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7. This research was supported by grant funds from the Medical Research Council of Canada and the Natural Sciences and Engineering Research Council of Canada. I thank C. Malinski for assistance with the experiments and Dr. Shepard Siegel for a critical reading of the original manuscript.

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Behavior of Antarctic Krill, *Euphausia superba:* Chemoreception, Feeding, Schooling, and Molting

Abstract. *Krill do not feed by passive, continuous filtration but use area-intensive searching and various rapid feeding behaviors to exploit local high food concentrations. Chemicals alone at low concentrations, not particles, trigger feeding. Krill form dense schools that move rapidly and migrate primarily horizontally. Abrupt disruption of a school can trigger mass molting, and molts may act as decoys.*

Euphausia superba is the dominant herbivore of the Southern Ocean. Today, in the virtual absence of southern baleen whales, the standing stock of "unutilized" krill is purported to equal the combined world harvest of all other marine species (*1*). Despite extensive investigation of krill (*2*), little is known of their behavior at sea or winter biology. In January and February 1982, we observed individual *E. superba* in aquariums at Palmer Station on Anvers Island off the west coast of the Antarctic Peninsula, and we used scuba to observe behavior of schools at sea (*3*). We describe a series of complex behavior patterns that may alter assumptions about euphausiid biology.

Euphausia superba feeds primarily on phytoplankton. Feeding experiments in laboratory flow chambers (*4*) showed that *E. superba* feeds episodically on phytoplankton and is not a continuous filter feeder. When not feeding, *E. superba* swims rapidly, pressing its six pairs of thoracic endopodites together to form a keel (Fig. 1a). When feeding, the euphausiid throws these legs out to enclose a packet of water and algae in a basket that closes ventrally and anteriorly. With the basket fully expanded, setae of adjacent endopodites overlap, forming narrow suture zones. When feeding begins the thoracic exopodites stop their metachronic beating and pronate 90° to flatten laterally against the suture zones (Fig. 1b). The dactyls fold back and also overlap the long setae of the endopodites. The result is a basket that is watertight, which was determined by adding fluorescein dye and phytoplankton to water presented to the euphausiid. Algae collect inside the basket on the setae while the euphausiid expels water by rapidly compressing the endopodites. The exopodites, like flapper valves, lift together in a horizontal direction as water is forced laterally through the setae in parallel jets. The feeding bout is repeated one to five times per second. After the mouthparts gather a food bolus the feeding bouts cease, the mandibular palps press the bolus against the mandibles, and ingestion ensues.

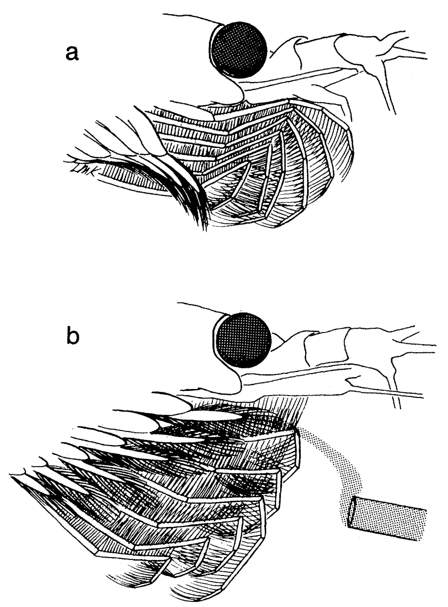

Fig. 1. Deployment of thoracic legs in *Euphausia superba*. Drawings were traced from photograph; intersetal distances are not to scale. (a) Swimming posture: *E. superba* presses endopodites tightly together into a streamlining keel; beating exopodites assist propulsion and steering. (b) Feeding posture: Opening basket draws in water and particles anteriorly; at full extension, ventral and anterior closure, folded dactyls, and exopodites flattened against suture lines between overlapping setae of adjacent endopodites make the expanded basket watertight.

We report that *E. superba* feeds in response to chemical cues. We tested 20 tethered *E. superba* with different concentrations of substances available at Palmer Station and used four or five individuals for each test (*5*). The lack of response to Miocene and Recent diatom skeletons indicates that particles alone do not trigger feeding. In the absence of particles, chemicals alone did elicit the full feeding bout, with a threshold concentration of $10^{-5}M$ for histidine, lactic acid, citric acid, and acetic acid.

