
LETTER TO THE EDITOR

Diversity of cues in zooplankton vertical migration—a reply to Ringelberg's comment

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Ringelberg (1995) states, 'From the recent literature, dealing with the role of predators, an impression can be obtained that the presence of predators or predator-mediated kairomones suffice to evoke DVM' and that 'light intensity changes are of no importance at all'. We were surprised to read the above statement from our esteemed colleague and are mystified as to how he could have gained such an 'impression'. We have certainly never stated—nor did we intend to imply—such a thing in any of our papers. Regarding the role of light, we have long been aware of its central importance in mediating vertical migrations [e.g. see Forward (1988) for a recent review of several decades of research on this topic] and we strongly suspect that the vast majority of aquatic ecologists can say the same thing. However, this does raise an important question: are changes in light intensity alone sufficient to evoke diel vertical migrations (DVM)?

There is now irrefutable evidence that some (but by no means all) species of zooplankton exhibit variable migration behavior, undertaking DVM at some locations and seasons, while at other times and places being non-migratory [e.g. Stirling *et al.*, 1990; Ringelberg *et al.*, 1991; Frost and Bollens, 1992; several papers in Ringelberg, 1993; Brancelj and Blejec, 1994; see also Bollens and Frost (1989a) for a review of many other, earlier studies]. These studies demonstrate that even when experiencing changing light intensities during sunrise and sunset, zooplankters (even of so-called 'migratory' species) may not exhibit DVM. This is certainly true of *Acartia hudsonica*, which exhibits seasonally variable migration behavior in Jakles Lagoon (Bollens *et al.*, 1992). Thus, we would modify the statement by Ringelberg in one small, but critically important way, to read: 'It is argued that changes in light intensity at sunrise and sunset are necessary *but insufficient* to evoke these migrations.' Some additional cue(s) are necessary to trigger DVM in many species of zooplankton, but what are these additional cues?

It was the recognition that variable migration behavior in field populations of zooplankton was statistically significantly correlated with abundances of their predators (Bollens and Frost, 1989a; Bollens *et al.*, 1992; Frost and Bollens, 1992) that led us to experimentally investigate the possibility that predator-mediated cues, in addition to light, are necessary to elicit DVM. Our earliest

experiments (Bollens and Frost, 1989b, 1991) showed that in the case of adult female *A. hudsonica* this additional cue is related to actively feeding planktivorous fish; we subsequently showed (Bollens *et al.*, 1994) that the nature of this predator-generated cue was mechanical or visual rather than chemical.

This latter finding is in contrast (but not, as Ringelberg states, 'in opposition') to many recent studies, cited in Bollens *et al.* (1994), of DVM in *other species and other environments* which show the inducing role of predator-released chemical exudates. As we pointed out (p. 561) in Bollens *et al.* (1994), *Acartia* may be unusual in possessing a large ratio of mechanoreceptors to chemoreceptors on their antennae (Barrientos Chacon De Avendano, 1980), and may prove to be the exception rather than the rule amongst marine copepods, but that in any case the exact cues eliciting DVM in zooplankton can be expected to vary between species. We would like to underscore this latter point, and recommend that the diversity of cues and responses in zooplankton DVM behavior be borne in mind in the design and execution of future studies.

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