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Light in the dark – the role of irradiance in the high Arctic marine ecosystem during polar night

Thesis for the degree of Philosophiae Doctor

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Norwegian University of Science and Technology
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Summary

Most research in the Arctic has been conducted during the time of year with daylight, but over the last years, the interest for the biological activity in the dark polar winter, the polar night, has grown. Recent studies show that part of the copepod community is still active in the upper parts of the water column during polar night, even performing diel vertical migration (DVM). The conventional paradigm of a "quiet" Arctic marine environment during polar night is thus about to be challenged, and with this, many interesting questions about the biology of the species present in the polar night are raised. As the intensity of the irradiance is far lower than at other times of year, the main light sources being background solar irradiance, moonlight, starlight (night sky irradiance), and aurora borealis, there are specific requirements to the visual capabilities of the different taxa. The ability of organisms to detect the downwelling irradiance is governed by sensitivity to absolute irradiance, as well as the spectral sensitivity of the species. In this thesis, patterns of DVM in the polar night were studied, and the vision of selected Arctic organisms was investigated by using hyperspectral imaging as well as behavioural experiments.

During polar night, patterns of bioluminescence and DVM were mapped in Kongsfjorden, Svalbard, using an autonomous underwater vehicle (AUV) as well as zooplankton net hauls. The AUV was equipped with a bathyphotometer for bioluminescence measurements and Acoustic Doppler Current Profilers (ADCP) providing relative acoustic backscatter from zooplankton. Bioluminescence was, as the first registration during the polar night, documented throughout the water column. The taxa contributing to the documented bioluminescence were dominated by dinoflagellates (mainly *Protoperidinium* spp.), copepod nauplii (e.g. *Metridia* spp.), the copepod *Oncaea borealis*, appendicularians, and krill. Diel changes in bioluminescence over depth were observed, with a significantly greater proportion of the more intense flashes occurring in surface layers during night and at depth during day. These changes were interpreted as indications of DVM, as no diel changes in the bioluminescence potential itself were documented. Investigations using acoustic backscatter as well as plankton net hauls supported that the larger zooplankton, like *Calanus* spp., performed DVM in Kongsfjorden during polar night.

To investigate the spectral characteristics of the eyes of different organisms, and thus their potential to detect irradiance in a low-light environment, the eyes of live specimens of different copepod and amphipod species were characterised using a hyperspectral imager. The spectral properties of the eyes were found to match the light climate of their habitats, sympagic and shallow-living pelagic species probably absorbing in blue and some in green wavebands, while deeper-living pelagic and hyperbenthic species absorbed mainly in blue. The sensitivity to ambient wavelengths may be part of the explanation to how organisms can stay active during the polar night, when ambient irradiance is very limited.

Calanus spp. is a genus highly important to the Arctic marine ecosystem, and it is one of the taxa suggested to contribute to the activity observed during the polar night. It was therefore selected for studies of their potential response to extremely low irradiance levels. An experimental setup was developed to investigate the phototactic behaviour (behavioural response to irradiance) of *Calanus* spp., and laboratory cultured *C. finmarchicus* were investigated in the first study. Using a white light stimulus, the lowest irradiance levels eliciting a phototactic response were

in the range of 1-10×10^{-6} μmol photons m^{-2} s^{-1}. This irradiance level is a minute fraction compared to the irradiance in periods with daylight, e.g. at mid-day during summer the irradiance is in the range of 10^3 μmol photons m^{-2} s^{-1}. Using parameters from spring phytoplankton bloom conditions, when attenuation of light is high, the irradiance threshold levels for *C. finmarchicus* were estimated to correspond to 48-57 m depth in a fjord (Trondheimsfjorden) and 158-186 m in open ocean (Norwegian Sea), which matched with reported depth ranges of natural *C. finmarchicus* populations.

Finally, using the same experimental setup as above, the phototactic behaviour of *Calanus* spp. sampled during polar night was investigated, to start revealing the visual capabilities of polar night acclimated organisms. Different wavebands of visible light were used, thus also investigating the spectral sensitivity of *Calanus* spp. The copepods displayed negative phototaxis, and showed highest sensitivity towards blue and green wavebands. The lowest irradiance levels eliciting a phototactic response in these wavebands were in the range of 0.3-4×10^{-6} μmol photons m^{-2} s^{-1}, and for the red waveband, the corresponding levels were about three orders of magnitude higher. The lower sensitivity to red suggests that *Calanus* spp. are adapted to the blue and green light climate of oceans and coastal areas, respectively. Correlating the lowest threshold level for response with estimations of polar night irradiance with depth, it was suggested that *Calanus* spp. may respond to irradiance from the night sky down to approximately 40-50 m, moonlight to 100-140 m, and aurora borealis down to 60-100 m depth. Thus, irradiance may be the proximate cue for the observed DVM patterns, and it was suggested that the background irradiance from the sun, moonlight, as well as aurora affect the pelagic ecosystem during the polar night.

Contents

List of papers

Paper I.

Berge J, **Båtnes AS**, Johnsen G, Blackwell SM, Moline MA (2012) Bioluminescence in the high Arctic during the polar night. Mar Biol 159:231–237

Paper II.

Moline MA, Berge J, Johnsen G, **Båtnes AS**, Blackwell SM (in revision) Bioluminescence flash kinetics characterize pelagic community structure. J Plankton Res

Paper III.

Båtnes AS, Thoen HH, Berge J, Johnsen G (submitted) Hyperspectral imaging of a crustacean's eye provides insight into its spectral sensitivity and general ecology. PLOS ONE

Paper IV.

Miljeteig C, Olsen AJ, **Båtnes AS**, Altin D, Nordtug T, Alver MO, Speed JDM, Jenssen BM (in revision) Sex and life stage dependent phototactic response of the marine copepod *Calanus finmarchicus* Gunnerus (Copepoda: Calanoida). J Exp Mar Biol Ecol

Paper V.

Båtnes AS, Miljeteig C, Berge J, Greenacre M, Johnsen G (submitted) Orchestrated movements of copepods in the dark conducted by the Moon, Sun, and aurora borealis. Polar Biol

Contributions

I performed all work on which this thesis is based.
Paper I: JB planned the field work and did the main part of writing the manuscript. ASB was responsible for carrying out the work both in the field and the laboratory, carried out all plankton enumerations, and was part of the writing process. SMB contributed to the data analyses and the writing process. GJ and MAM participated in planning and field work, and contributed to the data analyses and writing process.
Paper II: MAM planned the field work and did the main part of writing the manuscript. JB and GJ participated in the field work, and contributed to the data analyses and writing process. ASB took part in the fieldwork, and carried out plankton enumerations. SMB contributed to the data analyses and the writing process.
Paper III: ASB planned and carried out the field work and hyperspectral imaging of the zooplankton, all data treatment and the main part of writing the manuscript. HHT participated in the field work and contributed to writing the manuscript. JB participated in the field work and contributed to the writing process. GJ carried out field work and hyperspectral imaging for the remaining species, and contributed to the writing process.
Paper IV: CM did the main part of developing the experimental setup, all experiments, and the main part of data analyses and writing the manuscript. AJO contributed to developing the experimental setup and writing the manuscript. ASB was involved in developing the experimental setup, did irradiance measurements, and contributed to writing the manuscript. DA contributed to developing the experimental setup and performing experiments, and commented on the manuscript. TN contributed to developing the experimental setup and commented on the manuscript. MOA performed the light modelling and commented on the manuscript. JDMS helped with data and statistical analyses and commented on the manuscript. BMJ commented on the manuscript.

Paper V: ASB performed the modification of the experimental setup (same setup as in Paper IV), field and laboratory work, data analyses, and the main part of writing the manuscript. CM did field and laboratory work, developed video/image analysis, and contributed to the modifications of the experimental setup, statistical analyses and writing the manuscript. JB helped with field work and commented on the manuscript. MG contributed to data and statistical analyses. GJ commented on the manuscript.

Abbreviations

ADCP	Acoustic Doppler current profiler
AUV	Autonomous underwater vehicle
BP	Bathyphotometer
cDOM	Coloured dissolved organic matter
Chl*a*	Chlorophyll *a*
CIV and CV	Copepodite stages IV and V (*Calanus* spp.)
CTD	Sensor for measuring conductivity (salinity), temperature, density
CVIf and CVIm	Adult females and adult males, respectively (*Calanus* spp.)
DVM	Diel vertical migration
HI	Hyperspectral imager
K(λ)	Spectral vertical diffuse attenuation coefficient
LED	Light emitting diode
OOI	Object of interest
R(λ)	Relative spectral reflectance
WP2 net	Plankton net with 180 μm mesh size and 0.25 m^2 opening
WP3 net	Plankton net with 500 μm mesh size and 1 m^2 opening
λ_{max}	Wavelength with maximum bioluminescence emission

Introduction

Background

The Arctic has been an area of interest for centuries, starting with the exploration of the region, and continuing with exploiting resources, like whaling, hunting, and coal mining. Today the Arctic is an indicator area for global climate changes, and there is also increasing interest and activity regarding fossil fuels, minerals, fisheries, tourism, and new transport routes. There is a strong interest for basic natural science research, both due to the mentioned activities and for the basic science itself. Development of new methods and information retrieval is highly needed for decision-making and a sound nature management in the Arctic. Thus, there is a need for knowledge about the Arctic ecosystems, both for mapping them as well as revealing the secrets of how they function, but also for monitoring over time as the Arctic changes.

Most research in the Arctic has been conducted during the time of year with daylight (spring, summer, and autumn). Little work has been done during the dark winter season, the polar night, mainly due to logistical problems. Outdoors activities are challenging because of the darkness, low temperatures and harsh weather. Also, and partly due to the absence of data, it was for a long time assumed that the Arctic marine ecosystems were "shut down" and in some kind of dormancy through the polar night because of the lack of sunlight to fuel the ecosystem (Piepenburg 2005; Smetacek and Nicol 2005; Berge et al. 2009). In the pelagic system, for instance, copepod populations have been shown to migrate to great depths, entering a resting state (diapause), over the winter (e.g. Falk-Petersen et al. 2009).

Over the last years, the interest for the biological activity in the polar night has grown. Recent studies show that part of the copepod community is still active in the upper parts of the water column in Arctic and sub-Arctic areas during winter (Sasaki et al. 2001; Sato et al. 2002; Berge et al. 2009; Fort et al. 2010). Amphipods are actively feeding (Kraft et al. 2013), and benthic and littoral organisms, as well as seabirds, are observed to be active (Weslawski et al. 1991; Kuklinski et al. 2013; Paper I). Thus, the conventional paradigm of a "quiet" Arctic marine environment during polar night is about to be challenged, and with this, many interesting questions about the biology of the species present in the polar night are raised.

As the lives of many marine species largely rely on vision, there are very specific requirements to their visual capabilities and sensitivity to irradiance, which are related to their habitat. Irradiance is defined as the power of electromagnetic radiation (light) per unit area and time at 400-700 nm, which is the spectral range of light perceived by most marine organisms. The light climate (intensity, spectral composition, and amplitude) in surface waters during polar night is very different from that during times with daylight, and may be comparable to that of far deeper water. For marine organisms, high sensitivity to irradiance, and eye pigments that can absorb the wavebands available, is thus needed to remain active during the polar night.

Vision and light climate in the marine environment

The eyes of marine animals are commonly highly adapted to their low-light environment (e.g. Warrant and Locket 2004), as a result of evolutionary arms races between e.g. predators and prey. Prey need to have a vision adapted to the ambient irradiance in order to avoid their visual predators, and a sufficient visual sensitivity to enable their descent to depths below their predators' limit for visually hunting (e.g. Zaret and Suffern 1976; Hays 2003). In this respect, both the sensitivity to absolute irradiance, as well as the spectral sensitivity, should be considered. The

depth at which an organism is able to see the downwelling irradiance is governed by these two factors, as the intensity decreases and the waveband of the available irradiance gets narrower with depth. The properties of the irradiance at different depths depend on the inherent optical properties of the water and its constituents. In clear oceanic waters, the blue wavebands penetrates deepest, as the vertical diffuse attenuation coefficient ($K(\lambda)$) for pure water is smallest for blue light (Fig. 1; e.g. Jerlov et al. 1968; Sakshaug et al. 2009). In coastal areas, the concentrations of chlorophyll *a* (Chl*a*) and cDOM (coloured dissolved organic matter) are higher, and due to the light absorbing properties of these substances, the $K(\lambda)$ generally increases. The spectral absorption of Chl*a* and cDOM also causes $K(\lambda)$ to shift and become lowest in green, making coastal waters appear green (Fig 1).

In addition to the downwelling irradiance, many marine organisms produce light themselves. This is called bioluminescence, and occurs among most phyla and for a variety of purposes (e.g. Haddock et al. 2010; Widder 2010). The bioluminescence emission maxima (the wavelength with peak intensity; λ_{max}) for most species are within the range from 450 nm to 490 nm, pelagic species emitting mostly in blue, while for benthic species there is a shift in λ_{max} towards green (Herring 1983). Most marine organisms will generally need highest spectral sensitivity within the range of blue and green light, as both downwelling irradiance and bioluminescence falls within this waveband. More accurately, the peak spectral sensitivities of different species is expected to vary according to the ambient light of their habitat, as well as the nature of the visual scene; whether it is diffuse downwelling light (extended source) or bioluminescence (point source; e.g. Warrant and Locket 2004).

In the polar night, the intensity of the downwelling irradiance is far lower than during times with daylight, and most of the polar night period is perceived as continuous darkness by the human eye.

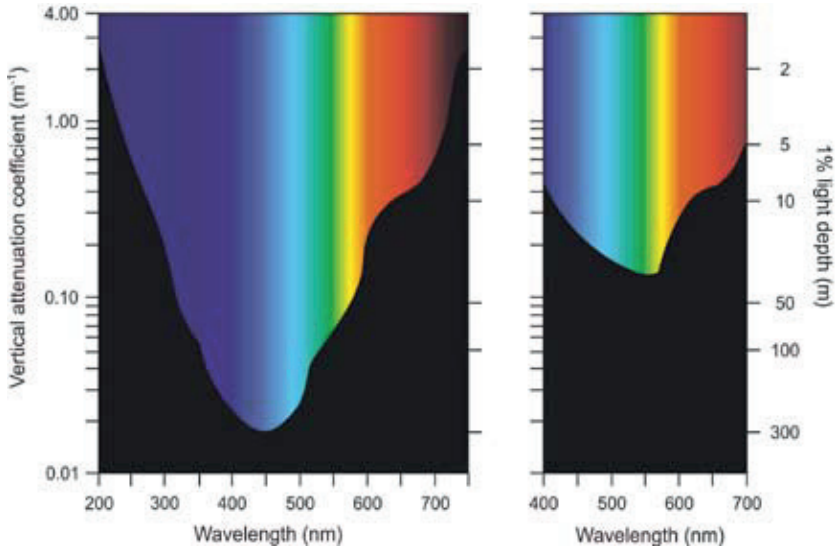


Fig 1. Vertical diffuse attenuation coefficients for different wavelengths for clearest ocean water (left image; mainly Sargasso Sea observations) and coastal water (right image; example from clearest Trondheimsfjord water; Chl*a* concentration <0.05 mg m^{-3}). Figure from Sakshaug et al. (2009), with permission.

The main light sources are background solar irradiance, moonlight, and starlight (night sky irradiance). The background solar irradiance has a 24 hour cycle, and in addition it varies with the time of year, the daytime irradiance varying with the solar elevation angle. The moonlight has an approximate 25 hour daily cycle as well as the 29 days lunar cycle. These light sources have spectral properties resembling that of sunlight, creating a light field of downwelling irradiance with depth that is relatively similar to that during times of year with sunlight (Fig. 1), but with lower intensity and thus a more limited depth range. In addition, aurora borealis (northern light) is frequently occurring in the areas experiencing polar night. The most common is the green aurora, which has an emission line at 557.7 nm. The $K(\lambda)$ in this waveband is relatively low, particularly in coastal water, so the aurora might potentially be visible to organisms at some depth. The aurora has a 24 hour cycle due to the Earth's rotation under the aurora oval. Thus, there is a periodicity in the polar night irradiance, which potentially may influence high-latitude ecosystems.

