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Lowered cameras reveal hidden behaviors of Antarctic krill

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Antarctic krill (*Euphausia superba*, hereafter 'krill') exemplify the methodological challenges of studying small, mobile, aggregating pelagic organisms[1]. Krill are a central species in the Southern Ocean food web, provide important biogeochemical functions and support a valuable commercial fishery[2]. Most of what we know about krill has been derived from acoustic surveys and net samples, the former being essential for estimating krill biomass and catch limits. However, understanding krill behavior, particularly in the poorly-studied autumn–winter seasons, is key for management and conservation. Here, we used seasonal video observations collected with a profiling camera system of krill along the Western Antarctic Peninsula to reveal krill vertical distribution, aggregation density and individual behaviors that have remained hidden from traditional sampling methods[3].

Using this camera system, we observed krill mating and feeding throughout the water column and at the seabed in both the productive and dark seasons. Traditionally, krill have been viewed as an epipelagic species, but the regularity of year-round seabed feeding observations marks a paradigm shift[4,5]. Using camera observations, we identified three different behaviors individual krill use to feed on the sediment: 'skimming' to collect the material on top of the seabed (Figure 1A); 'nose diving', previously described[4], to stir up a small amount of sediment (Figure 1B); and 'flip-flopping' to stir up more sediment (Figure 1C). In late autumn, we also observed hundreds of individuals forming tight, organized 'balls' on the seafloor, working together to resuspend large plumes of sediment (Figure 1D). Our observations of individuals feeding on the seabed in both seasons, and particularly our

observations of cooperative feeding in late autumn, support the hypothesis that benthic feeding is a normal behavior and not due to chance interactions of krill with the seabed[4,5].

Lowered camera systems can provide information on how krill vertical distributions, aggregation density, individual motility and differences in orientation change seasonally (Figure 1E,F). We observed krill in
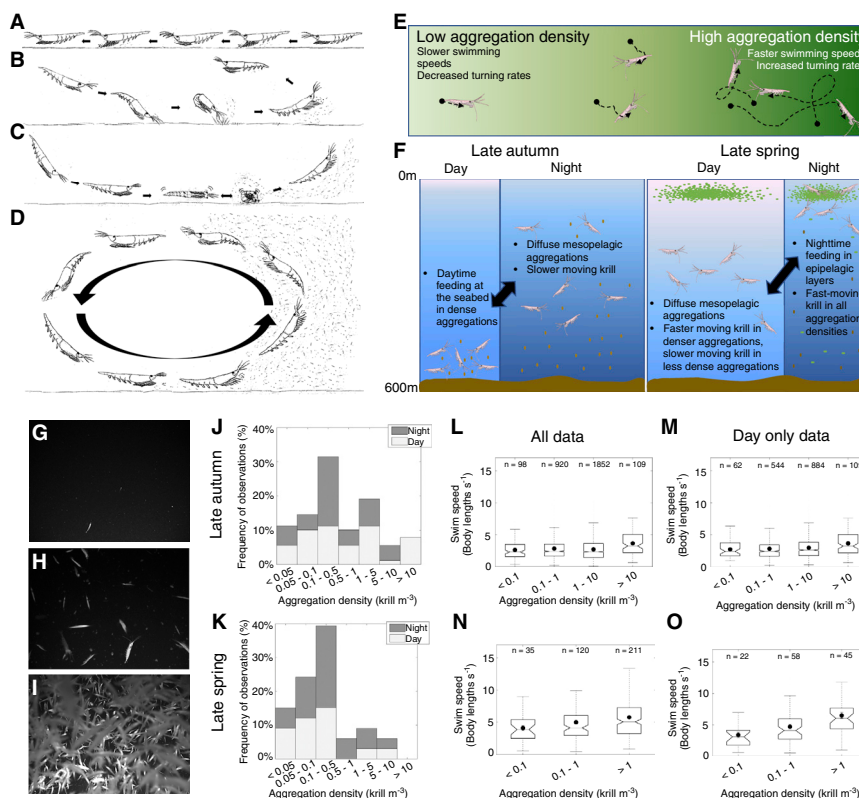

Figure 1. Antarctic krill benthic feeding behaviors, frequency of aggregation densities and relation between individual swimming speed and aggregation density.
(A–D) Krill benthic feeding strategies. Individuals can: (A) "skim" the seabed to collect food; (B) "nose dive" into the sediment and tail-flick backwards to stir up sediment; or (C) "flip" onto their sides, and "flop" around on the seabed by undulating their body several times to produce a plume of sediment. (D) Aggregations of krill can work together in a "ball" to stir up sediment into the water column. Individual krill move towards the center of the "ball" at the seabed (right), then upward to filter the suspended sediment; krill then move towards the outside of the "ball" (left) before moving back down towards the seabed. (E) Schematic showing how, in both late autumn and late spring, individual krill motility increased with increasing aggregation density; example tracks here are from krill observed in late autumn in low (left), medium (middle), and high aggregation densities (right). (F) Changes in krill feeding and vertical distributions influence benthopelagic coupling in late autumn and late spring. (G–I) Example images of krill seen in aggregation densities of 0.653 krill m^{-3} (G), 8.9 krill m^{-3} (H), and > 50 krill m^{-3} (I) in the water column. (J,K) Frequency of observations of krill aggregation densities in late autumn (J) and late spring (K). (L–O) Individual krill swimming speeds at different aggregation densities for all data in late autumn (L) and late spring (N), and for data collected during the day in late autumn (M) and late spring (O); there was no correlation between krill swimming speeds and aggregation density at night in either season. Krill swimming speeds were separated by aggregation densities (see Supplemental Experimental Procedures). Boxes represent 25th to 75th percentiles, notched lines the median values, and error bars the 10th and 90th percentiles of swimming speed distributions. Filled circles with error bars represent the means and standard errors (for weighted linear regression analyses, see Figure S1A (late autumn) and Figure S1F (late spring)).

