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Sex and life stage dependent phototactic response of the marine copepod *Calanus finmarchicus* (Copepoda: Calanoida)

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ABSTRACT

Irradiance thresholds for phototactic response were determined for the marine calanoid copepod *Calanus finmarchicus* (Gunnerus). *C. finmarchicus* is one of many zooplankton species that exhibit diel vertical migration. Light is considered the main proximate cause of diel vertical migration, but irradiance sensitivity is unknown for many ecologically important zooplankton taxa, including *C. finmarchicus*. Here we studied phototaxis in *C. finmarchicus* in response to low levels of irradiance using a custom-made experimental setup under controlled laboratory conditions. The setup consisted of an aquarium with a light stimulus in one end of a raceway. A video camera and near-infrared light for illumination were applied to monitor the response to light in the horizontal plane. Low levels of irradiance were achieved using a white LED and a combination of absorptive neutral density filters and diode pulsing.

Stage V copepodites and adult females displayed negative phototaxis, and the threshold for phototactic response was 9.8×10^{-6} μmol photons m^{-2} s^{-1}. Adult males displayed positive phototaxis and the corresponding threshold value was 9.9×10^{-7} μmol photons m^{-2} s^{-1}. The results from the experiments were used to estimate the depths at which phototaxis is elicited in natural light conditions by conducting light simulations for an ocean scenario and a fjord scenario during peak spring bloom conditions. The estimated depths for irradiances that elicit a phototactic response corresponded to approximate depths of 158–186 m in the ocean scenario and 48–57 m in the fjord scenario. These depths are within the range of depth distributions of *C. finmarchicus* reported for ocean and fjord populations.

1. Introduction

Diel vertical migration (DVM) is a widespread phenomenon among zooplankton taxa, including *Calanus* species, and may represent the largest synchronised animal migration on the planet in terms of biomass (Hays, 2003). The most common migration pattern for zooplankton populations involves staying in deeper water layers during daytime, and active migration towards the surface at night. A widely supported hypothesis for this activity is the predator avoidance hypothesis, stating that the animals reduce the risk of predation from visually hunting predators by staying away from the upper photic and phytoplankton-rich zone during daytime and ascending to feed during the night (e.g. Hays, 2003; Lampert, 1989), although other explanation models have also been suggested (e.g. Williamson et al., 2011).

For decades, various features of daily light changes have been considered the most important exogenous cue for timing of DVM (Cohen and Forward, 2009). The three major hypotheses on how light influences DVM are based on (1) absolute light intensity threshold, (2) relative rate of irradiance change and (3) preferred light intensity or isolume, and all three hypotheses are supported by field and laboratory evidence (Cohen and Forward, 2009). Other factors may also influence DVM, for example Ringelberg (1995) proposed a hierarchy of causality factors, with light being the primary which induces and maintains the movement. Secondary causal factors such as fish kairomones and food concentration may influence DVM dynamics by enhancing or inhibiting the effect of the primary cue. Also, environmental factors, such as temperature and oxygen gradients, may modulate the behaviour of the animals once the movement has been triggered (Ringelberg, 1995).

DVM does not only appear in response to solar light cycles. Nocturnal light and lunar cycles have also been shown to influence DVM in zooplankton (Alldredge and King, 1980; Benoit-Bird et al., 2009). Accordingly, Berge et al. (2009, 2012) reported DVM in Arctic

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zooplankton during the polar night and suggested that DVM in the polar night is regulated by solar and lunar irradiance that are below human perception and below the detection limit for most standard irradiance meters.

Calanus finmarchicus (Gunnerus) is considered an ecological key species in the North Atlantic pelagic ecosystem (Mauchline, 1998). The species contributes to a large fraction of the total plankton biomass (Planque and Batten, 2000), and constitutes a crucial component of the food web, transferring energy from the primary production of phytoplankton to e.g. fish species such as cod *Gadus morhua* L. and herring *Clupea harengus* L. (Green et al., 2004). The amplitude of DVM in *C. finmarchicus* may vary from a few metres to hundreds of metres. Studies investigating the stage-specific spatial distribution report that depth distribution is age-dependent (e.g. Baumgartner et al., 2003; Cottier et al., 2006; Dale and Kaartvedt, 2000; Durbin et al., 1995; Kwasniewski et al., 2003; Rabindranath et al., 2011; Unstad and Tande, 1991). During daytime, the early copepodite stages (CI–CIII) are primarily found in the upper water layers, whereas copepodite V (CV) and adult females (CVIf) are found in the deeper water layers (e.g. Kwasniewski et al., 2003; Unstad and Tande, 1991). Large proportions of *C. finmarchicus* CV and CVIf have been reported at depths of around 200 m during daytime, although it is uncertain whether these stages were actively migrating or in diapause (e.g. Baumgartner et al., 2003; Kwasniewski et al., 2003; Unstad and Tande, 1991).

For most crustacean plankton, DVM is generally considered a crucial life history trait and intimately related to the ecological success of the species (Hays, 2003). However, with respect to environmental cues regulating DVM, many mechanisms are still poorly understood or characterised. In the present study we examined behavioural responses of *C. finmarchicus* to light stimuli of different intensities by using a video-recording system that recorded position over time relative to a light stimulus. The main aim of the study was to examine the behavioural sensitivity and specificity (phototactic response) in response to stimulation by a broad-spectrum light (400–700 nm), within a range of irradiances including those found in the deep ocean or in the dark polar night (Clarke, 1970). To do this a new experimental laboratory set-up was developed, that allowed us to confidently measure phototactic behaviour in *C. finmarchicus* even at very low irradiances. Furthermore, light model simulations using available field data were included to estimate the ocean or fjord depths that correspond to the irradiance threshold for phototactic response.