Bioluminescence has to my knowledge not previously been investigated during the high Arctic polar night, but was documented for the first time in Paper I. Bioluminescence is ubiquitous, and has a variety of functions, like attracting prey, intraspecific communication, and "counter-illumination" (e.g. Haddock et al. 2010). At times with very limited external (downwelling) light, it is reasonable to believe that bioluminescence may significantly contribute to the total light budget of an ecosystem (Paper I), and in this respect, it may be an important feature of the Arctic ecosystem during polar night.

The genus *Calanus*

Calanus spp. is a genus highly important to the Arctic marine ecosystem (e.g. Falk-Petersen et al. 2009, Berge et al. 2012), and it is one of the taxa suggested to contribute to the activity observed during the polar night (Sato et al. 2002; Berge et al. 2009). On this basis it was selected for this thesis for closer investigations of the influence of downwelling irradiance (Papers III, IV, and V). In the Arctic, the genus mainly comprises the species *C. finmarchicus*, *C. glacialis*, and *C. hyperboreus* (Fig. 2). *Calanus* spp. are considered to be primarily herbivores, but do also feed on ciliates, and thus assimilate large amounts of energy from primary and secondary production (e.g. Vadstein 2009; Wold 2012). The energy taken up during spring bloom is stored as lipids in an oil sac, making *Calanus* spp. energy rich prey items (e.g. Sargent and Falk-Petersen 1988; Lee et al. 2006; Falk-Petersen et al. 2009). The biomass of *Calanus* spp. is very large, constituting over 90 % of the zooplankton biomass in some areas (e.g. Blachowiak-Samolyk et al. 2008). They are the main food of a variety of predators, including other copepods, amphipods, gelatinous zooplankton, fish, and whales, and are thus a key link in the food web, transferring large amounts of energy from phytoplankton to higher trophic levels (e.g. Falk-Petersen et al. 1990; Auel and Werner 2003; Baumgartner and Mate 2003; Karnovsky et al. 2003). *Calanus* spp., being highly desirable prey organisms, have evolved different strategies for reducing the predation risk and thus increasing their fitness. One important strategy, which is common among a variety of planktonic organisms, is diel vertical migration (DVM; e.g. Ringelberg 1995; 2010). The most common migration pattern is nocturnal DVM. This involves an ascent to surface waters, where food organisms are abundant, at sunset to feed in the darkness. At sunrise, the zooplankton descend to deeper waters and stay there during the time of daylight to hide from visual predators. The ultimate cause for DVM is considered to be the optimising of feeding at the same time as minimising the risk of being predated (the predator evasion hypothesis; e.g. Lampert 1989; Hays 2003).

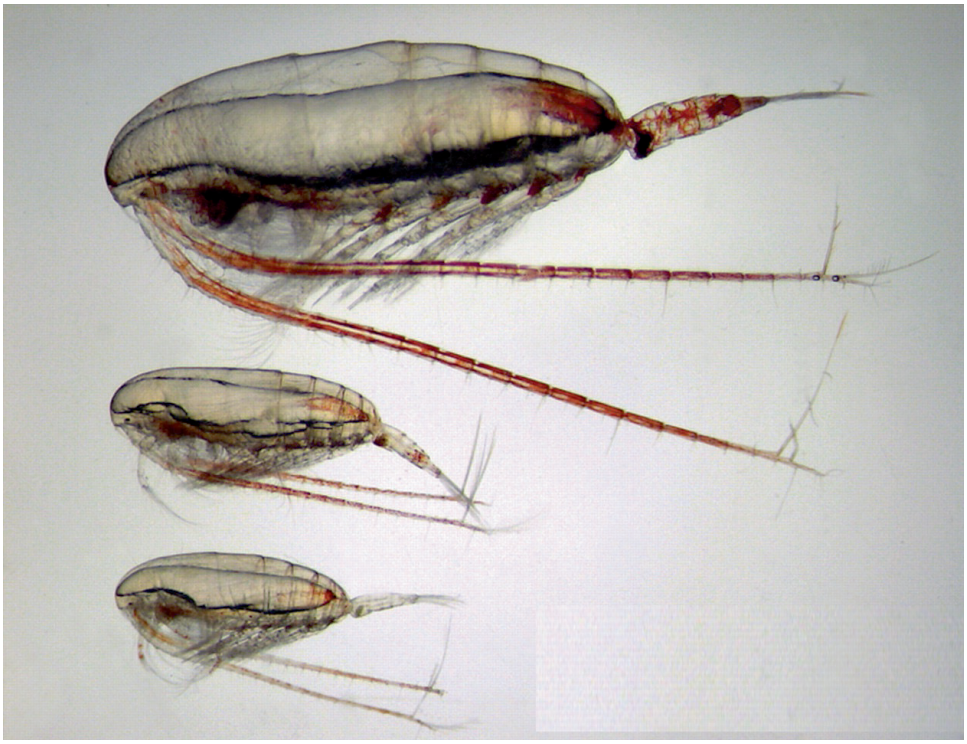


Fig 2. The three *Calanus* species that are common in the Arctic, from top to bottom: *C. hyperboreus, C. glacialis*, and *C. finmarchicus*. Figure from Berge et al. (2012), with permission.

The primary proximate cause of DVM is considered to be the use of light (irradiance) as an exogenous cue (e.g. Cohen and Forward 2009). Light perception is thus an important feature for *Calanus* spp.

DVM has been documented for *Calanus* spp. in the Arctic (e.g. Dale and Kaartvedt 2000; Fortier et al. 2001; Cottier et al. 2006; Rabindranath et al. 2011), and typical migration depths are 100-150 m. These investigations were performed during a time of year with daylight, when light cues obviously may be the proximate factor controlling the DVM behaviour. In a recent study Berge et al. (2009) found, using acoustic backscatter, a DVM signal during the darkest part of the year in the high Arctic. The diel variation in irradiance is very small at these latitudes during the polar night, and this study opened for the possibility of irradiance governing the observed DVM behaviour in zooplankton. It was suggested that *Calanus* spp. were one of the taxa contributing to the vertical displacement signal. The possibility of irradiance governing DVM even during the dark polar night is new insight and it is important to study this further to increase our knowledge of ecological processes in the Arctic marine ecosystem.

Objectives

The topic for this PhD work was investigating the role of irradiance in the Arctic marine (primarily pelagic) ecosystem during the polar night.

The first part investigates bioluminescence and DVM during the polar night. The objectives were to document and characterise, if present, bioluminescence and DVM patterns, as well as to investigate the contributing taxa (Papers I and II).

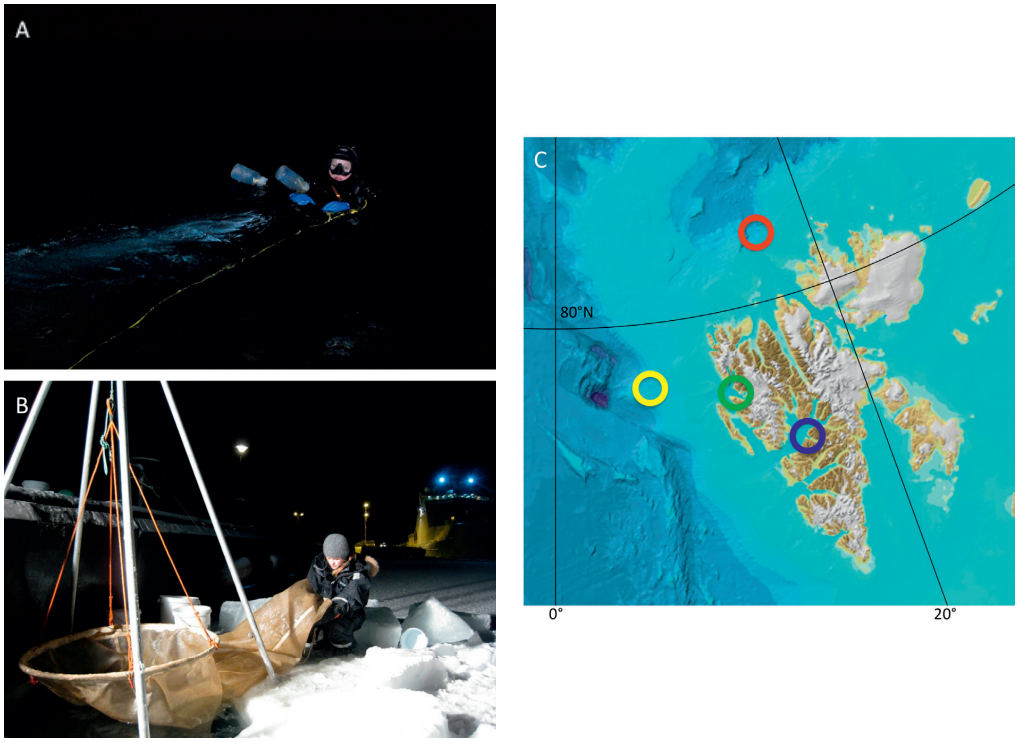


Fig 3. A) Sampling by SCUBA diving in Kongsfjorden, January 2010. Photo: Sanna Majaneva. B) Field work in Adventfjorden, sampling with a WP3 plankton net, in January 2011. Photo: Cecilie Miljeteig. C) Map over the Svalbard archipelago with field work locations indicated. Kongsfjorden (green circle): field work for Papers I, II, and III. Kongsfjordrenna (yellow circle) and ice edge (red circle): field work for Paper III. Adventfjorden (blue circle): field work for Paper V. The map was obtained from Jakobsson et al. (2012).

The second topic was the spectral sensitivity of crustaceans from different oceanic habitats. Hyperspectral imaging was used as a new method for investigating the spectral characteristics of the eye of copepods and amphipods, and the aim was to compare these characteristics to the habitat of the specific taxa, as well as to evaluate hyperspectral imaging as a tool for this kind of investigation (Paper III).

The third part of this work investigated the phototactic behaviour of *Calanus* spp. Using a newly developed experimental setup, the aim was to determine threshold levels for response of lab cultured *C. finmarchicus* to irradiance in the visible range, and relate the results to the irradiance in their natural habitat (Paper IV). Then, using *Calanus* spp. sampled in the high Arctic during polar night, the irradiance thresholds for response to different wavebands of visible light were determined, thus also investigating the spectral sensitivity of *Calanus* spp. The results were related to the light sources present in the polar night, and the final aim was to evaluate the possibility of irradiance affecting the observed DVM behaviour of *Calanus* spp. during the darkest part of the year (Paper V).

Methods

Study area

The field work for this study was conducted in the high Arctic archipelago of Svalbard (78-81°N; Fig. 3). The region is influenced by both Atlantic and Arctic

Fig 4. The REMUS-100 AUV. The green section with red circles is the ADCP (upward- and downward-looking). The nose cone contains the BP, and the organisms passing through the BP detector are captured by the attached plankton nets. Photo: Geir Johnsen.

water masses, giving a mix of species originating in Atlantic (*C. finmarchicus*, *Themisto abyssorum*) and Arctic areas (*C. glacialis*, *Themisto libellula*) (e.g. Hirche 1991; Unstad and Tande 1991; Dalpadado et al. 1994; Hop et al. 2006). The polar night at these latitudes lasts for around four months, from November to February.

Autonomous Underwater Vehicle (AUV)

AUVs are battery-powered vehicles that provide continuous spatial sampling of the marine environment, using large payloads with different scientific sensors. The AUV used in this study (Papers I and II) was a REMUS-100 (Moline et al. 2005; Fig. 4), which is propeller-driven and developed for high-resolution surveys in near-shore coastal areas. The AUV was fitted with different equipment for registering environmental variables. The nose cone contained a bathyphotometer (BP) developed for integration into the AUV (Moline et al. 2005). The BP is designed to measure bioluminescence, and the instrument adapted to the AUV consists of a light measuring section and an instrument interface section. An impeller pump creates a water flow from the nose cone water inlet and into a light-measuring chamber, at the same time creating turbulence that stimulates bioluminescent organisms to emit light. A photomultiplier tube measures the stimulated bioluminescence. Next to the nose cone is an Acoustic Doppler Current Profiler (ADCP), consisting of four upward- and four downward-looking transponder beams, operating at 1200 kHz. The ADCP was configured to provide relative acoustic backscatter as an estimate of scattering volume, instead of current velocities, which in combination with the frequency makes it ideal for studying the distribution of zooplankton. Incorporated into the AUV are also a fluorometer and a CTD sensor (Moline et al. 2005). The AUV was also equipped with cylindrical plankton nets (20 µm mesh size), which were fitted to each of the two exhausts of the BP (Moline et al. 2009), capturing all organisms passing through the light-measuring chamber.

The BP was also detached from the AUV and used for continuous observation at a single location (2 m depth) to investigate possible variations in bioluminescence activity over time.

Sampling marine organisms

Plankton nets used for zooplankton sampling consist of a cone-shaped net that has a cod-end in the narrow end to collect the organisms. Vertical net hauls were performed with plankton nets according to WP2 (0.25 m^2 opening, 180 µm mesh size; Papers I and III) and WP3 (1 m^2 opening, 500 µm mesh size; Paper V) standards. SCUBA divers used both hand held nets as well as an underwater electric suction sampler (Lønne 1988) for capturing larger zooplankton as well as sympagic fauna. For

capturing deep-sea scavenging amphipods, baited traps with acoustic releasers were deployed on the seafloor for 4-6 days (Thoen et al. 2010).

Hyperspectral imaging

Over the last years hyperspectral imaging has been used for remote sensing of objects of interest (OOI) from platforms such as airplanes and balloons. It has been used for e.g., mapping of coral reefs, seagrass, kelp forests, and distribution of phytoplankton/Chl*a* (e.g. Andréfouët et al. 2003, 2004; Dierssen et al. 2003; Volent et al. 2007). More recently, it has been used on smaller scales, like underwater mapping of corals and sponges (Pettersen et al. submitted), and also mounted on a stereomicroscope, looking at the spectral properties of micro- and macroalgae (Volent et al. 2009) and copepods and amphipods (Paper III).

The hyperspectral imager (HI) captures slices (Δx) where each slice is an image with hyperspectral profiles (Fig. 5). Δx is the spatial resolution in the direction of movement, dependent on the entrance slit width. The hyperspectral image scan is saved in video format, and computer software assembles the images into a spectral image cube. This is called the push broom technique. The HI used (Sigernes et al. 2000) was designed with a front focusing lens (L1), entrance slit (S) with the slit direction perpendicular to the direction of movement, collector lens (L2), grating and prism (grism; P), and a silicon charge coupled device imaging detector (CCD) with a camera lens (L3). When mounting the HI a stereomicroscope, the imager is stationary, so a moving table is used to

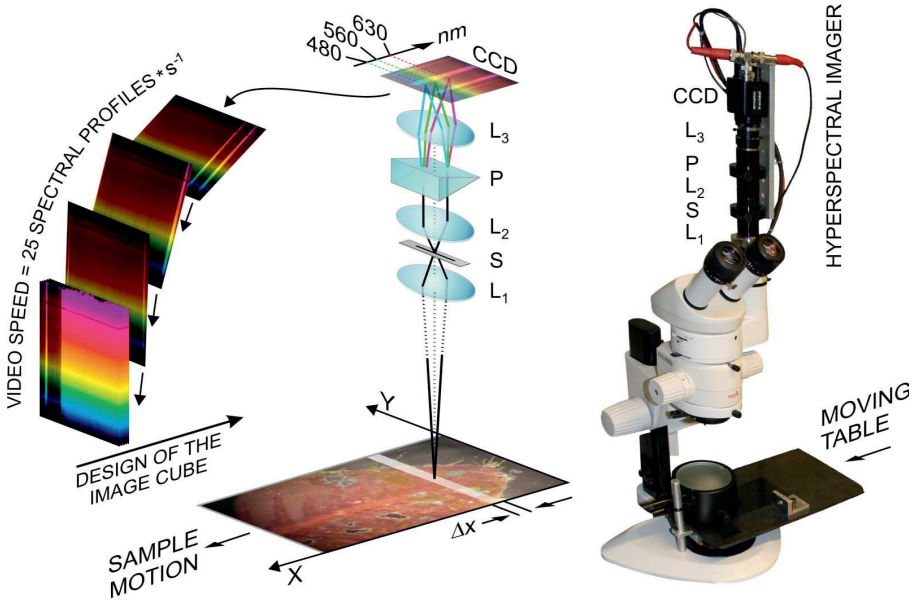


Fig 5. Principle of hyperspectral imaging: Left image illustrates the capturing and stacking of the hyperspectral profiles into a spectral image cube. The configuration of the hyperspectral imager in the middle shows L1 = front lens, S = entrance slit, L2 = collector lens, P = grism, and L3 = camera lens and CCD (imaging detector). Δx is the spatial resolution in the moving direction dependent of the entrance slit width. Right image shows the configuration of the moving table, stereomicroscope, and the hyperspectral imager. Figure from Volent et al. (2009), with permission.

move the OOI past the imager. After assembling the spectral image cube, monochromatic images of the OOI can be created, or reflectance spectra from the areas of interest can be extracted (Volent et al. 2007, 2009). As reflectance is the inverse of absorption, the spectral reflectance of the OOI also gives information about its spectral absorption characteristics. Looking at the bodies of crustaceans or other organisms, this information is useful regarding e.g. camouflage. In this work, the eyes of different amphipods and copepods were characterised *in vivo* using the HI, and the relative spectral reflectance ($R(\lambda)$), and thus the potential absorption, was related to the ambient light climate in the habitats of the different taxa.

