

A number of the species undertake diurnal vertical migration, rising to nearer the surface and dispersing at night. This has been shown clearly in *M. norvegica*, whereas in *E. superba* vertical migration appears to be highly variable and may depend on local physical conditions, surface predator affects, and predation effects from below, particularly in areas of the shelf. In addition to the importance of predation effects the behavioral tracking of particular isolumes has been suggested as a mechanism involved in diurnal vertical migration and some species appear to show an endogenous rhythm.

Seasonal changes in the pattern of aggregation and vertical migration have also been noted in some species. In one area it has been observed that during spring aggregations of *E. superba* are of the order of 0.7–2 km in length, whereas they are smaller and more dense in summer, and larger and less dense in autumn and winter. In the same study many of the swarms occurred in the upper 70 m during the summer, while in winter many were below 100 m deep. Other studies have found no such vertical change in depth distribution during the year, although diurnal vertical migration did change, being marked only during the spring and autumn.

## Role in the Food Web

### Krill as Consumers

Krill show a range of feeding strategies from complete herbivory to total carnivory, with a full range of capabilities and flexible feeding strategies in between. In the Antarctic they can have a major impact on the large diatoms that form the major components of the intense blooms associated with the summer retreat of the sea ice. Antarctic krill are also known to consume copepods and negative correlations have been shown between the krill occurrence and the density of copepods and the phytoplankton concentration. This indicates that euphausiids are important in the plankton dynamics of these regions. They generate large fecal pellets which have high rates of sinking, suggesting that they can be important in the export of carbon from the surface layers. Rapid grazing of diatom blooms in some areas can therefore lead to a rapid flux of material to deeper ocean regions. The highly aggregated nature of the distributions is also likely to be important in determining the plankton dynamics, not just in terms of producing an interactive mosaic of production and consumption, but also in terms of the nutrient regime. Large krill swarms will generate high concentrations of ammonia that may favor the production of particular size groups of phytoplankton, leading to complex interactions in the plankton. Their role as consumers continues to be studied, but across the order they clearly have the capacity to feed on a wide range of food sources including diatoms, coccolithophores, dinoflagellates, chaetognaths, copepods, and other crustaceans; cannibalism has also been shown in some species. On the basis of observed variations in feeding strategies, it has been suggested that most species of euphausiids can adapt their feeding to utilize what is available, modifying their feeding strategies depending on the food they encounter.

### Krill as Prey

Krill are prey of many higher trophic level predators and as such play a key role throughout the oceans by transferring energy up the food chain. The baleen whales are the most well known predator, eating krill throughout their range, and despite the massive depletion of their populations due to harvesting they are still important krill predators. So for example, dense aggregations of *M. norvegica* and *T. raschii* in the Gulf of St Lawrence are associated with high abundances of fish (capelin) and a range of whale species including minkes, fin, blues, humpbacks, sperm, and beluga.

Seals are also major predators of euphausiids in many areas. In Arctic waters, for example, harp seals consume *M. norvegica* and *T. inermis*, while in the Southern Ocean, crabeater seals consume *E. crystallorophias*. Further north, around some of the sub-Antarctic islands such as South Georgia, the previously exploited fur seal populations that are now very large consume a considerable quantity of *E. superba*.

Euphausiids also comprise a key component of the diet of a wide range of fish species, many of which are, or were, exploited. In the North Atlantic these include herring, cod, haddock, whiting, and mackerel. *M. norvegica* is probably the key species consumed, but others such as *T. raschii, T. inermis* and *T. longicaudata* are also important. In the North Pacific and adjacent regions *E. pacifica* is eaten by most commercial fish species, including Pacific cod, walleye pollack, chub mackerel, and sand lance. Other krill taken include *T. raschii* and *T. inermis*. The importance of euphausiids in the diet of many commercially exploited fish species is seen throughout the world. So for example around Australia *N. australis* is eaten by bluefin tuna and striped tuna, while in the Antarctic *E. superba* is eaten by the Mackerel icefish.

Seabirds are also important predators of euphausiids throughout the world. In the North Atlantic a wide range of bird species consume *M. norvegica* and *T. inermis* including gulls, puffins, kittiwakes, and fulmars. The importance of seabirds as predators of krill is highlighted in the Southern Ocean where *E. superba* is a key item in the diet and consumed in vast numbers by penguins (gentoos, macaronis, and Adelies) and by flying seabirds including albatrosses such as grey-headed and black-browed albatross.

This broad range view of euphausiids as prey emphasizes the important role that krill play in transferring energy to higher trophic levels in marine food webs worldwide. One of the key reasons for the importance of euphausiid species in food webs is the heterogeneity of krill distribution on a range of spatial and temporal scales. Different predators exploit the aggregation pattern with different foraging strategies, so exploiting different scales of pattern in the prey field. The pattern generated by the biological or biological–physical interactions will thus determine which predators can exploit the prey and hence the structure of the food web.