In aquariums and in slow-swimming schools at sea individuals occasionally opened the thoracic basket briefly, presumably to test for the presence of food. When they encountered food in the aquarium, the euphausiids swam fast and in tight circles, rapidly filling the feeding basket. When a food bolus accumulated, feeding stopped and the euphausiid swam away to process the food. Area-intensive foraging occurred at the surface also in response to phytoplankton or attractive chemicals floating in local high concentrations. Krill then rolled upside down against the surface, made rapid spinning turns, and quickly swept the surface with the feeding legs. Area-intensive foraging permits rapid food acquisition, indicating that grazing rate calculations made with the assumption of continuous filtration at low food concentration are probably not correct. Feeding behavior of other herbivorous euphausiids should also be reexamined.

In another mode of surface feeding individuals swim forward horizontally, just beneath the surface, and hold one branch of each antennule out of the water. Floating particles are flicked out of the surface film for inspection and sometimes eaten. A school of *E. superba* fed this way at dawn in the Gerlache Strait during a flat calm in February 1982. Thousands of antennules protruded through the surface, leaving tiny wakes on the flat water as the school swam slowly forward.

Another feeding mode, studied only in the laboratory, has implications for winter biology of polar euphausiids. We concentrated and refroze algae that live attached to sea ice into blocks which were floated in the aquarium. As the algae softened, *E. superba* beneath the ice located the food by an area-intensive search. They then fully extended the dactyls of the thoracic endopodites and raked algae into the food basket, working along the submerged surfaces or

Fig. 2. Inverted *Euphausia superba* molts. When startled by divers, many euphausiids in a school molted instantaneously. The school dispersed with rapid tail-swimming and left the molts, possibly as decoys for predators.

holding in place at sites of high algal concentration. Occasionally an animal would wrest algae out of another's basket as they swam away from the ice. This feeding mode is so distinctive that it may be a natural behavior that permits winter feeding. If so, *E. superba* may feed throughout the year, and population growth parameters may need reevaluation.

Most euphausiids are reputed to swarm at high densities (*6*), but the term "schooling" is appropriate for *E. superba*. We observed schooling in aquariums (*7*) and underwater in the Drake Passage near Livingston Island and in the Gerlache Strait near the Antarctic Peninsula. In the ocean aggregated *E. superba* always oriented uniformly. Schools ranged in size from tiny groups with about 150 members in 2000 cm^3 to schools so vast that the edges were invisible to the divers when phytoplankton was scarce and horizontal visibility exceeded 30 m. Schools also occurred in areas of dense diatom blooms where horizontal visibility was only about 3 m. Almost all euphausiids were within schools, and adjacent schools were separated by clear water. In 1969, Russian divers visually estimated densities in *E. superba* schools at 50,000 to 60,000 per cubic meter (*8*). Our estimate was 20,000 to 30,000 per cubic meter. Upper estimates from vertical net tows taken through swarms visible from the surface (*9*) are in the same range; lower density estimates reflect undersampling by towed nets or net avoidance.

Shapes of schools seemed to vary infinitely, but undisturbed schools changed shape slowly. Most schools had at least one narrow dimension. A school swimming horizontally might be 10 m deep, 100 m long, but only 3 to 4 m wide. Curtain-like schools only a few meters thick moved forward across a broad front. Huge hemispherical schools that appeared solid from above would prove to be dome-shaped when examined by divers. Because an individual within a school is generally only a few meters from clear water in at least one direction, potential problems associated with dense aggregation, such as local food or oxygen depletion, would be diminished.

Krill schools seem to be maintained primarily by rheotactic cues supplied by the wake of preceding animals. Schooling apparently does not require vision, for we repeatedly saw organized nonluminescing schools at night. Even in daylight krill schools move forward with a slow amoeboid character without the almost instantaneous cross-school synchrony of many fish schools. Directional changes caused by an obstruction such as a diver's arm persisted at exactly the same location even after the obstacle was removed. Each euphausiid copied the precise local detour made by its predecessors until the entire school traced the exact course of the leaders. Such rheotactic schooling would be effective in the long periods of winter night and ice cover.