Experimental setup for light responses of *Calanus* spp.

Hyperspectral imaging gives indications on the spectral sensitivity of the species. However, to assess the irradiance that elicits a signal reaching the brain (the light actually available for the individuals) as well as the sensory processing, behavioural experiments are needed. With behavioural experiments the absolute irradiance thresholds for response can also be investigated, which is of interest for low-light environments. An experimental setup

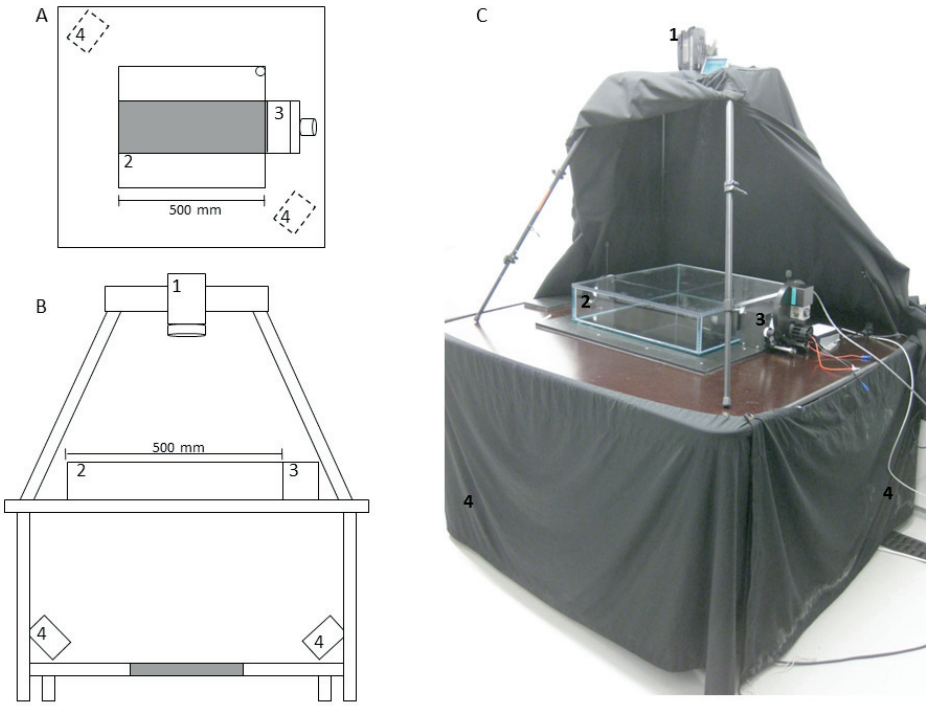


Fig. 6. A schematic overview of the experimental setup used to detect phototactic behaviour in *Calanus finmarchicus* from above (A) and the side (B) and a photograph of the experimental setup from the side (C). The experimental setup consisted of a camera (1), an aquarium (2) with a projection area in the middle (shaded area; partitioned by internal walls) fitted to the width of the light stimulus (3). The light stimulus unit consisted of a computer controlled filter wheel and a LED. On the table legs two near-infrared lamps (4) were attached with adjustable brackets. Figure from Paper IV.

was developed to investigate the behavioural response of *Calanus* spp. to irradiance (Fig. 6). The individuals were kept in an aquarium, illuminated by near-infrared light (which did not elicit any response in the copepods), and the movements of the copepods were recorded with a video camera. The light stimulus unit consisted of a LED (light-emitting diode) and a filter wheel with neutral density filters to adjust the irradiance (Papers IV and V). Experiments were firstly performed with *C. finmarchicus* from a lab culture originating from individuals caught in Trondheimsfjorden (SINTEF/NTNU Centre of Fisheries and Aquaculture, Trondheim, Norway; Hansen et al. 2007). The phototactic responses of copepodite stage V (CV) as well as adult males and females (copepodite stage CVI; CVIm and CVIf) were investigated using a white LED. The threshold irradiance eliciting a response was then related to the depth of corresponding irradiance in Trondheimsfjorden as well as in open ocean (station in the Norwegian Sea) during a time of spring bloom.

Secondly, we investigated the light responses of *Calanus* spp. (*C. finmarchicus* and *C. glacialis*; using the available developmental stages) sampled during the polar night. Due to transporting the equipment to Svalbard, the experimental setup was modified, using a smaller aquarium and a fitted table, as well as a different set of N-IR lamps (Paper V). Initially, we investigated potential diel variations in the phototactic response by comparing experiments run during daytime and during night-time. Then, we focused on the spectral sensitivity of *Calanus* spp. Experiments were performed with stages CIV and CV as well as CVIm and CVIf, using different wavebands of visible light (white, blue, green, aurora green, and red). We investigated the threshold irradiance levels eliciting a significant phototactic response to the different wavebands. The results from the behavioural experiments were then related to the available irradiance in the polar night.

Results and discussion

Bioluminescence in the pelagic ecosystem during the polar night (Papers I and II)

Using a REMUS-100 AUV equipped with a BP, the bioluminescence potential and acoustic backscatter (from the ADCP) at 15, 45, and 75 m were sampled during day and night in January 2010. Bioluminescence was detected throughout the water column, and the amount of bioluminescence (photons L^{-1}) was higher at depth during daytime and in surface (<45 m) during night-time (Fig. 1d in Paper I). The mean bioluminescence intensity per flash (photons $flash^{-1}$) at the different depths was also different from day to night, the highest intensity found at 75 m during day and at 15 m during night (Table 1). This indicates that the largest organisms, having the most intense flashes (Moline et al. 2009), migrated to surface waters during night and stayed deeper during day. Variability in bioluminescence from day to night may, however, be a result of circadian rhythms in the bioluminescence activity instead of diel migrations (Batchelder et al. 1992). We therefore investigated bioluminescence over 18 hours in a shallow bay (max depth 5 m), where migrations would be restricted, and found no significant diel variations (Fig. 2 in Paper I).

The estimates of relative backscatter (10-m swath around the AUV) showed the same pattern as the bioluminescence data at the different depths. The differences in S_v (relative backscatter coefficient) are shown in Table 1, the backscatter being significantly stronger at 40-50 m and 10-20 m during night.

For the daytime deployments, cylindrical plankton nets attached to the BP exhaust captured all organisms passing through the BP at each of the depths. Enumerations showed highest concentrations of organisms at 45 m, the main taxa being copepod nauplii and eggs, as well as tintinnid ciliates (Table 3 in Paper I). Other main contributors were the dinoflagellates *Ceratium* spp. and *Protoperidinium* spp., as well as the copepods *Microcalanus* spp., *Pseudocalanus* spp, and *Oithona* spp. The taxa contributing to the measured bioluminescence were dinoflagellates, mainly *Protoperidinium* spp., copepod nauplii (e.g. *Metridia longa* nauplii; Lapota et al. 1988), the copepod *Oncaea borealis*, appendicularians, and possibly krill. The highest concentration of known bioluminescent taxa was at 45 m (slightly higher than at 75 m), which was not consistent with the BP data with highest bioluminescence intensity at 75 m. However, copepod nauplii probably consist of both luminescent (*Metridia* spp.) and

Table 1. Mean bioluminescence intensity (photons) per flash (± SE) surveyed by the AUV at the three different depths during the daytime and night-time deployments (LT is local time). Table from Paper I.

Depth (m)	Mean intensity/flash ($\times 10^8$) daytime (10:30-14:25 LT)	Mean intensity/flash ($\times 10^8$) night-time (21:30-22:30 LT)	Mean S_v difference (day-night)
15	9 ± 2 [a]	160 ± 142 [b]	- 16
45	7 ± 2	8 ± 3	- 35
75	18 ± 6 [ac]	4 ± 1 [bc]	17

Significant differences were found between depths using Mann–Whitney ([a] $P = 0.016$, n = 1,030; [b] $P = 0.025$, n = 286; [c] $P = 0.022$, n = 126), and additionally, the differences in the mean acoustic backscatter coefficient (S_v) between day and night are shown for each depth. The differences in S_v between day and night were significant (Mann–Whitney, $P < 0.001$) at all depths.

non-luminescent (e.g. *Calanus* spp.) taxa, and the distribution of these with depth is not known. The highest concentration of bioluminescent nauplii may have been at 75 m, which would explain the observed bioluminescence pattern.

The plankton community sampled at the same depth intervals as the AUV, using a WP2 plankton net, showed the same pattern as the bioluminescence and acoustic backscatter data. There was increased abundance above 60 m of the majority of the most abundant taxa during night, e.g., *Calanus* spp., *Microcalanus* spp., *Pseudocalanus* spp, *Oithona atlantica*, *O. similis*, and *Thysanoessa* spp. (Table 2). Based on bioluminescence, acoustic backscatter, and plankton net haul data, we concluded that the diel variation in plankton distribution probably was due to DVM performed by the larger zooplankton.

Paper II re-investigated this data set, looking at the bioluminescence flash kinetics as a means of delineating the distribution of the planktonic community. The flash kinetics parameters used were the maximum flash intensity, the mean bioluminescence intensity, the time to

Table 2. Concentrations of the plankton captured by the 180 μm WP2 plankton net during the day and at night for depth intervals 30–0, 60–30 and 90–60 m (data missing for 90–60 m at night). Asterisks indicate organisms known to be bioluminescent. Table from Paper I.

Taxa	Depth (m)	ind./m^3 (day)	ind./m^3 (night)	Taxa	Depth (m)	ind./m^3 (day)	ind./m^3 (night)
Calanus finmarchicus	0−30	50	82	*Heterorhabdus norvegicus**	0–30	<1	<1
	30–60	41	148		30−60	<1	6
	60–90	89	–		60–90	4	–
Calanus glacialis	0–30	4	10	*Harpacticus chelifer*	0–30	9	50
	30–60	31	31		30–60	54	30
	60–90	147	–		60–90	<1	–
Calanus hyperboreus	0–30	<1	1	Harpacticoida spp.	0–30	2	<1
	30–60	<1	<1		30–60	11	<1
	60–90	4	–		60–90	<1	
Pseudocalanus spp.	0–30	3,100	10,300	*Oithona atlantica*	0–30	388	725
	30–60	<1	16,820		30–60	<1	555
	60–90	775	–		60–90	<1	–
Microcalanus spp.	0–30	563	2,300	*Oithona similis*	0–30	400	825
	30–60	163	1,900		30–60	<1	1,335
	60–90	63	–		60–90	131	–
*Metridia lucens**	0–30	3	17	Appendicularia*	0–30	17	15
	30–60	4	18		30–60	3	3
	60–90	6	–		60–90	96	–
*Metridia longa**	0–30	<1	<1	*Limacina helicina*	0–30	2	<1
	30–60	<1	3		30–60	<1	1
	60–90	11	–		60–90	12	–
Acartia longiremis	0–30	175	375	*Sagitta elegans*	0–30	<1	2
	30–60	<1	385		30–60	5	11
	60–90	<1	–		60–90	12	–
Paraeuchaeta norvegica	0–30	<1	<1	*Eukrohnia hamata*	0–30	4	30
	30–60	1	<1		30–60	2	21
	60–90	<1	–		60–90	11	–
*Diastylis lucifera**	0–30	<1	<1	*Thysanoessa longicaudata**	0–30	<1	2
	30–60	1	<1		30–60	3	7
	60–90	<1	–		60–90	2	–
Bradyidius similis	0–30	<1	1	*Thysanoessa inermis**	0–30	<1	<1
	30–60	<1	3		30–60	<1	22
	60–90	6	–		60–90	<1	–
*Oncaea borealis**	0–30	12	<1				
	30–60	51	200				
	60–90	<1	–				

Table 3. Centroid vectors of the four parameters used to assign observations into 3 groupings using K-means cluster analysis, including maximum bioluminescence (BL_{max}, photons s^{-1}), mean bioluminescence (BL_{mean}, photons s^{-1}), time to reach maximum bioluminescence (T_{max}, sec.) and the sum of bioluminescence until the maximum is reached (Σ_{max}, photons). Two values are presented under each depth and time of day. The first (left) is the percent of flashes per liter (%F L^{-1}) contributed by each grouping (G1, G2, and G3) at each depth for either daytime (DT) or nighttime (NT). The second number is the percent of flashes per liter (%F L^{-1}) contributed by each group at all three depths for each time of day. The bold numbers for G3 illustrate the differences in the depth distribution of that group for DT versus NT, with higher percentages at 75 m during DT and 15 m at NT. Finally, the number of individual flashes observed for each group is also shown. Table from Paper II.

Cluster	Flash Parameters				%F L^{-1} 15m		%F L^{-1} 45m		%F L^{-1} 75m		
Grouping	BL_{max}	Bl_{mean}	T_{max}	Σ_{max}	DT	NT	DT	NT	DT	NT	# of obs
G1	3,24E+08	1,59E+09	0,051	8,39E+09	67|25	63|23	71|37	64|27	63|38	73|48	1308
G2	6,89E+09	2,84E+09	0,217	4,69E+10	29|25	29|29	26|32	33|34	30|43	23|37	546
G3	1,62E+11	4,70E+10	0,163	1,00E+12	4|**17**	8|**46**	3|22	3|19	7|**61**	4|**35**	79

reach maximum intensity, and the cumulative sum of bioluminescence until the flash reached its maximum intensity (see Table 3). As different taxa display different flash characteristics, the bioluminescent part of the planktonic communities may be characterised on the basis of the parameters (Moline et al. 2009). When using an AUV, this may be done relatively efficiently, covering large areas and revealing horizontal as well as vertical distribution patterns. The bioluminescence observations were analysed and assigned to 3 groups: one dinoflagellate group (G1), and two zooplankton groups (small and large zooplankton; G2 and G3; Table 3). Investigating the vertical distribution of the three groups, there was a homogeneous distribution of dinoflagellates, and a heterogeneous distribution of the two zooplankton groups. The proportions of group G3 was higher at 75 m during day and at 15 m during night.

Bioluminescence has to our knowledge not earlier been documented in these latitudes and time of year. As the amount of downwelling light is very limited, bioluminescence may be a significant part of the total light budget of the ecosystem. In this study, the diel variation in bioluminescence also provided circumstantial evidence for DVM.

Berge et al. (2009) found, using acoustic backscatter, evidence for DVM in the Arctic during the polar night, and the same has been documented in the Antarctic (Cisewski et al. 2010). The results from Papers I and II support that DVM occurs in the planktonic community, and suggest that mainly larger zooplankton, e.g. *Calanus* spp., account for the migrations. These findings raise questions about the possibility of DVM being governed by downwelling irradiance, even though the irradiance amplitude through day and night is too small for the human eye to detect. The ability to detect irradiance at depth would depend on a high sensitivity to low-intensity irradiance, as well as a spectral sensitivity adapted to the waveband of the ambient light.

