Summary and Introduction

Just as there are growing seasons on land, so there are growing seasons in the ocean as well. In the Gulf of the Farallones, the growing season begins in early spring, when the first phytoplankton blooms (large increase of microscopic plants) of the year fuel growth at higher levels of the marine food web. In California, as in many parts of the world, euphausiid shrimp, commonly called “krill,” are one of the beneficiaries of this early-season production and are a critical link in the marine food web. Feeding on phytoplankton (microscopic plants) and small zooplankton (animals), krill populations expand and by being eaten by other marine animals, transfer energy from the lowest (primary producer) level into the upper levels of the marine food web. They are often referred to as “keystone” species because they play such an important role in the functioning of many marine ecosystems.

Krill hatch from free-floating eggs and pass through larval and juvenile stages before maturing into adults. This development process involves a series of molts (casting off the rigid outside skeleton that restricts growth), during which segments and appendages are gradually added. While the new outside skeleton is still soft, the individual can increase its size. Adult euphausiids have the unique ability to actually shrink in size after a molt if food resources are scarce. Because krill can increase and decrease their size, it can be difficult to determine their age or the age distribution of a population of animals from their sizes.

Krill have legs called “swimmerets” that have evolved to look like small feathers and function like fins, giving them great mobility and agility for life in the water column. They feed while swimming, using their modified front legs to form a food basket that strains food from the water while they swim.

Krill are typically very gregarious, which means they are often found in large, concentrated groups, including dense swarms with as many as 100,000 krill per cubic meter of ocean water. This swarming behavior makes krill especially vulnerable to predators. Swarming activity starts sometime in spring and continues through the fall. These aggregations can commonly be located in the Gulf of the Farallones by finding flocks of diving seabirds or clusters of birds picking at the surface. Fishermen use these feeding flocks to help them locate salmon feeding on the undersides of the krill swarms. Lunging humpback whales that break the surface of the water are also a good indication that krill are swarming at or near the surface. Surface swarms provide ideal feeding conditions for these large filter feeders. With its huge mouth, a gaping humpback (and other baleen whales) is capable of engulfing a large volume of krill in a single gulp. These dense aggregations of prey provide the several tons of food per day required by these whales during the summer feeding season.

In the Gulf of the Farallones, the two most abundant species of krill are *Thysanoessa spinifera* and *Euphausia pacifica* ([fig.1]). They are typically about 15 to 20 mm (approx. 3/4 in.) long and live for about 2 years. *Thysanoessa spinifera* is found mostly in shallower water over the continental shelf, whereas *Euphausia pacifica* is usually found in deeper water towards the margin of the shelf and beyond. Between them they are a major food source for salmon (krill pigments give salmon flesh its characteristic pink to orange color), rockfish, seabirds, and whales. Krill are the main reason hungry humpback and blue whales visit the gulf in the sum-
mer—to fatten up for the rigors of the coming year. Both of these krill species demonstrate special adaptations that enable them to succeed despite constant predation pressure. From spring through fall, *Thysanoessa spinifera* swarm at the surface during the day. Though it is unclear what is driving this behavior, the benefits must outweigh the cost, which is increased predation.

*Euphausia pacifica*, controlled by light intensity, migrate out of ocean depths and into surface waters each night. As dawn approaches, they return to deep water for the day. This migration pattern is shared with many other organisms in the ocean, and during the day krill form part of the so-called “deep scattering layer” that fishermen see on their depth sounders. The timing of this daily event in response to changing light intensities provides *Euphausia pacifica* with several advantages. By moving upward at night, *Euphausia pacifica* minimizes exposure to daytime predators, while grazing in surface waters where food is abundant. They also realize an energy gain by returning during the day to the colder deep water, where metabolism slows. Releasing eggs in warmer surface waters speeds development times, thus reducing the time exposed to predators; it also ensures that hatching larvae are in productive waters when they start feeding, increasing their chances of survival.