## Krill Fisheries

There are extensive fisheries for *E. superba* in the Southern Ocean, while in the Pacific off Japan there are important fisheries for *E. pacifica*. There is a more limited *E. pacifica* fishing off western Canada and there have also been intermittent fisheries for other species. The Southern Ocean fishery for *E. superba* is the largest and started at beginning of the 1970s, peaking in the early 1980s at 0.5 million tonnes. The fishery has since declined with changes in its economic basis. Catches over recent years have been $< 100\,000$ tonnes. The *E. superba* fishery in the Scotia Sea region is linked to seasonal sea ice changes. During winter the fishery operates in the north around South Georgia, it moves further south in the spring with the ice, to the area near the South Orkney Islands, and then during summer the fishery exploits krill around the Antarctic Peninsula.

The management regime for *E. superba* takes account of krill recruitment variability, growth, and mortality to examine effects of various harvesting levels. Decision rules are included to maintain stocks at a level that takes into account the dependent predators. At the current time, catch levels are much lower than the allowable catch ($< 10\%$) and future expansion of the fishery depends on the development of new products utilizing krill. An ecosystem approach is being developed for managing Southern Ocean fisheries and extensive predator monitoring programs are operating. The challenge here is to develop management decision rules that consider not just the target species, the krill, but also incorporate ecological information from a number of levels in the food web, taking into account dependent species as well as environmental links. This ecosystem rather than species-based approach is one that will be increasingly relevant elsewhere.

## Krill Variability

There is considerable evidence of the importance of variation in the physical environment and circulation systems of the oceans in determining the distribution and abundance of krill. For example, links have been noted between variations in the oceanographic regimes associated with El Niño events and the recruitment of *E. pacifica* in the North Pacific, while water temperature variations have been linked to 2–3 year variations in *T. inermis* populations. Biological processes associated with the environmental variation are also important in generating the variation observed in euphausiid populations. For example, there are marked interannual variations in the abundance of *E. superba* in the Southern Ocean, where recruitment strength has been linked to variations in the extent and concentration of sea ice. The current view is that increased sea ice cover and extent lead to favorable conditions for spawning and larval survival. The sea ice is thought to provide better overwinter conditions for the krill. Salps compete with krill for phytoplankton – in poor sea ice years salp numbers are increased and krill recruitment is reduced. Further north in their range, *E. superba* abundance is dependent on the transport of krill in the ocean currents as well as fluctuations in the strength of particular cohorts.

Given the importance of euphausiids in marine food webs throughout the world's oceans, they are potentially important indicator species for detecting and understanding climate change effects. Changes in ocean circulation or environmental regimes will be reflected in changes in growth, development, recruitment success, and distribution. These effects may be most notable at the extremes of their distribution where any change in the pattern of variation will result in major changes in food web structure. Given their significance as prey to many commercially exploited species, this may also have a major impact on harvesting activities. A greater understanding of the large-scale biology of the euphausiids and the factors generating the observed variability is crucial. Obtaining good long-term and large-scale biological and physical data will be fundamental to this process.

## See also

**Antarctic Circumpolar Current. Baleen Whales. Copepods. Phalaropes. Plankton. Sea Ice: Overview. Seals. Sperm Whales and Beaked Whales.**

## Further Reading

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# KUROSHIO AND OYASHIO CURRENTS

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## Introduction

The Kuroshio and Oyashio Currents are the western boundary currents in the wind-driven, subtropical and subarctic circulations of the North Pacific Ocean. Translated from Japanese, Kuroshio literally means black ('kuro') stream ('shio') owing to the blackish – ultramarine to cobalt blue – color of its water. The 'blackness' of the Kuroshio Current stems from the fact that the downwelling-dominant subtropical North Pacific Ocean is low in biological productivity and is devoid of detritus and other organic material in the surface water. The subarctic North Pacific Ocean, on the other hand, is dominated by upwelling. The upwelled, nutrient-rich water feeds the Oyashio from the north and leads to its nomenclature, parent ('oya') stream ('shio').

The existence of a western boundary current to compensate for the interior Sverdrup flow is well understood from modern wind-driven ocean circulation theories. Individual western boundary currents, however, can differ greatly in their mean flow and variability characteristics due to different bottom topography, coastline geometry, and surface wind patterns that are involved. For example, the bimodal oscillation of the Kuroshio path south of Japan is a unique phenomenon detected in no other western boundary current of the world oceans. Similarly, interaction with the semi-enclosed and often ice-covered marginal seas and excessive precipitation over evaporation in the subarctic North Pacific Ocean make the Oyashio Current considerably