The spectral sensitivities of crustaceans, investigated by hyperspectral imaging (Paper III)

Organisms tend to have spectral sensitivities matched to the light climate of their habitats, which is important as it enables optimising of different behaviour, like feeding and predator avoidance. Using a HI, we measured the relative reflectance

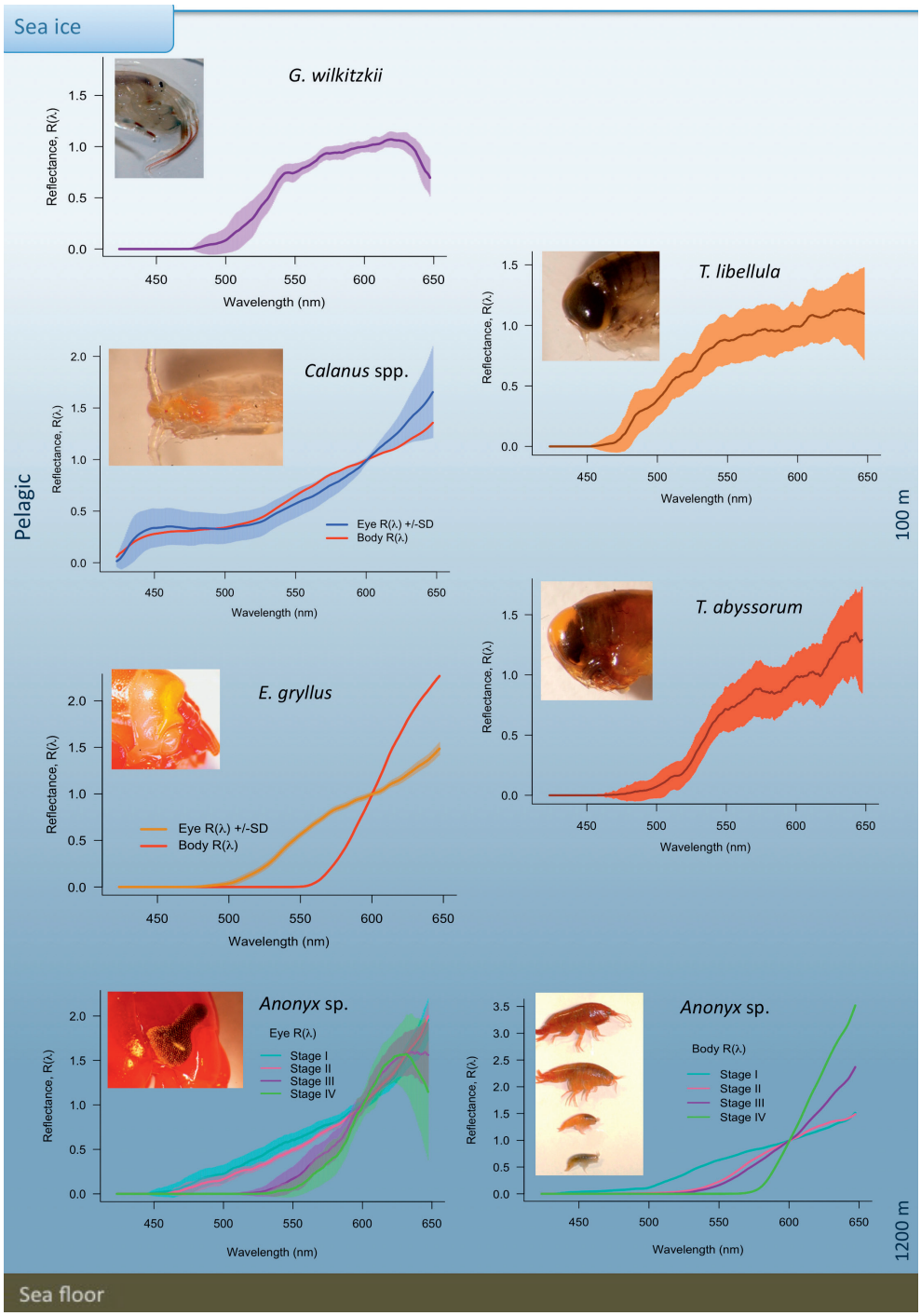


Fig 7. Reflectance (R(λ)) spectra (±SD) (normalised to 600 nm), derived by hyperspectral imaging, from the eyes of copepods and amphipods, related to habitat. For *Calanus* spp. and *E. gryllus*, body R(λ) is also shown. For *Anonyx* sp., body R(λ) spectra are shown in a separate figure. Data from Paper III.

of the eyes of the sympagic (sea ice-associated) amphipod *Gammarus wilkitzkii*, the pelagic amphipods *Themisto libellula* and *T. abyssorum*, the pelagic copepods *Calanus*

spp., and the hyperbenthic amphipods *Eurythenes gryllus* and *Anonyx* sp. As reflectance is the inverse of absorption, we assumed that the reflectance spectra gave indications on the absorption characteristics of the eye, and thus the spectral sensitivity of each taxon.

The spectral properties of the eye of the different species matched well with their different habitats. *G. wilkitzkii* eyes reflected increasingly from green to red wavebands, indicating major absorption in blue and some in the green waveband (Fig. 7), being adapted to the under-ice habitat. *G. wilkitzkii* are assumed to feed using mechanosensory methods, thus not using vision for foraging (e.g. Werner 1997; Lønne and Gulliksen 1991), but vision may have other functions, like detecting predators in the surrounding environment and thus omitting them.

Calanus spp. reflected increasingly from green towards red, probably absorbing in blue and green. *Calanus* spp. is very abundant in both open ocean and coastal areas, where the light field is predominantly blue and green, respectively. For *Calanus* spp. it is important to have a well-matched spectral sensitivity, as well as a generally high sensitivity to irradiance, to be able to perform DVM to depths where they become unavailable to visual predators. *Themisto* spp. are examples of visual predators that hunt *Calanus* spp. and other pelagic organisms (Scott et al. 1999; Auel et al. 2002; Dalpadado et al. 2008; Kraft et al. 2013), and thus need the same type of sensitivity. *T. libellula* eyes had lowest reflectance in the blue wavebands, and slightly increasing reflectance from green towards red (Fig. 7), thus probably absorbing over a wide waveband. This is consistent with its distribution in the upper water layers (Dalpadado et al. 2001; Dalpadado 2002), where wider wavebands of irradiance are available. The eye reflectance of the deeper-dwelling *T. abyssorum* increased steeply from 500 nm, indicating absorption mainly in blue. It thus seemed to be more blue-sensitive than *T. libellula*, which is consistent with adaptations to the blue light field in deeper water. The spectral sensitivity of pelagic species may be part of the explanation of the ability to remain active, feed, and perform DVM during the Arctic polar night (Berge et al. 2009; Kraft et al. 2013; Papers I, II and V).

The hyperbenthic amphipod *E. gryllus* had eye reflectance resembling that of *T. abyssorum*, probably absorbing mainly in blue wavebands (Fig. 7). *Anonyx* sp. eye reflectance (older stages) was more red-shifted, probably additionally absorbing some in green. The eye of *E. gryllus* has structural adaptations to enhance the light-gathering abilities (Hallberg et al. 1980), and the same might be suggested for *Anonyx* sp. due to the similarities in ecology as well as the relatedness to *E. gryllus*. This study thus supports that *E. gryllus*, and probably also *Anonyx* sp. (the species in this study has not yet been described; Thoen et al. 2010), are adapted to the deep-sea light climate, where there is very little or no downwelling irradiance, the main light source being bioluminescence.

We concluded that the eyes of the organisms investigated had spectral characteristics that matched their habitat, the deep-living species absorbing primarily in the blue waveband, while shallower-living additionally absorbed in green. Hyperspectral imaging was judged to be a relatively simple method for retrieving information about the spectral properties of different organisms (Johnsen et al. 2012), as it is suitable for use in the field, and by mounting the HI on a stereomicroscope, even small organisms can be investigated. Hyperspectral imaging may thus be a good, non-invasive method for investigating the spectral properties of living marine organisms compared to the traditional, more time-consuming and complicated methods like behavioural studies and electrophysiology.

Phototactic behaviour of *Calanus finmarchicus* (Paper IV)

The DVM behaviour of *Calanus* spp. is well documented (e.g. Dale and Kaartvedt 2000; Fortier et al. 2001; Cottier et al. 2006; Rabindranath et al. 2011), and light is considered to be the main proximate cue for the migrations (e.g. Cohen and Forward 2009). However, the phototactic behaviour of *Calanus* spp. has not previously been examined with respect to finding the irradiance threshold needed to elicit a phototactic response, and regarding spectral sensitivity, the only information

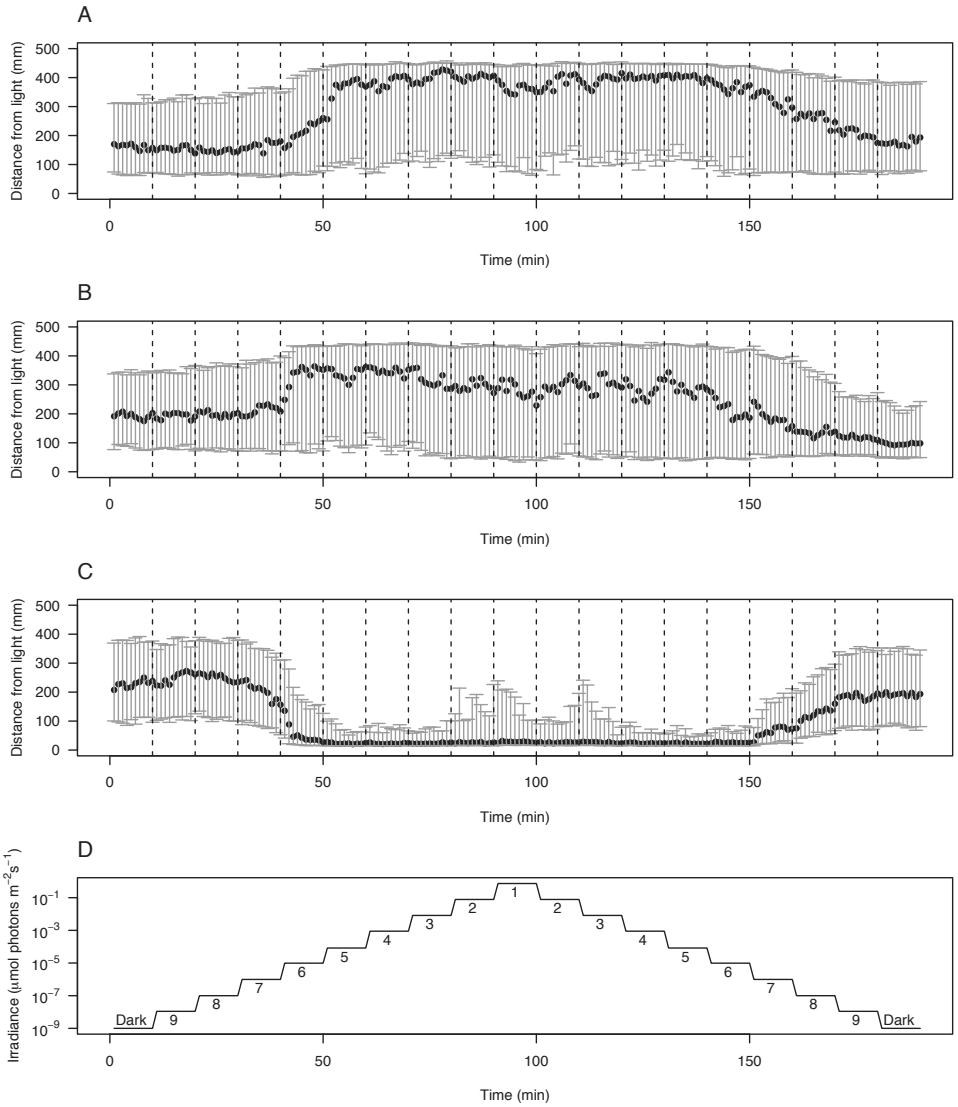


Fig 8. Median distance (± interquartile range) to light source for A) copepodite stage V (CV) B) adult females (CVIf) and C) adult males (CVIm) exposed to increasing and decreasing irradiance of white light. Dashed lines indicate change in irradiance. The total length of the projection area was 500 mm. D) A schematic view of the stepwise changes in irradiance related to OD level. Figure from Paper IV.

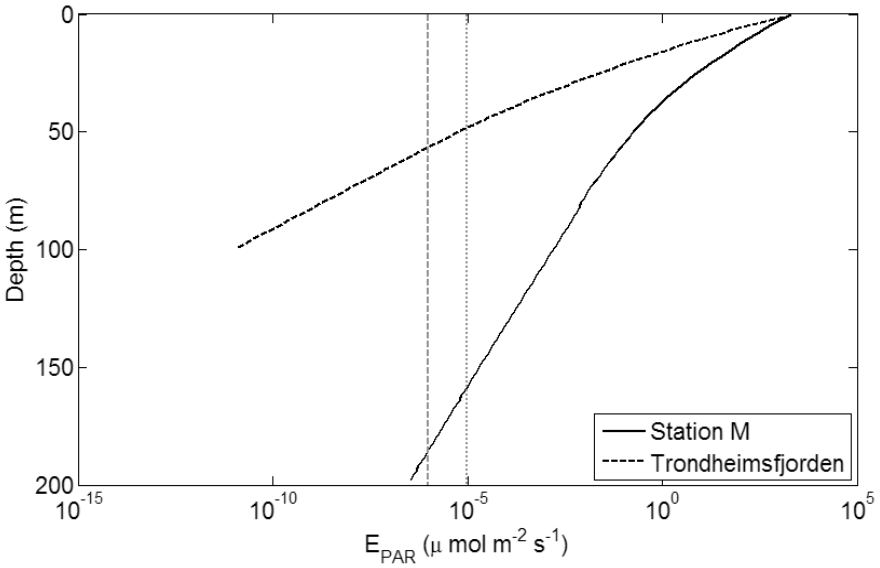


Fig 9. Estimated irradiance (E_{PAR}) plotted against depth for an ocean scenario (Station M, solid line) and a fjord scenario (Trondheimsfjorden, Norway, dashed line) at noon during the spring bloom. Vertical lines indicate the irradiance thresholds for phototactic response of *C. finmarchicus* (0.99×10^{-6} and 9.8×10^{-6} μmol photons m^{-2} s^{-1}). Figure from Paper IV.

available is from studies on other copepod species (Stearns and Forward 1984; Cohen and Forward 2002) as well as the hyperspectral imaging of *Calanus* spp. eyes (Paper III). An experimental setup (Fig. 6) was developed for investigating the phototactic behaviour of *Calanus* spp., and laboratory cultured *C. finmarchicus* were used for the experiments (Paper IV). The experimental setup was designed in the horizontal plane in order to separate the active, directional phototactic responses from the effects of gravitation as well as buoyancy. As details of the spectral sensitivity of the species were unknown, a white LED was used as light stimulus. Experiments were performed with stage CV as well as CVIf and CVIm. The copepods were exposed to stepwise increases as well as decreases in irradiance, spanning from levels so low that there were no phototactic response, to levels beyond where clear responses had occurred.

Stages CV and CVIf displayed negative phototaxis, moving away from the light stimulus when irradiance increased (Fig. 8A,B). Negative phototaxis was expected because the older developmental stages of *C. finmarchicus* (particularly CV and CVIf) perform nocturnal DVM, which involves moving away from the increasing irradiance at sunrise. CVIm, however, displayed positive phototaxis, and the response was strong and uniform (Fig. 8C). CVIm spend most of their time on mate-finding, and have been suggested to migrate upwards to a specific layer of water to search for mates (Hayward 1981; Tsuda and Miller 1998), which may account for the positive phototaxis. When irradiance decreased, there was no clear response at any irradiance level, and the individuals seemed to disperse randomly rather than actively swimming towards the light stimulus. Due to the horizontal orientation of the setup, the specimens were unable to actively swim upward, and the lack of clear response with decreasing irradiance may indicate that during DVM, some gravitational effect is involved in the ascent towards surface waters at sunset.

The lowest irradiance eliciting a significant phototactic behaviour was 9.8×10^{-6} µmol photons m^{-2} s^{-1} for CV and CVIf, and 0.99×10^{-6} µmol photons m^{-2} s^{-1} for CVIm. This is within the range of irradiance thresholds found for other copepod species, e.g. *Calanopia americana* (blue-green irradiance at approximately 0.2×10^{-6} µmol photons m^{-2} s^{-1}; Cohen and Forward 2005) and *Acartia tonsa* (approximately 0.5×10^{-6} µmol photons m^{-2} s^{-1}; Stearns and Forward 1984). Regarding predator evasion, copepods would be expected to migrate deeper than their visual predators can feed (Ringelberg 1995). Herring and larval cod are known to feed on *C. finmarchicus*, and both were able to feed at irradiance levels down to approximately 2×10^{-5} µmol photons m^{-2} s^{-1} (Batty et al. 1990; Vollset et al. 2011). This is around one order of magnitude higher than the threshold irradiances for response in *C. finmarchicus*, which supports that *C. finmarchicus* use vision to enable a descent to depths where they are unavailable to visual predators.

