Cues, not an endogenous rhythm, control the water-column entry by benthic copepods

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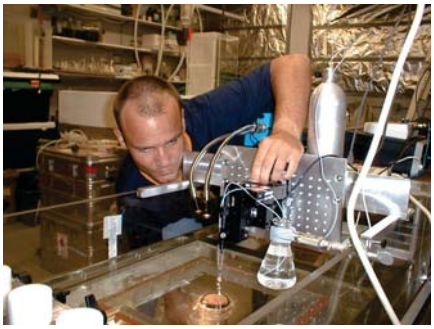

Figure 1. Photograph showing the working section of a seawater flume, the surface of a sediment core inserted through the flume bottom, and a microelectrode attached to a micromanipulator.

INTRODUCTION

Individuals of benthic copepod species can be entrained by near-bottom flows and thus moved into the water column. In addition, individuals of some species swim into the water column, i.e., they emerge. Both emergence and entrainment are of interest, e.g., for their roles in benthopelagic coupling, but the controlling factors are poorly understood.

Field studies have revealed that a pulse of benthic copepods emerges near sunset (e.g., Service and Bell 1987). Laboratory studies have shown that darkness or a correlate of it can cause this behavior (e.g., Teasdale et al. 2004), but its trigger in the natural environment remains unknown.

PROBLEM

At least three possibilities exist to explain the timing of emergence. (1) Given the biology of other crustaceans, an endogenous rhythm could be involved. (2) Many shallow-water benthic copepods have light-sensing organs, so the onset of darkness could be a direct cue. (3) The onset of darkness could indirectly cue emergence.

EXPERIMENTAL

Experiment 1: *Does an endogenous rhythm control emergence?* We inserted sediment cores into a laboratory seawater flume (**Figure 1**) to test the emergence response of copepods to a delay in the onset of darkness. We found that a delay in the onset of darkness caused a delay of their emergence pulse (**Figure 2**).

Experiment 2: *Do benthic copepods emerge in daylight when benthic photosynthesis stops?* We stopped photosynthesis of benthic microalgae chemically in the middle of the day (**Figure 3**) and found that a pulse of emergence occurred (data not shown).

DISCUSSION

We showed that factor(s) associated with the onset of darkness, rather than an endogenous rhythm, controls the dusk emergence of benthic copepods. In all experiments and in the field, we found that the oxygenation of the sediment pore water decreased markedly in the minutes after the onset of complete darkness (**Figure 4**). This decrease or correlated chemical change could therefore cue the emergence pulse.

Furthermore, we suggest that entrainment and emergence are not independent processes but that they can interact in at least two ways. Firstly, light-induced changes in oxygenation of the sediment pore water may affect the entrainment flux of benthic copepods. Secondly, if large numbers of individuals are entrained in the time leading up to sunset, few will remain in the sediment to be part of the dusk peak in emergence.

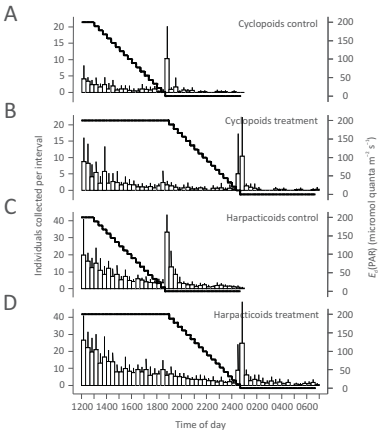

Figure 2. Experiment 1. Average (n = 7) number of (**A**, **B**) cyclopoids and (**C**, **D**) harpacticoids collected in the tail sieve of the flume during each 20-min interval, showing the dramatic increase in emergence rate at the onset of darkness. The irradiance of photosynthetically active radiation, E_d(PAR) is indicated by the dashed line. Error bars are one standard deviation.

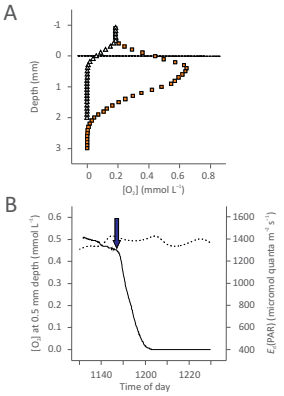

Figure 3. Experiment 2. (**A**) Microprofiles of pore-water [O$_2$] in daylight (E_d(PAR) = 1200 µmol quanta m^{-2} s^{-1}) before (squares) and after (triangles), showing the arrest of photosynthesis by addition of DCMU. Notice the difference in oxygen penetration. Dashed line indicates position of the sediment surface. (**B**) Time series of photosynthetically active radiation (dashed line) and pore-water [O$_2$] (solid line), showing the abrupt decrease in oxygen concentration when 3-(3′, 4′-dichlorophenyl)-1,1-dimethylurea (DCMU) was added (arrow).

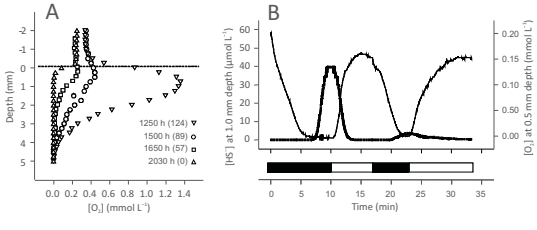

Figure 4. (**A**) Microprofiles of pore-water [O$_2$] in subtidal fine sand showing the in situ decrease in O$_2$ penetration as light intensity decreased. The number in parentheses is the irradiance of photosynthetically active radiation, E_d(PAR) (µmol quanta m^{-2} s^{-1}). (**B**) Laboratory time series of pore-water [O$_2$] at 0.5-mm depth (solid line) and [HS$^-$] at 1-mm depth (dotted line), showing the abrupt change that occurs at the transition from light to darkness. Horizontal bar indicates times when the core of intertidal mud was exposed to darkness (black) or to E_d(PAR) of 200 µmol quanta m^{-2} s^{-1}.

Service SK, Bell SS (1987) Density-influenced active dispersal of harpacticoid copepods. Journal of Experimental Marine Biology and Ecology 114:49–62

Teasdale M, Vopel K, Thistle D (2004) The timing of benthic copepod emergence. Limnology and Oceanography 49:884–889.

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