The role of rheotaxis was particularly obvious when separate schools collided. Approach of one school to another from below and behind resulted in upward movement and smooth merging of the lower school into the upper one. Swimming turbulence is directed obliquely downward, and the lower school perceived the upper but not the reverse. Approach from above and behind often resulted in simple overflight with no merging of schools. Oblique or head-on collision disrupted both schools as krill tail-flipped 1 to 2 m in random escape jumps. Large disturbances propagated rapidly as disoriented animals landed amid organized groups which then reacted similarly. A major disturbance could totally disperse a school.

Schools are composed of similar sized individuals, perhaps because of lifetime integrity of the school (*10*), but also because of segregation by swimming speeds (*11*). We caused a small school with bimodal size distribution to swim faster but not panic, and the larger, faster-swimming krill moved to the front of the school, which elongated until it pinched in half.

Molting within a school presents problems because the molt must be shed among cannibalistic colleagues (*12*). We watched normal, undisturbed *E. superba* in the ocean swim up out of the school to shed the molt in less than a second, swim forward for perhaps a minute, then sink and slip suddenly back into the school. External stimuli also can trigger molting. When divers frightened a school, it scattered as the krill tail-flipped backward like tiny lobsters in random directions at up to 100 cm/sec (*13*). But a number of krill first would instantaneously and synchronously molt and abandon the molts in place of the now-departed school. The visual impression was that the school was still present; the molts presumably served as decoys for visual predators (Fig. 2). Crustaceans are widely believed to molt only in response to hormonal cues. Neurological control of sudden molting is noteworthy in *E. superba* and would have obvious adaptive advantages for other pelagic crustaceans as well.

Schooling *E. superba* swim steadily for days at 419.4 to 467.7 m per hour (*14*). Rapid swimming is accompanied by ventral compression of thoracic endopodites into a keel, metachronic beating of pleopods and thoracic exopodites, and compression of the antennules into a rigid spear pointing forward. Schooling euphausiids swim horizontally; a school dives gradually at no more than a 5° to 10° angle. During tight schooling and rapid swimming the feeding basket is never opened. Rapid klinokinetic turning increases the likelihood of finding concentrated and patchy food, but at the same time it totally disrupts the oriented swimming normally associated with schooling. It is apparent that rapid feeding and schooling are incompatible. Schooling promotes long-distance horizontal or vertical search patterns; rapid bout-feeding promotes efficient use of concentrated, patchy foods. *Euphausia superba*, therefore, does not randomly feed but actively forages. Krill schools resemble schools of juvenile clupeid fishes, and management of these resources must be planned accordingly.

Note added in proof: In our second season (January–February 1983) we dove eight times with *E. superba*. On seven dives all animals were in oriented schools, but on one dive all were in an unoriented swarm, rapidly feeding.

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4. A thread or glass rod glued to the dorsal carapace suspended individuals in a flow chamber (60 cm long, 10 cm wide, and 10 cm high) supplied with a constant laminar current of oxygenated seawater at ± 1°C. Suspended animals swam and fed normally in place. We used horizontally mounted stereoscopic optics, videotapes, and 35-mm macrophotography to analyze functional morphology of feeding.
5. Test substances, mixed with seawater and fluorescein dye, were injected through a pipette into the current flowing toward a tethered euphausiid (*4*). The full feeding bout, a stereotypic all-or-none response, was the bioassay. Euphausiids did not respond to fluorescein dye alone, Recent or Miocene diatoms (diatomaceous earth), sucrose, maltose, galactose, D(+)-mannose, fructose, L-glutamine, or EDTA. They performed full feeding bouts in response to live diatoms, Miocene diatoms mixed with citric acid, Maxi-Crop seaweed extract, Difco marine broth, dextrose, glycine, L-arginine, histidine, neopeptone, acetic acid, lactic acid, ascorbic acid, and citric acid. They actively rejected methionine and L-tyrosine.
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The Terminal Nerve: A New Chemosensory System in Vertebrates?