Simulations of irradiance changes with depth were conducted using input parameters from a spring phytoplankton bloom scenario, which is the time of year with the highest attenuation of light, for an ocean scenario (Norwegian Sea) and a fjord (Trondheimsfjorden) scenario. The threshold irradiances for phototactic response correspond to approximate depths of 158-186 m in the ocean scenario and 48-57 m in the fjord scenario (Fig. 9). The results correspond well to observed migration depths for *C. finmarchicus* (e.g. Tande 1988; Unstad and Tande 1991; Dale and Kaartvedt 2000).

The results support that *Calanus* spp. are highly sensitive to irradiance and that irradiance governs the DVM behaviour. As the modelling of light with depth was performed using a spring bloom scenario, the depths should be regarded as minimum depths for detection of irradiance, and these copepods may probably respond to irradiance far deeper in the water column when the optical properties of the water are different. During winter in the Arctic, for instance, the content of cDOM, Chl*a*, and inorganic particles is low, creating a low $K(\lambda)$ particularly in the blue waveband (Sakshaug et al. 2009). Thus, the water transparency is high, and light may penetrate deep into the water column. The limitations in this area during winter, however, are the extent of sea-ice as well as the limited irradiance from natural light sources.

Phototactic behaviour and spectral sensitivity of *Calanus* spp. during the polar night (Paper V)

After investigating the light responses of lab cultured *C. finmarchicus*, we took the experimental setup further, looking at the responses of high Arctic, polar night-acclimated *Calanus* spp. The *Calanus* spp. were negatively phototactic, moving away from the light stimulus as the irradiance increased (Fig. 10). When investigating the phototactic response over 24 hours, we did not detect significant changes in response during daytime compared to night-time (Table 3 in Paper V). For the threshold level experiments, using five different wavebands of visible light, there were significant results for at least one waveband for each stage (Table 4). The number of replicates was low, and variability between replicates may account for the lack of significant threshold levels in some experiments as well as variable results in some wavebands. In general, the copepods responded to very low irradiance levels in blue, green, and white wavebands, the lowest irradiance eliciting a significant response ranging from 0.34 to 42×10^{-6} µmol photons m^{-2} s^{-1} for CV, CVIf, and CVIm (Table 4). The lowest irradiance threshold was found in experiments with CVIf, using green irradiance (emission peak 525 nm). For the red waveband, the threshold was about three orders of magnitude higher ($310\text{-}1800\times10^{-6}$ µmol photons m^{-2} s^{-1}). These results support the

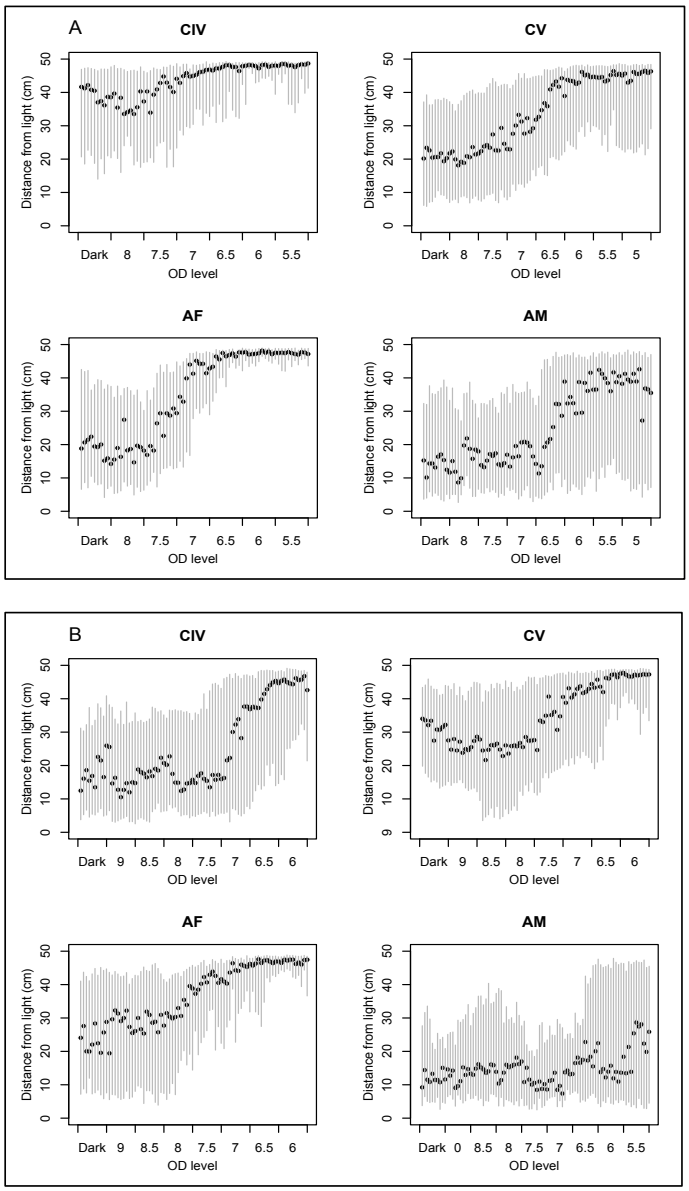
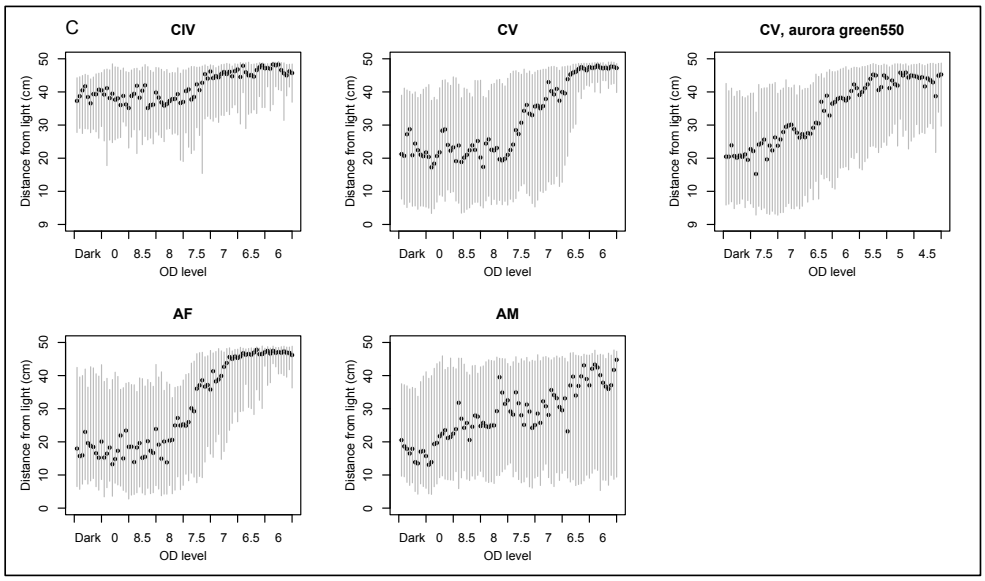


Fig 10. Median distance from light (cm; each black dot representing one minute) with interquartile range (grey bars) over the duration of each experiment (2-3 replicates per experiment, see Table 2 in Paper V) for A) white, B) blue, C) green525 and aurora green550 (the latter only for stage CV), and D) red wavebands. Developmental stage/sex is indicated above each panel. Each irradiance level lasted 10 minutes. Dark is the initial dark period; subsequent OD levels are indicated (see Table 1 in Paper V for the irradiance range used in each experiment). Figure from Paper V.



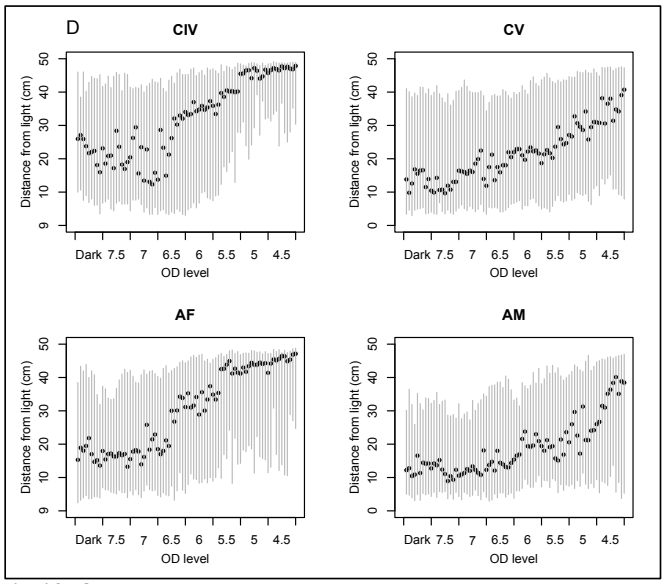


Fig 10. Cont.

investigations of spectral reflectance of *Calanus* spp. eyes (Paper III), where the results suggested that the eye absorbed mainly in blue and green wavebands (Fig. 7). *Calanus* spp. was thus confirmed to be adapted to the light climate of coastal and oceanic areas, where green and blue penetrate deepest. The sensitivity to absolute irradiance was in the range of that of lab cultured *C. finmarchicus* (Paper IV) as well as other copepod species (Stearns and Forward 1984; Cohen and Forward 2005).

The next step was to investigate the ecological relevance of our findings. We used approximate surface irradiance values for the different light sources during the

polar night (derived from literature; see Paper V), and compared these to the threshold levels for response of *Calanus* spp. (Table 4). Where a threshold level for phototaxis could be detected for blue and green wavebands, the threshold irradiance corresponded to <0.86% of surface moonlight and 1-43% of surface night sky irradiance. The threshold level for phototaxis for green and aurora green corresponded to <2.1% of surface aurora borealis irradiance.

Using a relevant extinction coefficient (Hovland et al. 2012), and assuming ice-free conditions, we estimated the irradiance changes with depth for the different light sources. Applying the lowest irradiance threshold for response, *Calanus* spp. may respond to irradiance from the night sky down to 40-50 m, moonlight to 100-140 m, and aurora borealis down to 60-100 m depth (Fig. 11). Our estimated depth range of night sky irradiance detection corresponds well to Berge et al. (2009) who reported that DVM occurred at a depth range of 30-60 m during the darkest time of the polar night (mid December to early January). As the solar elevation angle increases after winter solstice, the solar background irradiance during midday will increase, as will the depth for irradiance detection. This is reflected in the data of Berge et al. (2009), where the depth of DVM increased to around 70 m in late January and beyond 90 m in February, as well as in Papers I

Table 4. Modelling summary (ANOVA; + or -) and irradiance threshold value (where significant; μmol photons m^{-2} s^{-1}) is given for all developmental stages and wavebands, as well as the fraction (%) of surface irradiance for each light source for the specific threshold value. Table from Paper V.

		White	Blue	Green525	Aurora green550	Red
CIV	**Model**	**+**	**-**	**-**		**-**
	Threshold	**-**				
	Moon					
	Night sky					
	Aurora borealis					
CV	**Model**	**+**	**+**	**+**	**+**	**+**
	Threshold	**4.7×10^{-6}**	**4.3×10^{-6}**	**2.1×10^{-6}**	**0.43×10^{-6}**	**1800×10^{-6}**
	Moon	0.052-0.94 %	0.048-0.86 %	0.023-0.42 %	0.0048-0.086 %	>20 %
	Night sky	15-47 %	14-43 %	7-21 %	1.4-4.3 %	>100 %
	Aurora borealis	0.12-4.7 %	0.11-4.3 %	0.053-2.1 %	0.011-0.43 %	>45 %
CVIf	**Model**	**+**	**-**	**+**		**+**
	Threshold	**0.47×10^{-6}**		**0.34×10^{-6}**		**1800×10^{-6}**
	Moon	0.0052-0.094 %		0.0038-0.068 %		>20 %
	Night sky	1.6-4.7 %		1.1-3.4 %		>100 %
	Aurora borealis	0.012-0.47 %		0.0085-0.34 %		>45 %
CVIm	**Model**	**+**	**+**	**-**		**+**
	Threshold	**42×10^{-6}**	**4.3×10^{-6}**			**310×10^{-6}**
	Moon	0.46-8.4 %	0.048-0.86 %			3.4-62 %
	Night sky	>100 %	14-43 %			>100 %
	Aurora borealis	1.0-42 %	0.11-4.3 %			>7.8 %

and II, where a DVM signal down to about 80 m was detected in late January. The irradiance from aurora and moonlight has higher intensity and will probably be detected deeper into the water column than night sky/solar background during mid-winter (Fig. 11). This is supported by the study of Berge et al. (2009), who reported a shift in DVM signal from a 24 hour cycle toward a 25 hour lunar cycle during the 3 days prior to and after full moon. Zooplankton performing reverse DVM during full moon, the moon rising during night and setting during day, has also been described in Svalbard in January (Webster et al. ssubmitted). The DVM signal has to our knowledge not been investigated in relation to the aurora borealis, but the intensity of auroras is probably high enough for affecting DVM (Fig. 11). The aurora available to the marine organisms will vary according to the intensity of the aurora as well as its frequency of occurrence. The latter was reported to be about 65 % on average for Longyearbyen, Svalbard (from 2000 through 2012; Pulkkinen et al. 2011 with additional data at http://www.space.fmi.fi/MIRACLE/ASC/AuroralOccurrence.html). Another factor important for the irradiance in the ocean is the frequency of nights with clear or partially clear skies. This has been reported to be 68 % for Longyearbyen (1986-1995; Simmons et al. 1996). Combining the information about frequency of occurrence for aurora as well as clear nights, it seems likely that aurora may, at least in periods, affect the zooplankton during the polar night.

Calanus spp. light perception thus seems to be highly adapted to life in the pelagic realm, and to the low-light environment during twilight or polar night, regarding absolute as well as spectral sensitivity. According to our findings, irradiance may be the cue for the observed DVM during polar night, and may affect the marine ecosystem during the darkest part of the year.

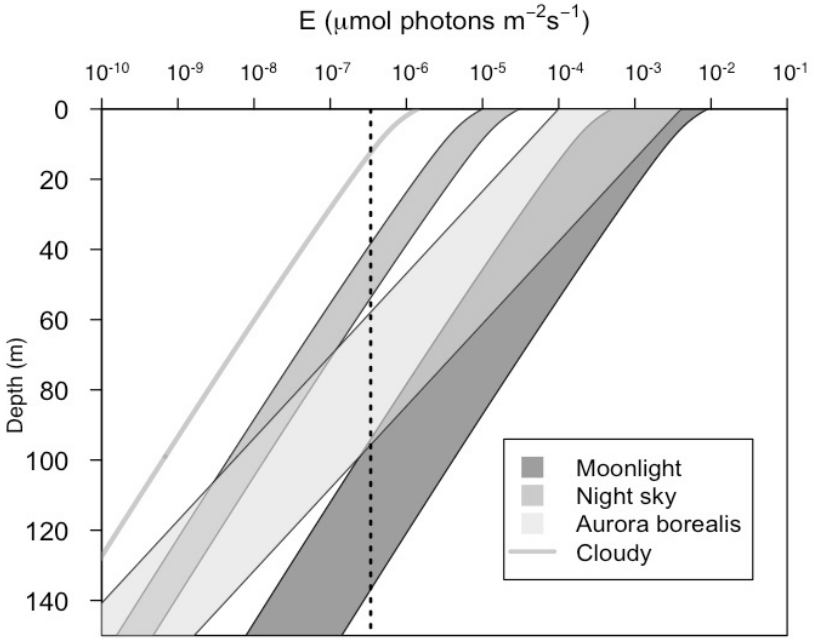


Fig 11. Irradiance in the polar night from the moon, night sky, and aurora borealis with depth. The vertical dotted line (0.34×10^{-6} μmol photons m^{-2} s^{-1}) represents the lowest E value for phototactic response in *Calanus* spp. Figure from Paper V.

Conclusions

Bioluminescence was documented for the first time during the high Arctic polar night in January 2010 using an Autonomous Underwater Vehicle equipped with a bathyphotometer (bioluminescence detector). The taxa contributing to the detected bioluminescence were dominated by dinoflagellates (mainly *Protoperidinium* spp.), copepod nauplii (probably *Metridia* spp.), the copepod *Oncaea borealis*, appendicularians, and krill. Diel changes in bioluminescence over depth were documented, a larger proportion of the more intense flashes occurring in surface during night and at depth during day. These changes were interpreted as indications of diel vertical migration (DVM) due to that no diel changes in the bioluminescence potential (photons L^{-1}) itself were documented. Investigations using acoustic backscatter as well as plankton net hauls supported that the larger zooplankton, like *Calanus* spp., performed DVM in the upper 80 m in Kongsfjorden during polar night.