2. Material and methods

2.1. Copepod culture

Experimental copepods were collected from the continuous *C. finmarchicus* culture at SINTEF/NTNU Centre of Fisheries and Aquaculture (Trondheim, Norway). The culture was established from copepods collected in Trondheimsfjorden, Norway (63°N, 10°E), in October 2004. More details on the culture conditions are given in Hansen et al. (2007). At the time of the experiments (autumn 2010) the culture had been running for 27 generations under laboratory conditions, including a light–dark cycle of 18:6 h, with 6 h of dawn and dusk in the first and last parts of the light period, respectively. This corresponds to light conditions in late April at 63°N. Endogenous rhythms may influence the phototactic response in the copepods, thus adaptation to a defined circadian rhythm is vital in order to obtain copepods in the same state for the experiments. The maximum light intensity experienced by the copepods in culture is 2.0 μmol photons m^{-2} s^{-1} (400–700 nm, measured at the surface during the light period; QSL100, Biospherical Instruments, San Diego, CA, USA). This is within the irradiance range measured in their natural environment, which can be up to 2000 μmol photons m^{-2} s^{-1} at the sea surface at midday (Sakshaug et al., 2009).

2.2. Experimental setup

The experimental setup included a 50 × 50 × 12 cm aquarium made of 10 mm glass (Pilkington Optiwhite, NSG Co., Ltd, Japan; Fig. 1). The aquarium was equipped with an overflow outlet (removing excess water), ensuring a water depth of maximum 8 cm during the experiments. There was no water renewal during experiments. A raceway was constructed inside the aquarium using glass plates (Pilkington Optiwhite, 8 mm) as walls, limiting the projection area available to the copepods to 48 × 13 cm. The walls of the raceway fit smoothly but not watertight to the outer walls of the aquarium, hence allowing water exchange with the rest of the aquarium.

The light stimulus source was a white light emitting diode (LED; Luxeon I Lambertian, 350 mA, Phillips Lumileds, LXHL-PW01) attached to a heat sink (ATSEU-077B-C2-R0, Advanced Thermal Solutions, MA, USA). To control the light intensity, absorptive neutral density filters (CVI Melles Griot, Netherlands) mounted in a computer controlled filter wheel (Tofra, Inc., Palo Alto, CA, USA) were positioned between the LED and the aquarium. The light intensity could be further adjusted over orders of magnitude (1–100%) using a 100 Hz pulse width modulation (PWM) signal generated by a computer controlled USB device (National Instruments, USB-6212). A Fresnel lens (95 × 135 mm, optical PVC, 3Dlens.com, Taiwan) was attached one focal length from the LED (12 cm) to make the light path in the raceway collimated. The LED, filter wheel and Fresnel lens were assembled in a single tailored light-proof unit to avoid stray light from the LED. Between replicate tests, the position of the light stimulus assembly was alternated between the two ends of the raceway.

The aquarium was placed on a table with a 48 × 48 cm opening for illumination from below. Two near-infrared lamps (~845 nm, Eneo, Germany) were attached to the table legs with custom-made adjustable brackets that allowed the lamps to be regulated in most directions to optimise image quality. Infrared longpass filters (Kodak Wratten #87C, Edmund Optics Ltd, York, UK, 0% transmission up to ~790 nm wavelength) were attached to the near-infrared lamps to cut off any traces of visible light. To prevent distortions from near-infrared stray light being reflected off the walls in the laboratory, the setup was enclosed in a custom-made black fabric cape. Preliminary experiments demonstrated no behavioural response to the near-infrared illumination.

The positioning and phototactic response of the copepods following light stimuli were recorded using a video camera (Sony Handycam HDR-XR520-VE, Sony) placed perpendicular to the aquarium on a quadrapod (Quadrapod Elite Copy Stand, Forensic Imaging, Inc., US). The movement of the copepods in the raceway relative to the light stimulus was monitored in the horizontal plane, to exclude the influence of buoyancy as well as gravitation on the light response movements. The copepods were recorded in high definition video (HD) and in "night shot" mode, in which the camera's internal glass filter for removing near-infrared light is physically displaced. A black polyethylene sheet was placed below the aquarium in the raceway area to provide a uniform background with high contrast against the illuminated copepods. The experiments were conducted in a conditioning room at air and water temperature of 10 (±2) °C in complete darkness, except for the light stimuli and near-infrared illumination.

2.3. Light stimulus

The range of irradiance used in the experiments was achieved using a combination of absorptive neutral density filters and diode pulsing. The absorptive neutral density filters used had an optical density (OD, absorbance, dimensionless) from 0.5 to 5 at 546 nm. By combining these filters with diode pulsing (diode pulsing was used on three of the light intensities), we obtained 9 irradiance levels over 9 orders of magnitude. These were for simplicity called OD1 through OD9.

Spectral irradiance was determined using a spectroradiometer (Fixed Imaging Compact Spectrograph, FICS SN 7743, Oriel Instruments,