Abstract. *Ganglion cells of the terminal nerve in goldfish are located in the olfactory nerve and bulb and send peripheral processes into the olfactory epithelium and central processes to the supracommissural nuclei of the telencephalon as well as to the retina. Correlations between terminal nerve projections and neurobehavioral studies suggest that the terminal nerve mediates responses to sex pheromones.*

Pheromones, presumably detected by the olfactory system, influence a number of reproductive responses in fishes (*1*). The medial olfactory tract (MOT) is specifically implicated in several of these responses; electrical stimulation of the MOT in cod elicits behavioral responses similar to those observed in normal courtship (*2*); bilateral transection of the MOT in goldfish drastically reduces male responses to pheromones of reproductively active females (*3*); and stimulation of the MOT in reproductively active male goldfish elicits sperm release (*4*). However, the axons of another cranial nerve, the terminal nerve (TN), course centrally into the forebrain in association with the MOT in a wide range of vertebrates (*5–8*). This raises the possibility that pheromone-mediated responses are detected by the TN instead of, or in addition to, the olfactory system.

Descriptive studies of the TN in fishes (*5–8*) have led to the proposal that this cranial nerve consists of ganglion cells located within, or ventral to, the olfactory nerves and bulbs. The peripheral processes of these ganglionic cells are reported to course rostrally and become distributed among the epithelial tissues of the olfactory organs, whereas their central processes course into and terminate among several cell groups closely associated with the anterior commissure of the telencephalon (*5–8*).

Large neuronal cell bodies (Fig. 1A) do occur within the medial half of the olfactory nerves and implantation cones of the olfactory bulbs (area of entry of olfactory nerve fibers) in goldfish (*Carassius auratus*), a pattern that was described from observations of carp (*6*). In order to determine whether these cells have peripheral processes that ramify in the olfactory epithelium, small pledgets of Gelfoam soaked in horseradish peroxidase (HRP) enzyme (40 percent solution dissolved in 1 percent lysolecithin) were applied unilaterally onto the olfactory epithelium of six goldfish (7 to 10 cm in total length). Two to 4 days later the fish were perfused with $0.1M$ phosphate buffer and then with a solution of cold, buffered 4 percent glutaraldehyde in $0.1M$ phosphate buffer. The brains, including the olfactory bulbs and organs, were removed, embedded in gelatin, and sectioned horizontally at 40 μm. Sections were processed with tetramethylbenzidine in order to visualize the HRP (*9*).

In these cases, HRP-labeled olfactory nerve fibers terminate in the glomerular layer of the ipsilateral olfactory bulb, but no labeling occurred in the mitral cell bodies nor in the majority of the olfac-

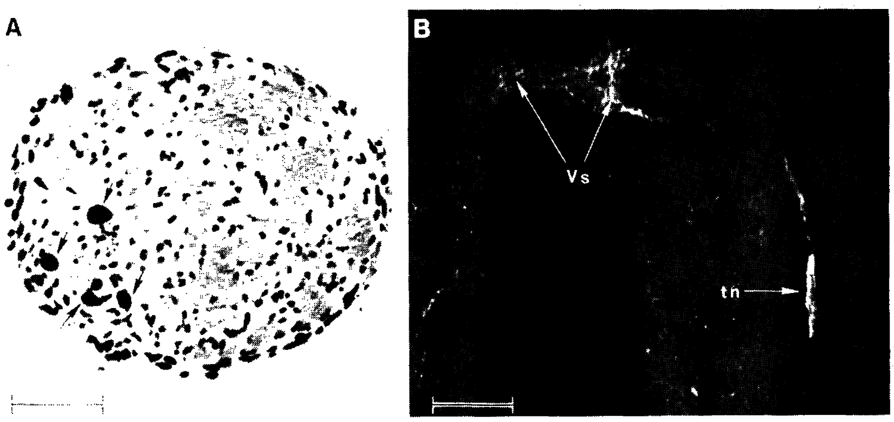

Fig. 1. (A) Transverse section of the right olfactory nerve of the goldfish stained by the Bodian method. The cell bodies of the terminal nerve are indicated by the arrows. Dorsal and medial surfaces are to the top and left of the figure, respectively (bar represents 50 μm). (B) Dark-field illuminated horizontal section through a ventral portion of the telencephalic hemisphere of the goldfish illustrating the central course of the terminal nerve fibers (*tn*) and their bilateral termination within the supracommissural nucleus of area ventralis (*Vs*) after HRP application to the left olfactory epithelium. Lateral and rostral planes are to the right and bottom of the figure, respectively (bar represents 100 μm).