Using a hyperspectral imager, the *in vivo* spectral properties of the eyes of different crustacean species were found to match the light climate of their habitats. Sympagic and shallow-living pelagic species probably absorbed in blue and some in green wavebands, while deeper-living pelagic and hyperbenthic species absorbed mainly in the blue waveband. The sensitivity to ambient wavelengths may be part of the explanation to how organisms can stay active during the polar night, when ambient irradiance is very limited. Hyperspectral imaging was suggested to be a relatively fast and easy way of gaining information on the spectral properties of crustacean eyes, and a method well suited for use in the field as well as for investigating small species.

Investigating the phototactic behaviour of laboratory cultured *C. finmarchicus* in an experimental setup, the lowest irradiance levels eliciting a phototactic response were in the range of $1\text{-}10\times10^{-6}$ μmol photons m^{-2} s^{-1}. Stages CV and CVIf displayed negative phototaxis, while CVIm displayed positive phototaxis, which probably reflected the different ecological requirements of the different stages and sexes. Using parameters from spring phytoplankton bloom conditions, the irradiance threshold levels were estimated to correspond to 48-57 m depth in a fjord (Trondheimsfjorden) and 158-186 m in open ocean (Norwegian Sea), which matched reported depth ranges for natural *C. finmarchicus* populations.

When investigating the phototactic behaviour of *Calanus* spp. sampled during the polar night, all stages and sexes displayed negative phototaxis. This matches with the nocturnal DVM observed in *Calanus* spp. The sensitivity was highest towards blue and green wavebands, and the lowest irradiance levels eliciting a phototactic response in these wavebands were in the range of $0.3\text{-}4\times10^{-6}$ μmol photons m^{-2} s^{-1}. For the red waveband, the corresponding levels were about three orders of magnitude higher, suggesting that the *Calanus* spp. are adapted to the blue and green light climate of oceans and coastal areas, respectively. This is consistent with the results from hyperspectral imaging of *Calanus* spp. eyes. Correlating the lowest threshold level for response with estimations of polar night irradiance with depth, it was suggested that *Calanus* spp. may respond to irradiance from the night sky down to 40-50 m, moonlight to 100-140 m, and aurora borealis down to 60-100 m depth. Thus, irradiance may be the proximate cue for the observed DVM behaviour, and it was suggested that the sun and moon as well as aurora might affect the pelagic ecosystem during the polar night.

Future perspectives

Due to the increased year-round human activity in the Arctic, such as utilisation of fossil fuels, fisheries, new transport routes, and tourism, there is a general need for further research on marine ecosystem dynamics during the polar night. Elucidating which organism groups are active, as well as the type of activity, is important information to be able to predict the consequences of incidents like oil spills, as well as the ongoing climate change. This thesis, elucidating the effect of natural light sources on DVM rhythms in zooplankton, is one of the first steps into looking at photobiology in the polar night. Light is a highly important environmental variable regulating biological activity, also during the polar night, and should be further investigated with respect to ocean heating/cooling (climate), weather, and temporal/spatial differences in light-regulating mechanisms, affecting physiology, ecology and functional genetics in all marine taxa.

Bioluminescence has now been documented for the first time during the polar night, and it would be interesting to delineate the proximate as well as ultimate reasons for this behaviour, both during the polar night and also whether it is comparable to those at other latitudes. Also concerning the DVM behaviour of *Calanus* spp. (and possibly other taxa), further research may involve the ultimate reasons for performing migrations during polar night. Pelagic predators like *Themisto* are active, so *Calanus* spp. performing predator evasion by descending to deeper waters seems apparent – but why ascend in the first place? Is there a sufficient amount of food in surface layers to gain advantages by migrating? *Calanus* spp. have been documented to undergo diapause during the winter, but the findings presented in this thesis indicate that only part of the population is in diapause and another part is active and migrating. Looking at the nutritional status of the two parts would be an interesting topic, and would probably also provide information about the ultimate reasons for DVM. Furthermore, more detailed investigations of the spectral sensitivity of *Calanus* spp. would give further insight into vision eco-physiology of copepods. This might reveal possible adaptations to different water masses or to specific light sources. Finally, the experimental setup developed for investigations of the phototactic behaviour of *Calanus* spp. has a large potential as a tool for further behavioural investigations, as it may be used for a variety of purposes as well as with many different taxa.

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Paper I

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SHORT COMMUNICATION

Bioluminescence in the high Arctic during the polar night

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Abstract This study examines the composition and activity of the planktonic community during the polar night in the high Arctic Kongsfjord, Svalbard. Our results are the first published evidence of bioluminescence among zooplankton during the Arctic polar night. The observations were collected by a bathyphotometer detecting bioluminescence, integrated into an autonomous underwater vehicle, to determine the concentration and intensity of bioluminescent flashes as a function of time of day and depth. To further understand community dynamics and composition, plankton nets were used to collect organisms passing through the bathyphotometer along with traditional vertical net tows. Additionally, using a moored bathyphotometer closed to the sampling site, the bioluminescence potential itself was shown not to have a diurnal or circadian rhythm. Rather, our results provide evidence for a diel vertical migration of bioluminescent zooplankton that does not correspond to any externally detectable changes in illumination.

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Introduction

Of the various behaviors and adaptations that have evolved in marine environments, bioluminescence stands out as one of the particular importance, given the fact that it has evolved independently more than 40 times (Haddock et al. 2010). While it does not necessarily give specific advantage to species in cold environments, the long periods of continuous darkness that characterize winters at high latitudes create an environment, at least with respect to light, that is similar to the deep-sea. Depending on which taxa are bioluminescent, a variety of adaptive advantages have been suggested. These include defensive functions such as the "counter-illumination," the "burglar alarm" and offensive mechanisms such as "prey attraction" and "intraspecific communication" (Haddock et al. 2010).

Other adaptations have evolved in both phytoplankton and zooplankton to survive in these harsh conditions that relate more to metabolic rates and the actual vertical space occupied in the water column within which a species spends the winter months. One such strategy is to enter a dormant state and overwinter at depth, seen for the copepods *Calanus glacialis* and *C. hyperboreus* which are commonly reported to enter a state of diapause at depth during winter months (Fortier et al. 2001; Falk-Petersen et al. 2008). They, then, return to shallower water in the summer to take advantage of the high productivity rates (Ashjian et al. 2003). Interestingly, Berge et al. (2009) for the first time provide acoustic evidence of active vertical migrations of zooplankton throughout the polar night in the high Arctic. More recently, this phenomenon was

corroborated in the Southern Hemisphere where diel vertical migration (DVM) was shown to continue through the Austral winter in the Lazarev Sea, but ceased during the Austral summer (Cisewski et al. 2010).

The goal of the current study was to characterize plankton abundance and distribution patterns during a time of year that has rarely been studied by means of vertical net tows and autonomous underwater vehicle (AUV) surveys. Fitted on the AUV were ADCPs, a CTD and a bathyphotometer designed to register bioluminescence potential in the water column.

Materials and methods

Data were collected off the coast of Ny Ålesund in Kongsfjord, Svalbard (78°57′ N, 11°56′ E) in ~120 m of water from January 19 to 22, 2010. Spatial and temporal dynamics of acoustic backscatter, salinity, temperature and bioluminescence were measured using a REMUS-100 AUV (Moline et al. 2005). The vehicle was equipped with upward and downward facing RD Instruments 1,200-kHz Workhorse navigator acoustic Doppler current profilers (ADCP), configured in this study to provide relative acoustic backscatter as an estimate of scattering volume, rather than current velocities, a Neil-Brown CTD and a bioluminescence bathyphotometer (BP; Moline et al. 2005). The BP utilizes an impeller to continuously draw a measured volume of water into a chamber through the front of the nosecone where bioluminescence is measured by a photomultiplier tube at 60 Hz [see Herren et al. (2005) for details]. For statistical purposes, we restricted our analysis to the non-zero observations.

The AUV was deployed at 10:27, 12:25 and at 13:40 (local time 19th of January) at depths of 15, 45 and 75 m, respectively. These missions were surveyed a transect of 1.5 km at each respective depth. The vehicle was also deployed at 21:30 (19th of January) along the same transect as during the "day" but ran one mission surveying the transect at 15, 45 and 75 m successively without breaks between each depth. ADCP data were processed to remove noise and calculate relative backscatter coefficient (S_v) according to Deines (1999) for the data collected between 0.5 and 5.0 m away from either side of the vehicle. Following the AUV deployments, continuous BP observations were made from 15:00 on January 21, 2010 until 09:00 on January 22, 2010 at 1 m depth at the Ny Ålesund harbor about 2 km from the study site. For logistical reasons (power supply, stable holdfast for the instrument and weather conditions), it was not possible to carry out the continuous BP observations in the fjord at the same place as the AUV deployments. However, given the short distance between the two locations and the absence of any physical barriers, the two sites are regarded as comparable for the examination of circadian rhythm (see also "Discussion"). Concurrent with the REMUS deployments, vertical net hauls were conducted using a WP2 plankton net, 180-μm mesh size with a 0.25 m^2 opening. In order to collect vertical net hauls from the same depths surveyed by the REMUS ADCP, two replicates from each depth were taken from 30–0 m, 60–0 m and from 90–0 m between 10:30–13:00 LT. During the nighttime AUV deployment, replicate hauls were taken between 30–0 m, but inclement weather resulted in only one sample from 60–0 m was collected and none between 90–0 m. To determine species composition and abundance for specific depth intervals of 60–30 m and 90–60 m, the results from 30–0 m were subtracted from those of 60–0 m, and results from 60–0 m from those of 90–0 m, respectively. Additionally, the REMUS BP was equipped with cylindrical plankton nets (20-μm mesh size), and these nets were fitted to each of the two exhausts of the BP (Moline et al. 2009), which hence provided two replicate samples from each of the depths (15, 45 and 75 m) sampled using the AUV. For all plankton samples, the nets were rinsed and samples collected and preserved in a 4% formaldehyde solution. Samples were later enumerated and identified to the lowest possible taxonomic unit using a Leica stereomicroscope with 6.3–40× magnification.

Results

The temperature, salinity and density profiles were similar between night and day during the sample period (Fig. 1) and did hence not reveal any major advection events that would otherwise influence the measurements and results presented below. Based upon Willis et al. (2006), physical parameters indicated that the water mass in Kongsfjord was of Artic Water origin. Bioluminescence was detected throughout the water column both night and day, with higher bioluminescence at depth during the day and increased surface bioluminscence at night (Fig. 1d). Comparison of the bioluminescence at the specific depths also provided that this result with significantly greater bioluminescence intensity per flash was observed at 75 m during the day and at 15 m at night (Table 1), suggesting that the organisms with more intense flashes, i.e., larger zooplankton (see Moline et al. 2009), had migrated toward shallower depths at night.

It is important when interpreting changes in bioluminescence signals that the circadian rhythms in the bioluminescence potential of planktonic organisms be taken into account (Batchelder et al. 1992). The continuous BP observations at the Ny Ålesund harbor showed no evidence of a circadian rhythm in the bioluminescence signal

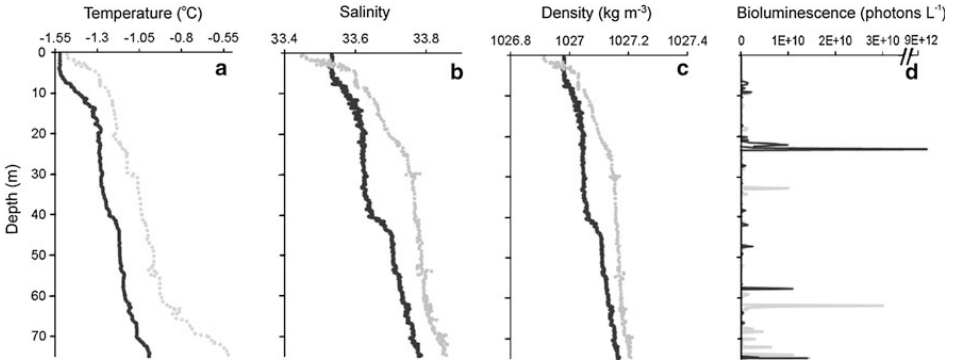

Fig. 1 Vertical profiles of **a** temperature (°C), **b** salinity (ppt), **c** density (kg m^{-3}) and **d** bioluminescence (photons/l) as a function of depth (m) taken from the REMUS AUV during the final ascents from 75 m during the day and night deployments. Daytime observations represented in *gray* and nighttime in *black*. For this profile, bioluminescence for the upper water column (<45 m) was significantly less than that for the lower water column during the day (Mann–Whitney, $P = 0.009$, $n = 102$) and higher bioluminescence in the upper water column at night

(Fig. 2) in a location (sheltered by the pier and with a max depth of 5 m) where vertical migration of zooplankton would be restricted. Organisms collected by net hauls next to the moored BP and by nets connected to the BP during this period using identical methods described above for the AUV showed >80% similarity to the study transects (data not shown), thus making these results applicable to the observations made by the AUV.

Estimates of relative backscatter coefficient as a relative measure of zooplankton biomass in a 10-m swath around the prescribed vehicle depths showed significantly higher intensity between 70 and 80 m during the day, and between 10 and 20 m and 40–50 m at night (Table 1). In combination with the changes in bioluminescence intensity, these data demonstrated a coordinated movement of biomass indicative of DVM.

Plankton enumerations from WP2 vertical net hauls show an increase above 60 m in the majority of the most abundant zooplankton taxa at night, including *Pseudocalanus* spp., Microcalanus spp., *Oithona* spp., *Calanus* spp., *Metridia* spp. and *Thysanoessa* spp. These genera have been reported to present throughout the year in this regions (Lischka and Hagen 2005). Table 2 provides specific species classification and shows that this increase above 60 m at night is also apparent in the enumerations of other less abundant taxa including *Calanus finmarchicus*, *Acartia longiremis*, *Oncaea borealis* and *Eukrohnia hamata*. Of these, *Metridia lucens, Metridia longa, Oncaea borealis, Thysanoessa inermis* and *Thysanoessa longicaudata* most likely account for the increase in high-intensity bioluminescent flashes at 15 and 45 m during the night (Table 1).

Plankton enumerated from the >20 μm net collection of the BP exhaust suggests that during the day, the greatest biomass occurred at 45 m and was dominated by copepod nauplii, copepod eggs and the Tintinnid *Acantostomella norvegica* (Table 3). The same three groups of organisms dominated the biomass at 15 and 75 m. Other major contributors at each of these three depths were *Ceratium* and *Protoperidinium* spp., *Salpingella acuminata Pseudocalanus* spp., *Microcalanus* spp., *Oithona similis* and *Oithona atlantica* (Table 3), consistent with the WP2 nets samples (Table 2).

Table 1 Mean Bioluminescence intensity per flash (±SE) surveyed by the AUV at the three different depths during the daytime and nighttime deployments (LT is local time)

Depth (m)	Mean intensity/flash ($\times 10^8$) daytime (10:30–14: × 25 LT)	Mean intensity/flash ($\times 10^8$) daytime (21:30–22:30 LT)	Mean S_v difference (day–night)
15	9 ± 2*	$160 \pm 142^{\dagger}$	−16
45	7 ± 2	8 ± 3	−35
75	18 ± 6*‡	$4 \pm 1^{\dagger,\ddagger}$	17

Significant differences were found between depths using Mann–Whitney (* $P = 0.016$, $n = 1{,}030$; † $P = 0.025$, $n = 286$; ‡ $P = 0.022$, $n = 126$), and additionally, the difference in the mean acoustic backscatter coefficients (S_v) between day and night is shown for each depth. The differences in S_v between day and night were significant (Mann–Whitney, $P < 0.001$) at all depths

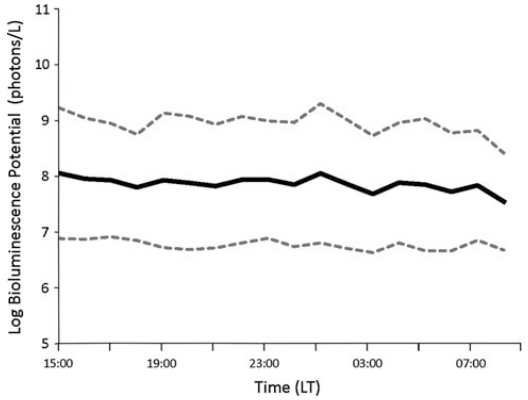

Fig. 2 Hourly means of log bioluminescence potential (*solid black line*) with standard deviations (*dotted black lines*) collected at 1 m depth from 15:00 LT on January 21 to 09:00 LT on January 22, 2010, ($n = 9{,}545$, non-zero observations). Flashes per unit time were also found to be consistent throughout the time series

Evident from organisms collected from both net sampling approaches is that the day/night changes in the vertical distributions of bioluminescence and acoustic scattering resulted from the larger zooplankton. Zooplankton taxa > 2.3 mm (*Calanus* spp., *Metridia* spp., *Thysanoessa* spp. and *Appendicularia*) collected by the WP2 vertical net tows showed decreased abundance at the surface (upper two depth layers) during the day than during the night and the highest abundance of this size class was found at depth during the day (Table 2). The smaller size class (*Pseudocalanus* spp, *Microcalanus* spp., *Oithona* spp.) did not show this trend. Histograms of the bioluminescence intensity (data not shown) in conjunction with plankton enumerations from each depth suggest that an underlying low-to-intermediate-intensity bioluminescence was consistent between day and night and likely attributed to the dinoflagellates, from *Protoperidinium* that occurred throughout the water column and to a lesser degree, *Ceratium furca* and *C. fusus* that were present in significantly lower abundances (Table 3).