Krill are a critical link in the Gulf of the Farallones marine food web and in marine food webs around the world. They directly or indirectly support the survival and well-being of many animals living in different oceans. Knowing the key position filled by krill in many marine ecosystems, we need to ensure that their populations remain healthy—for the well-being of all.

### Occurrence and Role in Marine Food Webs

Just as there are growing seasons on land, so there are growing seasons in the ocean as well. In the Gulf of the Farallones, the growing season begins in early spring, when the first phytoplankton blooms (large increase of microscopic plants) of the year fuel growth at higher levels of the marine food web. In California, as in many parts of the world, euphausiid shrimp, commonly called krill, are one of the beneficiaries of this early-season production. Feeding on phytoplankton and small zooplankton (animals), krill populations expand and become a critical link in many marine systems. Krill are the bridge, converting energy from the primary producer level into a form that is usable by animals in the upper levels of the marine food web. They are commonly referred to as “keystone” species because they play such an important role in the functioning of many marine systems. In the Gulf of the Farallones, euphausiids are a major food source for salmon (krill pigments give salmon flesh its characteristic pink color), rockfish, seabirds, and a myriad of lesser-known species. The main reason why hungry humpback and blue whales visit the gulf in the summer is to fatten up on krill for the rigors of the coming year. In many of the world’s oceans, krill are a critical source of energy for seabirds, penguins, seals, sharks, octopi, and many species of whales. Without krill, our oceans would be a very different place.

Currently, 85 species of euphausiids have been identified from different oceans around the world. They live in habitats ranging from abyssal depths (5,000 m [16,000 ft]) to nearshore kelp beds (10 m [33 ft]), from warm tropical seas to the freezing Antarctic Ocean. The Antarctic species, *Euphausia superba*, can be as long as 65 mm (2 1/2 in.) and may live for 7 years or more. The two most common species in the Gulf of the Farallones, *Thysanoessa spinifera* and *E. pacifica*, are typically 15 to 20 mm long (approx. 3/4 in.) and live about 2 years. *T. spinifera* is found mostly in shallower water over the Continental Shelf, whereas *E. pacifica* is generally found in deeper water toward the margin of the shelf and beyond. All euphausiids are marine and
pelagic; that is, they live in the water column full time. They have legs called “swimmerets” that have evolved to look like small feathers and function like fins, giving them great mobility and agility for life in the water column. Krill feed while swimming, using their modified front legs to form a food basket that strains food from the water while they swim. Most euphausiids hatch from free-floating eggs and pass through larval and juvenile stages before maturing into adults. This development process involves a series of molts (casting off the rigid outside skeleton that restricts growth), during which segments and appendages are gradually added. While the new outside skeleton is still soft, the individual can increase its size. Adult euphausiids have the unique ability to actually shrink in size after a molt if food resources are scarce. Because krill can increase and decrease their size, it can be difficult to determine their age or an age distribution from a population of animals.

Swarming and Other Behaviors

Krill are typically gregarious; that is, they are commonly found in concentrated aggregations. Like many organisms that live in the water column, these aggregations of krill in the Gulf of the Farallones are patchy, with 1 to 10 individuals per cubic meter of ocean. However, denser patches called shoals have concentrations of 10 to 100 krill per cubic meter, and swarms have 1,000 to 100,000 krill per cubic meter. This “schooling” behavior may be an effective defense mechanism for confusing smaller visual predators that isolate and take single individuals. Within the aggregation, single krill are capable of some truly remarkable maneuvers. Researchers in the Antarctic have documented an amazing response by individual Euphausia superba. When the aggregation was disturbed by divers, krill scattered in all directions. Some individuals in the group instantaneously and synchronously molted, leaving behind only their floating exoskeletons. These castings presumably act as decoys to further confuse predators as the krill rapidly swim away, much as an octopus leaves behind an ink cloud. Swarming, however, does little to protect krill from the considerable risk posed by larger predators, such as the great whales, who are not targeting single prey. Swarms can extend 10 m (33 ft) or more in diameter and commonly elicit a frenzied feeding response from whales and other predators, such as fish and birds, particularly when these aggregations are in the upper part of the water column and escape routes are restricted by the ocean’s surface.