densities ranging from solitaries to aggregations too dense to count (Figure 1G–I). Previously, we found krill scattered throughout the water column in late spring and deeper than 50 m in late autumn, with the greatest densities near the surface in spring and near the seabed in autumn[3]. We also found individual motility increased between late autumn and spring[3]. Aggregation densities where krill were successfully

tracked ranged from 0.014 to 52 krill m^{-3} in autumn and from 0.014 to 8.9 krill m^{-3} in spring; the most frequently observed aggregation densities were ≤0.5 krill m^{-3} in both seasons (Figure 1J,K). Differences in orientation between tracked krill neighbors were consistent across seasons, averaging 63° ± 33° in autumn and 65° ± 33° in spring, rather than the parallel orientation expected for schools. These results suggest that krill occur frequently in sparse aggregations in the water column, although tight schools may be more difficult to locate and may avoid sampling devices.

Footage from lowered cameras allows us to relate krill aggregation densities to individuals' swimming behaviors. In late autumn, greater aggregation density correlated with faster individual swimming speed (Figure 1L), accelerated turning rate (Figure S1B), more upward body orientation (Figure S1C), and decreasing nearest neighbor distance (NND) (Figure S1D,E). These correlations were stronger during the day than at night (Figure 1M and Figure S1B–E). In late spring, higher aggregation density correlated with faster individual swimming speed (Figure 1N), greater upward vertical velocity (Figure S1H), more downward body orientation (Figure S1J), and increasing minimum NND (Figure S1L). During the day, increasing aggregation density correlated with faster swimming speed (Figure 1O), accelerated turning rate (Figure S1G), more upward vertical velocity and swimming direction (Figure S1I), and increasing average and minimum NNDs (Figure S1K,L). These correlations were weaker or non-existent at night.

Limitations of our camera study include: restricted water column depth (≤700 m) of the study area relative to the >2000 m depths krill can migrate to[4]; limited ability to track individuals in dense aggregations; and the limited depth of field, due in part to the red LEDs used in most deployments[3]. However, we are confident that the camera system, and its associated lights, did not influence krill abundances or individuals' behaviors (Supplemental Information).

Because all methods used to survey krill have strengths and weaknesses[1,2,5], the most pragmatic approach is to combine them. Large-scale coverage from acoustics is essential for biomass estimates[2], while nets provide

experimental material and indices of multidecadal population dynamics[6]. Camera observations complement these approaches by providing small-scale observations of animal behaviors throughout the water column. Integrating multiple methods to study pelagic organisms, such as krill, *in situ* enables a more holistic understanding of pelagic ecology.

Our camera observations of changes in krill behaviors due to season, time of day and aggregation density, as well as their benthic feeding behaviors, improve our understanding of how krill influence food web and biogeochemical cycles (Figure 1E,F). We observed krill actively swimming and feeding in late autumn as well as in spring. Food web processes during the dark season are poorly understood, and whether krill feed during winter is debated[2,7]. Whatever season, denser aggregations may intensify the contribution of each krill to nutrient recycling and benthopelagic coupling due to increased individual motility and elevated energetic costs[3,5,8,9]. Epipelagic aggregations foraging on phytoplankton would enhance nutrient recycling and the biological carbon pump[5,9,10]. Seabed feeding could resuspend sediment and reintroduce limiting nutrients to shallower waters via vertical migration[3,5,8,10]. Overall, our findings from lowered cameras shed new light on the diverse and complex role of krill in food web dynamics, biogeochemical cycling and benthopelagic coupling.

SUPPLEMENTAL INFORMATION

Supplemental Information including one figure and methods can be found with this article online at https://doi.org/10.1016/j.cub.2021.01.091.

AUTHOR CONTRIBUTIONS

Conceptualization, M.K.K., S.M.-D. and A.A.; Methodology, M.K.K., A.A., and S.M.-D.; Investigation, M.K.K.; Writing – Original Draft, M.K.K., A.A., and S.M.-D.; Writing – Review and Editing, M.K.K., A.A., and S.M.-D.; Funding Acquisition, S.M.-D., M.K.K., and A.A.; Resources, M.K.K. and S.M.-D.; Supervision, A.A. and S.M.-D.

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