Discussion

Though ubiquitous in the world's oceans and important from an ecological and evolutionary perspective (for review see Haddock et al. 2010), few studies have described bioluminescent communities and their distributions in the Arctic, particularly during the winter darkness. Buskey (1992), and Lapota et al. (1989, 1992) examined bioluminescence distributions and community structure with the goal of developing methodology to use bioluminescence as a way to measure total biomass and light budgets of a given water mass during the spring in the Greenland Sea, during the fall in the Beaufort Sea and in summer in a Norwegian Fjord, respectively. In contrast, this study quantified the bioluminescent community during the polar night and demonstrated the absence of circadian rhythm in bioluminescence.

Furthermore, both the diurnal distribution of bioluminescence intensity and concurrent changes in acoustic backscattering provide independent evidence for an active DVM of the larger bioluminescent zooplankton (and likely non-bioluminescent zooplankton) within the upper 75 m of the water column. Histograms of intensities showed the major differences between day and night occurring at the highest intensities, which is consistent with larger zooplankton (Lapota et al. 1992; Moline et al. 2009) and with the enumerations in this study. Bioluminscence and acoustic backscatting may in fact not be directly linked, but the circumstantial evidence provided herein suggests that the diurnal signal in bioluminescence is in fact caused by vertically migrating organisms. Numerous studies have examined proximal triggers for DVM (Forward 1988; Ringelberg 1995; Ringelberg and Van Gool 2003; Benoit-Bird et al. 2009), and many others have looked at triggers for the inhibition of bioluminescence as related to its circadian rhythm (Batchelder et al. 1992; Kelly and Katona 1966; Raymond and DeVries 1976; Swift et al. 1995). Interestingly all studies have in one way or another implicated a relative or absolute change in irradiance intensity, angle or daylength as a means of regulation for both DVM and the circadian rhythm of bioluminescence. Although changes in light during the time of this study are not visible to the human eye, it is possible that they were sufficient to initiate DVM in the organisms present at the time of the study as was suggested in the study by Berge et al. (2009). However, while external light cues may play a role in regulating DVM, it might not be the only factor relevant to consider for understanding this behavior. It has been well established for photosynthetic dinoflagellates and for heterotrophic dinoflagellates of the *Protoperidinium* genus that the bioluminescent inhibition occurs when light intensities are greater than the intensity of bioluminescence of the organisms themselves (Sweeney et al. 1959; Buskey et al. 1992). This phenomenon could explain why no circadian rhythm existed in bioluminescence during December and January in Antarctica (Raymond and DeVries 1976) and may also be related to the absence of a circadian rhythm in bioluminescence in the current study. Previous studies have found that *Protoperidinium* spp contributed between 20 and 90% of the total light budget from the surface to a depth of 100 m in the Beaufort Sea (Lapota et al. 1992) and that dinoflagellates were estimated to account for 96% of the total light budget in Vestfjord,

Table 2 Concentrations of the plankton captured by the 180 μm WP2 plankton net during the day and at night for depth intervals 30–0, 60–30 and 90–60 m

Taxa	Depth (m)	ind./m^3 (day)	ind./m^3 (night)	Taxa	Depth (m)	ind./m^3 (day)	ind./m^3 (night)
Calanus finmarchicus	0–30	50	82	*Heterorhabdus norvegicus**	0–30	<1	<1
	30–60	41	148		30–60	<1	6
	60–90	89	–		60–90	4	–
Calanus glacialis	0–30	4	10	*Harpacticus chelifer*	0–30	9	50
	30–60	31	31		30–60	54	30
	60–90	147	–		60–90	<1	–
Calanus hyperboreus	0–30	<1	1	Harpacticoida spp.	0–30	2	<1
	30–60	<1	<1		30–60	11	<1
	60–90	4	–		60–90	<1	
Pseudocalanus spp.	0–30	3,100	10,300	*Oithona atlantica*	0–30	388	725
	30–60	<1	16,820		30–60	<1	555
	60–90	775	–		60–90	<1	–
Microcalanus spp.	0–30	563	2,300	*Oithona similis*	0–30	400	825
	30–60	163	1,900		30–60	<1	1,335
	60–90	63	–		60–90	131	–
*Metridia lucens**	0–30	3	17	Appendicularia*	0–30	17	15
	30–60	4	18		30–60	3	3
	60–90	6	–		60–90	96	–
*Metridia longa**	0–30	<1	<1	*Limacina helicina*	0–30	2	<1
	30–60	<1	3		30–60	<1	1
	60–90	11	–		60–90	12	–
Acartia longiremis	0–30	175	375	*Sagitta elegans*	0–30	<1	2
	30–60	<1	385		30–60	5	11
	60–90	<1	–		60–90	12	–
Paraeuchaeta norvegica	0–30	<1	<1	*Eukrohnia hamata*	0–30	4	30
	30–60	1	<1		30–60	2	21
	60–90	<1	–		60–90	11	–
*Diastylis lucifera**	0–30	<1	<1	*Thysanoessa longicaudata**	0–30	<1	2
	30–60	1	<1		30–60	3	7
	60–90	<1	–		60–90	2	–
Bradyidius similis	0–30	<1	1	*Thysanoessa inermis**	0–30	<1	<1
	30–60	<1	3		30–60	<1	22
	60–90	6	–		60–90	<1	–
*Oncaea borealis**	0–30	12	<1				
	30–60	51	200				
	60–90	<1	–				

Asterisks indicate organisms known to be bioluminescent

Norway (Lapota et al. 1989), so it is reasonable to assume that they were significant contributors to the overall light budget during this study. Wherein the lack of sunlight facilitated an environment where the intensity of bioluminescence was not inhibited by light greater than the bioluminescence of the organisms themselves. While this regulatory factor has been established for dinoflagellates, it is possible that it plays a role in other bioluminescent taxa as well, such as copepods, appendicularians and Arctic krill as in the case of this study.

Conclusions and perspectives

The most notable finding in this study is the detection of bioluminescent activity among zooplankton during the

Table 3 Concentrations of the plankton captured by the 20 μm plankton nets covering the REMUS BP exhaust for daytime deployments at 15, 45 and 75 m

Taxa	Depth (m)	ind/m^3	Taxa	Depth (m)	ind/m^3
Ceratium arcticum	15	229	Copepod nauplii*	15	1,409
	45	352		45	2,726
	75	246		75	1,403
*Ceratium fusus**	15	9.6	Copepod eggs	15	903
	45	91.3		45	1,631
	75	80.3		75	1,372
Ceratium furca	15	<1	*Oncaea borealis**	15	5
	45	13		45	52
	75	4		75	4
Protoperidinium spp.*	15	211	*Harpacticoida* spp.	15	7
	45	391	*Microsetella norvegica*	45	7
	75	387		75	4
Diatom spp.	15	10		15	5
	45	59		45	7
	75	80		75	4
Acantostomella norvegica	15	1,252	*Oithona atlantica*	15	67
	45	2,023		45	117
	75	827		75	59
Salpingella acuminata	15	241	*Oithona similis*	15	72
	45	163		45	111
	75	122		75	108
Heliocostomella subulata	15	2	*Eukrohnia hamata*	15	<1
	45	13		45	1
	75	<1		75	<1
Parafavella denticulata	15	7	Gastropoda larvae	15	23
	45	33		45	33
	75	45		75	11
Calanus finmarchicus	15	8	Appendicularia*	15	11
	45	8		45	39
	75	11		75	21
Paraeuchaeta norvegica CIII	15	<1	Membranipora larvae	15	19
	45	1		45	20
	75	<1		75	21
Acartia longiremis	15	29	Bivalve larvae	15	<1
	45	7		45	7
	75	18		75	<1
Pseudocalanus spp.	15	205	*Limacina helicina*	15	<1
	45	215		45	<1
	75	154		75	4
Microcalanus spp.	15	137	*Thysanoessa longicaudata**	15	<1
	45	437		45	<1
	75	140		75	1

Asterisks indicate organisms known to be bioluminescent

polar night, which may be an important ecological feature. While the ultimate and proximate explanations for both the bioluminescence and the DVM behavior detected during the campaign fall outside the data collected during this study, these results provide evidence for both endogenous and exogenous control of poorly understood or previously unknown processes. Also, during this expedition, which took place during the darkest period of the polar night, we observed five different species of seabirds actively foraging at sea; little auk (*Alle alle*), black-legged kittiwake (*Rissa tridactyla*), northern fulmar (*Fulmarus glacialis*), black guillemot (*Cepphus grylle*) and brünnich's guillemot (*Uria*

lomvia). These seabirds have, to the best of our knowledge, not been reported to overwinter at these latitudes. Whether bioluminescence and/or DVM are playing roles in the foraging behavior of these visual predators is an exciting possibility, although still an open question. Despite the limited scope of this study, results open new lines of enquiry regarding the function and process during a time of year when classical paradigms of Arctic ecosystems postulate that organisms are predominately in a state of hibernation (see Berge et al. 2009). Ultimately, these questions also have implications for human activities (i.e., oil exploration) in the high Arctic, which up until to now has been considered "without life" during the polar night.

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Paper II

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Paper III

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Paper IV

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

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Abstract

Irradiance thresholds for phototactic response were determined for the first time 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 study 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 was 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.

Copepodites stage V 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.

Keywords: zooplankton, physiology, behaviour, diel vertical migration, light response

1 Introduction

Diel vertical migration (DVM) among zooplankton taxa, including *Calanus* species, is a widespread phenomenon 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. The widely supported hypothesis for this energetically costly 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. Lampert, 1989; Hays, 2003), 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 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.

Crustacean plankton quantitatively dominate the zooplankton communities in the North Atlantic and Norwegian Sea. Copepods constitute the main taxon within the group, and in these waters the calanoid copepod genus *Calanus* is generally considered the most important in terms of biomass, energy turnover and general ecosystem impact (Mauchline, 1998). *Calanus* species hence constitute a crucial component of the food web, transferring energy from the primary production of phytoplankton to fish species such as cod *Gadhus morhua* L. and herring *Clupea harengus* L. (Green, et al., 2004). *Calanus finmarchicus* Gunnerus is the dominant *Calanus* species in the northern part of the North Sea, the Norwegian Sea and the Atlantic inflow region to the Barents Sea (Planque and Batten, 2000). In these waters the species contributes to a very large fraction of the total plankton biomass (>90% in the southern Norwegian Sea; Planque and Batten, 2000), and *C. finmarchicus* is accordingly considered an ecological key species in the North Atlantic pelagic ecosystem (Mauchline, 1998).

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. Unstad and Tande, 1991; Durbin, et al., 1995; Dale and Kaartvedt, 2000; Baumgartner, et al., 2003; Kwasniewski, et al., 2003; Cottier, et al., 2006; Rabindranath, et al., 2011). During daytime, the early copepodite stages (CI-CIII) are

primarily found in the upper water layers, whereas copepodite V (CV) and adult females (copepodite VI; CVIf) are found in the deeper water layers (e.g. Unstad and Tande, 1991; Kwasniewski, et al., 2003). Large proportions of *C. finmarchicus* CV and CVIf are found at depths of around 200 m during daytime, although it is uncertain whether these stages were actively migrating or in diapause (e.g. Unstad and Tande, 1991; Baumgartner, et al., 2003; Kwasniewski, et al., 2003).

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 white light, within a range of irradiances including those found in the deep ocean or in the dark polar night. 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 (Hansen, et al., 2007). At the time of the experiments (autumn 2010), the copepod culture had been running for 27 generations under laboratory conditions. The culture is maintained in running seawater in polyester containers (280 L) at ~10 °C, and the culture copepods are reared on a mixture of the unicellular algae *Rhodomonas baltica* Karsten, *Isochrysis galbana* Parke and *Dunaliella tertiolecta* Bucher.

At the time of the experiments the culture had been kept for several generations in a light-dark cycle of 18:6 hours, with 6 hours of dawn and dusk in the first and last part 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.

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, California, 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. The edges of the opening were cut at an approximate angle of 45 degrees to the plumb line to avoid shadowing effects. 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 were conducted to ensure that near-infrared illumination did not interfere with the experiments, and these demonstrated no behavioural response to the illumination.

The positioning of the copepods in the aquarium raceway and their phototactic response following light stimuli was 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 nightshot 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. To ensure no stray light would reach the experimental compartment, a custom made entry passage made in optically dense material and with an inner zipper door was fitted inside the entrance door. A second compartment in the entry passage contained the computer for remotely controlling the light stimulus, as well as a monitor displaying live video viewing from the camera. Thus, the experiments could be monitored and controlled without entering the experimental area.

2.3 Light stimulus

The range of irradiance used in the experiments were achieved using a combination of absorptive neutral density filters (CVI Melles Griot, Netherlands) controlled by WheelTool v1.0 software (Tofra Inc.) and diode pulsing maintained by a PWM signal controlled by LabView 8.2.1 (National Instruments). 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, USA; Fig. 2). The detector of the instrument was placed in front of the aquarium on the opposite side of the light source and the irradiance of white light was measured for several OD levels. The spectrometer was calibrated with a

Quartz Tungsten Halogen lamp (Model no. 63358, 45 W, 6.5 A, Oriel Instruments) to obtain the irradiance measurements in μW nm^{-1} m^{-2}, which then were converted to μmol photons nm^{-1} m^{-2} s^{-1} (Baker and Romick, 1976).

As the detector was not waterproof, the measurements were conducted outside the aquarium, thus detecting lower irradiance than the copepods experienced in the raceway. The measurements were therefore adjusted for the attenuation of irradiance through one Optiwhite glass wall (transmittance: 0.91). Total irradiance of the light stimulus applied was calculated for OD4 to OD6 as the integrated spectral-specific data over photosynthetic active radiation (PAR; 400-700 nm). Irradiance below OD6 and above OD4 were outside the linear response of the instrument, so the log linear relationship (R^2=0.998, $P<0.05$) of the measured OD levels was used to calculate the irradiance of the remaining OD levels (Table 1).

2.4 Experiments

Experimental runs were conducted with adult males (copepodite VI; CVIm), CVIf and CV copepodites, respectively, and each run was replicated 5 times. A total of 50 (CVIm) or 60 (CV and CVIf) individuals were used in each experiment replicate, amounting to a total of 300 CVIf and CV and 250 CVIm. All experiments were conducted with copepods in the same diurnal phase, i.e. during daytime between 0900 and 1500 hrs. The copepods were sampled from the culture tanks shortly after 0900 hrs and sorted to developmental stage and sex using a stereo microscope and dim light conditions. Only apparently healthy individuals were selected. The copepods were not fed during the experiments. The collected copepods were transferred to the aquarium raceway, and then acclimated in darkness for 1 h before the experiment started.

The distribution of the copepods in the raceway during the last 10 minutes of the acclimation period was assumed to represent the general distribution in darkness, and applied as the basis

positioning prior to light exposure. The irradiance was then increased stepwise from the lowest irradiance level (OD9) to the highest level (OD1) through a total of 9 steps, each with a tenfold (log_{10} unit) increase in intensity (Table 1). Each light intensity level lasted for 10 minutes. The order of the stepwise change was then reversed from the highest irradiance (OD1) to the lowest (OD9), followed by a final 10 minute period in darkness.

