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How are the vertical migrations of copepods controlled?

Konrad Thorisson *

Marine Research Institute, P.O. Box 1390, 121, Reykjavik, Iceland

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Abstract

Using *Calanus finmarchicus* (Gunnerus) as a model organism, a hypothesis is suggested to explain the diel and seasonal vertical migrations of herbivorous copepods in boreal and polar waters. The hypothesis is based on the following assumptions. Hungry copepods are assumed to react to food smell by increased swimming. High lipid content is assumed to turn the copepods upside down. Light avoidance is assumed to operate solely while the copepods are satiated. The following three major peaks in downflux of phytoplankton remains are assumed to reach 1000 m depth or more: pre- and post-spring bloom peaks and the autumn increase. A minor "afternoon peak" in short-range downflux of phytoplankton is also assumed to exist. The assumptions are used to explain the following main traits in copepod migrations. The afternoon increase in downflux of phytoplankton material induces upward swimming of hungry copepods. If satiated, light avoidance brings them down again at dawn. The late stages of many species of copepods accumulate large amounts of lipids and if the above assumptions are valid, they will be turned upside down and swim down if activated. During midsummer, the downflux does not reach deep water and the copepods are assumed to spend some time in midwater until they moult. Copepods moulting from stage V into female adults use up to half of their lipids to produce eggs, which are more anteriorly located. This is assumed to turn their bodies back into an upright position and the copepods are assumed to swim up to the surface again when they smell sinking phytoplankton remains. Fat copepods are assumed to follow the downflux of phytoplankton material down to diapause depths, especially at the end of the spring bloom and in autumn. It is assumed that enough lipids are used up during the diapause to turn the copepods into head-up position again. The smell of fast-sinking fecal pellets containing prebloom phytoplankton is assumed to bring the copepods up from diapause again in late winter. The probable implications for the survival of cod larvae are discussed.

Keywords: *Calanus finmarchicus*; Cod larvae; Diel migrations; Phytoplankton; Seasonal migrations

1. Introduction

In the marine environment, a major part of the energy transfer from primary production to fish passes through the zooplankton. Through their extensive diel and seasonal vertical migrations, the zooplankton animals also make some of the energy from the euphotic layer available to deeper layers (Longhurst and Williams, 1992). The most prominent group of animals in this flow of energy are the copepods, in particular the oldest stages. This especially holds true at higher latitudes, where a single species of copepods e.g. *Calanus finmarchicus* can comprise more than half of the zooplankton biomass over extensive areas (Jaschnov, 1970; Heath et al., 1999; Planque and Batten, 2000).

Due to their importance in the marine food web, copepods have been studied intensively for more than a century. As detailed descriptions of the various forms of vertical migrations are easily obtained (e.g. Cushing,

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* Tel.: +354 5752000; fax: +354 5752001.
E-mail address: konrad@hafro.is.

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1951; Hutchinson, 1967), only those aspects that are necessary to explain the proposed hypothesis will be mentioned here. However, it may be helpful to mention a brief history of some of the ideas and hypotheses that led to our present understanding of zooplankton migrations. In 1882, T. Fuchs suggested that the diel vertical migrations of some freshwater crustaceans might be influenced by the light intensity (Longhurst, 1976). Both Rose and Russel later added to the hypothesis and formulated it more precisely for marine copepods (Russel, 1926). Since then, many attempts have been made to explain both the mechanism (Ostvedt, 1955; Rudjakov, 1970; Yayanos et al., 1978; Bollens et al., 1994; Heath, 1999) and the advantages (Hardy, 1956; McLaren, 1963; Zaret and Suffern, 1976; Kerfoot, 1985; Backhaus et al., 1994; Hays, 1995) of these massive migrations. Hardy and Gunther (1935) suggested that migrating behaviour may be modified by hunger and, later, the hunger–satiation hypothesis emerged (Conover, 1968; Pearre, 1979), supported by the laboratory experiments of Huntley and Brooks (1982). The predator evasion hypothesis has some explaining power and has been gaining increasing support (Zaret and Suffern, 1976; Stich and Lampert, 1981; Bollens and Frost, 1989). The effect on copepod buoyancy of the high compressibility and large thermal expansion of wax esters is also slowly emerging (Yayanos et al., 1978; Visser and Jonasdottir, 1999; Campbell and Dower, 2003). All these milestones and many others were important additions to our understanding of the vertical migrations. Some details are still missing, however, especially concerning the seasonal migrations.

The hypothesis presented here is one possible way of fitting most of the existing, complicated, and sometimes contradictory evidence on the vertical migrations of copepods into one framework. The hypothesis rests on a few assumptions which do not seem to contradict present knowledge but have not been proven either. Herbivorous copepods in boreal and polar waters are the main subjects of the hypothesis. The model animal is the intensively studied *C. finmarchicus*, but data on other (mostly) herbivorous copepod species are also used to fill in the picture. In a few cases data on cladocerans from fresh water are also mentioned, as similar behaviour of these animals hint at a wider appeal of some aspects of the present model (Clarke, 1932; Johnsen and Jakobsen, 1987). Different species of copepods have different life strategies, however (Head et al., 1985; Hays et al., 2001; Gislason, 2003), and the overwintering survival strategies of some copepods are radically different from those of *C. finmarchicus*. Some copepod species produce resting or diapause eggs (Johnson, 1980; Lindley, 1990), other species are active all year round (Heinrich, 1962) and lipid storage is very variable between species (Davis, 1976; Tiselius, 1992; Norrbin, 1994). In spite of these differences, some of the basic principles may apply to a variable degree to other herbivorous and omnivorous copepod species, to other areas, to some carnivorous copepod species and even to some freshwater cladocerans.

2. The hypothesis

The assumptions of the present hypothesis are the following:

- Satiated copepods maintain low activity, but avoid bright light
- Hungry copepods increase their swimming activity when they smell food
- High lipid content may reverse the direction of swimming.

To make the hypothesis work, there are two additional requirements concerning the phytoplankton: 1) there needs to be an afternoon/evening increase in the downflux of phytoplankton material during the productive season; 2) there also needs to be a considerable increase in downflux of marine snow to deep water, a) shortly before the spring bloom, b) right after the spring bloom, and c) during the autumn maximum in phytoplankton. There are some indications that these requirements may be fulfilled and supporting references will be given when appropriate. The scope of this paper, however, only permits a limited discussion of the phytoplankton-related topics. To simplify the description of the hypothesis that follows, let us assume that the assumptions above are valid.

2.1. Diel migrations

Starting in the mixed surface layer in the early hours of a summer day, satiated copepods are hanging motionless or slowly sinking with their antennae stretched out, in a head-up position. At sunrise, the satiated copepods start swimming downwards to avoid the bright daylight. Many copepod species end up below the thermocline, at say 50–150 m depth, where the light level is presumably more comfortable. The copepods rest down there for a few hours, until they become hungry again. Even if hungry, however, the copepods maintain their low level of activity as long as they do not smell food. It is suggested here that the amino acids released from the decomposing phytoplankton cells