The formation of swarms at or near the surface has been reported for 18 species of euphausiids worldwide. In the Gulf of the Farallones, Thysanoessa spinifera demonstrates this behavior by forming large swarms at the surface during daylight hours. Swarming activity starts sometime in spring and continues through the fall. These aggregations can commonly be located in the gulf by finding flocks of diving seabirds or clusters of birds picking at the surface (fig. 4). Fishermen use these feeding flocks to help them locate salmon feeding on the undersides of the krill swarms. Lunging humpback whales that break the surface of the water are also a good indication that krill are swarming at or near the surface. Surface swarms provide ideal feeding conditions for these large filter feeders. With its huge mouth, a gaping humpback (and other baleen whales) is capable of engulfing a large volume of krill in a single gulp. These dense aggregations of prey provide the several tons of food per day required by these whales during the summer feeding season. It’s perplexing why krill form these huge swarms at the surface during the day when it makes them so vulnerable to predation.

Ideas about what is driving this swarming behavior range from physical influences through biological cues to a combination and interaction of both. Some researchers believe that physical
factors, such as passive transport by tides or ocean currents, are the reason why krill are at the surface during the day. Other researchers believe that biological factors, such as increased feeding opportunities associated with higher phytoplankton densities or increased reproductive success relating to faster incubation times in warmer surface waters, are reasons for this behavior. It is unclear at present what specifically is driving this behavior, because it varies by species and location. A combination of several factors that change slightly from year to year is probably involved. If biological forces are involved, however, the presence of this daytime surface-swarming behavior must provide a net benefit for the species; that is, the advantages gained by daytime, surface swarming must outweigh the associated costs of increased predation.

Although they don’t form daytime surface swarms in the Gulf of the Farallones, the other common euphausiid, *Euphausia pacifica*, demonstrates a behavior that is equally fascinating. Each night, as if on cue, these krill rise from the deep ocean into the upper levels of the water column. As dawn approaches, they descend from the upper water column and return to ocean depths for the day. This migration pattern is shared with many other organisms in the ocean, and during the day krill form part of the so-called “deep scattering layer” that fishermen see on their depth sounders. The timing of this daily event in response to changing light intensities provides *E. pacifica* with advantages relating to predation, feeding, energy, and reproduction. By moving upward at night, *E. pacifica* minimizes exposure to certain daytime predators, while grazing in surface waters where food is abundant. They also realize an energetic gain by returning during the day to the colder deep water, where metabolism slows and converting food into energy and growth is more efficient. Releasing eggs in the warmer surface layers speeds development times and reduces the time exposed to predators; it also ensures that hatching larvae are in productive waters when they start feeding, increasing their chances of survival.

**Conclusion**

Euphausiid shrimp or krill are a critical link in the Gulf of the Farallones marine food web and in marine food webs around the world. They directly or indirectly support the survival and well-being of many animals living in different oceans around the world. Although scientists still have many questions about the population dynamics and complex behaviors exhibited by krill, active fisheries are currently exploiting abundant krill populations in Antarctica. Experimental fishing to determine the feasibility of harvesting krill off the California coast has been conducted. Knowing the key position filled by krill in many marine ecosystems, we need to ensure that their populations remain healthy for the well-being of all.

**Further Reading**


Figure 1. The two species of krill common in the Gulf of the Farallones are *Euphausia pacifica* (A, photograph courtesy of Steven Haddock) and *Thysanoessa spinifera* (B, photograph from Gulf of the Farallones National Marine Sanctuary.)
Figure 2. Krill and other plankton collected in the Gulf of the Farallones. (Photograph courtesy of Jamie Hall.)
Figure 3. Lunging humpback whales feeding on surface swarms of krill are a common site in the Gulf of the Farallones in the summer. (Photograph by Thomas R. Kieckhefer, Pacific Cetacean Group.)

Figure 4. Birds feeding on swarming krill in the Gulf of the Farallones. (Photograph from Gulf of the Farallones National Marine Sanctuary.)