2.5 Image analysis

The positioning and change in distribution of the copepods in the raceway in the test aquarium were analysed using image frames extracted from HD video. One image was extracted from the HD video per minute using Picture Motion Browser video software (v 4.2, Sony Corporation), providing a total of ten images representing each level of irradiance. The images were processed and analysed with ImageJ software (Rasband, 2009). Prior to particle analysis the images were organised in stacks with all ten images from each irradiance level, and the image quality was enhanced by increasing the contrast and subtracting the background using a rolling ball filter. Edges, air bubbles and other stationary irregularities were removed by calculating a median image based on all the images in the stack and subtracting it from all images in the same stack. Thresholding (by adjusting brightness and saturation) was used to create binary images for particle analysis (Fig. 3). Particle analysis provided data for size (area in square pixels) and coordinates of each particle; which was further organised and analysed in the R environment (R Development Core Team, 2011). The particles were sorted by size, and the 50, 60 and 60 (for CVIm, CV and CVIf, respectively) largest particles in each image were defined as the copepods and extracted for further analysis. A manual count was compared to the positions extracted from the automated particle analysis, and the positions were highly correlated ($r=0.997$, $p<0.001$, Pearson correlation). Thus, the simplified method of automated particle analysis based on particle size

was deemed reliable. The coordinate position obtained for each particle (i.e. individual copepod) provided information on its distance (mm) from the light stimulus.

2.6 Statistical analysis

The phototactic response for each developmental stage and sex was tested through Gaussian family linear mixed-effects modelling, with replicate as a random factor to account for the repeated measurements nature of the design. Likelihood ratio tests (ANOVA F-tests) were used to test the significance of irradiance level as a predictor of copepod distribution with the level for retention set to $\alpha < 0.05$. The distribution of copepods at each irradiance level was then contrasted to the distribution of copepods during the initial dark period. The median position of the copepods over the time span of each irradiance level, i.e. 10 minutes, was used as the core unit in the analysis with one set of copepod positions relative to the light stimulus per minute. Statistical analyses were conducted in the R environment (R Development Core Team, 2011) using the package nlme (Pinheiro, et al., 2011).

2.7 Light simulations

Light simulations were conducted using Hydrolight, which is a radiative transfer rate-based numerical model of light propagation in water (Mobley, 1994). The inherent optical properties of pure water were based on the Pope and Fry (1997) model. The chlorophyll absorption spectrum was based on Prieur and Sathyendranath (1981), and chlorophyll scattering as a function of wavelength was modelled according to Loisel and Morel (1998). Coloured dissolved organic matter (CDOM) absorption was modelled using an exponentially decaying function of wavelength:

$$a_{CDOM}(\lambda) = a_{CDOM}(\lambda_0) \exp^{(-S(\lambda - \lambda 0))}$$

where λ is the wavelength, λ_0 is a reference wavelength and S is a parameter that depends on the composition of the CDOM.

Two scenarios were simulated. One scenario represented the ocean at the location of a permanent station in the Norwegian Sea (Station M; 66° N, 2° E), where extensive measurements were made during 1997 and 1998. The other scenario was representative of a Norwegian fjord using data from the station Trollet (63° N, 10° E) in Trondheimsfjorden. For the Station M scenario, chlorophyll (Chl *a*) data were obtained from Irigoien et al. (1998) and the solar angle at noon, 47.4°, was used. For the Trondheimsfjorden scenario, Chl *a* data from the station Trollet over several years were averaged, and a representative profile for 15 April, during the spring bloom, was chosen. The solar angle at noon in this case was 51.9°. In both scenarios, clear sky was assumed and Hydrolight's semi-empirical sky model based on RADTRAN (Gregg and Carder, 1990) was used. For Station M, CDOM absorption parameters ($a_{CDOM}(\lambda_0)$=0.23 m^{-1}, λ_0=350 nm and S=0.0169) were obtained from Stedmon and Markager (2001). For Trondheimsfjorden, the parameters ($a_{CDOM}(\lambda_0)$=2.0 m^{-1}, λ_0=340 nm and S=0.0135) were obtained from Kjeldstad (2006). The average wind speed at Station M in May of approximately 7 m s^{-1} was used in the simulation (http://www.ecmwf.int/, data from 1997-1999). For Trondheimsfjorden, 1 m s^{-1} was used. Approximate depths based on the irradiance thresholds were extracted from both models.

3 Results

Irradiance (OD level) was a significant predictor for the distribution of the CV copepodites in the raceway (mixed effect model, F=9.39, P<0.001, replicate as random factor; Table 2). When increasing the irradiance, there were no significant differences in distribution of the CV copepodites at OD9 to OD7 compared to the baseline dark period (Fig. 4A).The distribution of CV copepodites became significantly different from the distribution in the initial dark period at OD6 (P<0.01), corresponding to 9.8×10^{-6} µmol photons m^{-2} s^{-1}. The distribution remained significant from the initial dark period from OD6 to OD1, the highest irradiance level. The distance from the light source increased in comparison to the

distribution in the dark period, thus demonstrating negative phototaxis (Fig. 3). When the irradiance was decreased in steps from OD1 to OD9, the distribution returned to random at OD8 ($P=0.14$), with a change in significance level at OD7 ($P=0.015$) compared to OD1 to OD6 ($P<0.001$).

Irradiance (OD level) was also a significant predictor for the distribution of the CVIf copepods in the experimental raceway (mixed effect model, $F=4.04$, $p<0.001$, replicate as random factor). When the CVIf copepods were exposed to increasing irradiances, the copepods were randomly distributed from OD9 to OD7 (Fig. 4B). The distribution of CVIf copepods became significantly different from the initial dark period at OD6 ($P<0.05$), corresponding to 9.8×10^{-6} µmol photons m^{-2} s^{-1}. . The distribution was significantly different from the initial dark period at OD6, OD5 ($P<0.001$) and OD4 ($P<0.01$), demonstrating a non-random distribution with negative phototaxis. The distribution of the CVIf copepods was not significantly different from the initial dark period at OD3 ($P=0.072$), OD2 ($P=0.070$) and OD1 ($P=0.30$), but had a significantly different distribution when the irradiance level was decreased to OD2 ($P=0.049$) and OD3 ($P=0.05$). The CVIf copepods stayed randomly distributed throughout the remaining part of the experiment (irradiances at OD4 -OD9; Table 2).

Irradiance (OD level) was also a significant predictor for the distribution of the CVIm copepods in the experimental raceway (mixed effect model, $F=43.60$, $p<0.001$, replicate as random factor). When the irradiance of the light stimulus was increased following the initial period in darkness, the distribution of the CVIm copepods were remained randomly distributed at OD9 and OD8 (Fig. 4C). The copepod distribution became significantly different from the initial dark period at OD7 ($P<0.001$), which corresponds to 9.9×10^{-7} µmol photons m^{-2} s^{-1}. The distribution remained significant from the initial dark period from OD7

to OD1. The distance from the light source decreased in comparison to the distribution in the dark period, thus demonstrating positive phototaxis (Fig. 3). When the irradiance decreased, the CVIm copepod distribution did not return to a random distribution during the duration of the experiment, however, the copepods started to disperse from OD7 (Fig. 4C).

Simulated irradiance (E_{PAR}) across depth was estimated for the ocean scenario (Station M) and the fjord scenario (Trondheimsfjorden; Fig. 5). The depths with PAR values closest to OD6 (CV and CIVf) and OD7 (CVIm), i.e. the lowest irradiances that elicited phototactic response, were determined. For Station M the depths were 158 m and 186 m, respectively, and for Trondheimsfjorden the depths were 48 m and 57 m.

4 Discussion

The data in the present study show phototaxis in *C. finmarchicus* in response to low levels of irradiance in controlled laboratory conditions. The direction of the phototactic response differed between the sexes, with CVIm displaying positive phototaxis and CVIf, as well as CV, displaying negative phototaxis. CVIm appeared to be more photosensitive than CVIf and CV, responding to irradiance levels of 9.9×10^{-7} µmol photons m^{-2} s^{-1} compared to 9.8×10^{-6} µmol photons m^{-2} s^{-1} for CV and CVIf. Previous studies investigating phototactic response in *C. finmarchicus* have used one or only a few irradiance levels and in general at relatively high irradiance, and have therefore not determined an irradiance threshold for response (e.g. Aarseth and Schram, 1999; Wold and Norrbin, 2004). Thus, the irradiance reported in those particular studies are not comparable with the threshold levels reported in the present study. However, absolute irradiance thresholds inducing a phototactic response have been reported in other zooplankton species (e.g. Barnes and Klepal, 1972; Stearns and Forward, 1984; Cohen and Forward, 2005). Adult females of *Calanopia americana* Dahl F. exposed to the blue-green spectrum of light in a vertical system showed a significant negative phototaxis

when the absolute irradiance was >1×10^{11} photons m^{-2} s^{-1} at daytime and >1×10^{14} photons m^{-2} s^{-1} during the night, which corresponds to ~1.7×10^{-7} and ~1.7×10^{-4} µmol photons m^{-2} s^{-1}, respectively (Cohen and Forward, 2005). Stearns and Forward (1984) reported that the intensity threshold for positive phototaxis in dark-adapted *Acartia tonsa* Dana was 2.8×10^{11} photons m^{-2} s^{-1}, which corresponds to ~4.6×10^{-7} µmol photons m^{-2} s^{-1}.. Thus, the irradiance thresholds that elicited phototactic response in *C. finmarchicus* are within the range of that reported for other zooplankton species.

Predator evasion is probably the most important ultimate reason for DVM (Hays, 2003). Thus, the ambient irradiance at the depths the zooplankton migrate to should be lower than the threshold irradiance at which visually hunting fish successfully can catch prey (Ringelberg, 1995). Consequently, zooplankton with DVM behaviour should be able to detect and respond to irradiances lower than the threshold irradiance at which fish can hunt by vision. Herring (*C. harengus*), one of the main predators of *C. finmarchicus* (Marshall and Orr, 1972), was offered a mixture of zooplankton including *C. finmarchicus*, at different irradiances to determine the irradiance threshold for visual feeding by biting (Batty, et al., 1990). The threshold proved to be at 0.001 lux, which corresponds to approximately 2×10^{-5} µmol photons m^{-2} s^{-1}. Furthermore, larval cod (*G. morhua*) were able to feed at light intensities of 3.67×10^{-6} W m^{-2} (Vollset, et al., 2011), corresponding to approximately 2×10^{-5} µmol photons m^{-2} s^{-1}. Hence, the irradiance thresholds for phototactic response in *C. finmarchicus* identified in the present study were one to two orders of magnitude lower than the irradiance necessary for successful visual hunting in herring and larval cod. This strengthens the view that *C. finmarchicus* is able to migrate to depths with irradiances below the irradiance necessary for successful hunting by its predators, and still be able to detect and respond to the low irradiance.

Both CV and CVIf elicited negative phototactic response to the light stimulus, whereas CVIm showed a positive phototactic response. Particularly the response in CVIm was strong and uniform, as seen from the small variation in the distribution of the copepods after the light response had been elicited (Fig. 4). Forward (1988) pointed out that positive phototaxis is not common among zooplankton and often this is a laboratory artefact resulting from a narrow stimulus beam or high light intensities. In our study, the copepods were exposed to low levels of irradiance and a relatively wide light field, thus the observed differences in light response between the developmental stages and sexes probably reflect their ecological requirements The CVIm copepod behaviour is primarily focused on mate-finding. They spend little time feeding and exhibit a higher swimming activity than CVIf, allowing them to cover large areas probably mainly to increase their chances of detecting female pheromones and finally mating (Kiørboe and Bagøien, 2005). However, in addition to requiring more energy, this behaviour also increases the chances for being detected and caught by predators (Irigoien, et al., 2000). CVIm are generally found in low abundance (e.g. Pasternak, et al., 2001; Niehoff, et al., 2002). Thus, because most investigations addressing phototactic behaviour or DVM in *Calanus* copepods have been field studies, few studies have been able to include phototactic behaviour of CVIm. CVIm appear earlier in spring than the CVIf, probably due to a faster development of the gonads compared to CVIf (Irigoien, et al., 2000). It has been suggested that male copepods migrate upwards and stop at a certain level, e.g. at a thermohaline layer, to increase their chances of mate-finding by restricting the search behaviour to certain strata of the water column (Hayward, 1981; Tsuda and Miller, 1998). Hence, an inherent strong light-governed behaviour evolved to increase mating success may help explain the positive phototaxis observed in the CVIm in the current experiments. On the other hand, temperature or salinity gradients that can act to modulate or reverse the positive phototaxis under field

conditions are not included in the experimental setup, which may be in accordance with the uniform positive phototaxis observed.

In contrast to CVIm, CVIf showed a less clear-cut response to the light stimulus throughout the experiment. This is evident by the larger variation in the distances from the light source in these groups (Fig. 4). In the present study, the copepods were selected based on their developmental stage or sex, and within-stage variation was not taken into account. There was probably a relatively large variation within the CVIf group with respect to age, ranging from newly molted unmated females through females with different stages of egg production and egg-laying females, to females that had exploited all their reserves for egg-laying. Several studies indicate that copepods can modulate their DVM behaviour depending on body condition, food conditions and predator presence (e.g. Hays, et al., 2001; Basedow, et al., 2010), and they may also modulate their behaviour in relation to reproductive status. Furthermore, copepods have been reported to have higher lipid content in deeper water compared to copepods in the surface water (Hays, et al., 2001; Bergvik, et al., 2012), which indicate that also lipid content can modulate copepod DVM behaviour. Individual variation in lipid content may thus also explain some of the observed variation in phototactic response found within the different groups in the present study.

Decreasing irradiance did not elicit as distinctive responses as those observed during the increasing irradiance. Rather, when the irradiance was decreased, the copepods appeared to become gradually redistributed towards random distribution as the stimulus decreased below the irradiance that produced a phototactic response during the gradual increase in irradiance. Ringelberg (1999) suggested that vertical movements are normal hop-and-sink swimming activity controlled by two balanced internal oscillators in a positive and negative mode. These two modes determine vertical displacement, and temporary dominance of one oscillator will

result in an individual gradually moving upwards or downwards. Changes in irradiance affects the upwards or downwards movements by increasing one mode and shortening the other, e.g. giving downwards movement by longer periods of sinking at increasing irradiances (Ringelberg, 1999). In the horizontal two-dimensional setup used in the present study, this hop-and-sink behaviour could not be investigated, only reactive and optically oriented swimming could be monitored. However, the slow redistribution of the copepods when the irradiances decreased below the threshold eliciting a phototactic response indicates that the copepods did not have a direct response to decreasing irradiance.

Light simulations estimated that the irradiances that elicited phototactic response in the copepods correspond to approximate depths of 158-186 m in an ocean scenario and 48-57 m at noon in a fjord scenario (Trondheimsfjorden). The simulations were conducted using input parameters from a spring bloom scenario, at the time of year with the highest attenuation of light. Thus, at other times of the year corresponding irradiances are expected to be found at greater depths. Furthermore, in Trondheimsfjorden the light attenuation is particularly high during spring, due to river run-off during snow melt (Sakshaug and Sneli, 2000). Nevertheless, the estimated depths are within the range of the depth distributions of *C. finmarchicus* of down to 200 m reported from field samplings in the open sea and in Arctic fjords with clear water (Unstad and Tande, 1991; Kwasniewski, et al., 2003). In Norwegian fjords, the depths at which *C. finmarchicus* are found are more variable, ranging from 20-40 m to 180 m (Marshall and Orr, 1972; Tande, 1988). At least some of this variation may be explained by the differences in light attenuation between fjords (Sakshaug, et al., 2009).

The white LED used in the light stimulus in the current study contained a considerable amount of red light (Fig. 2). In seawater the red light is absorbed very quickly and at depths below the surface layer the spectral composition of the light is either blue (ocean) or blue-

green (fjord; Sakshaug, et al., 2009). It is unlikely that animals have a substantial spectral sensitivity to wavebands that are attenuated quickly in the water column (Forward, 1988), and studies on several marine copepods do show highest spectral sensitivity in wavebands generally below ~600 nm (Stearns and Forward, 1984; Cohen and Forward, 2002). Although the spectral sensitivity of *C. finmarchicus* is presently unknown, it is reasonable to assume that *C. finmarchicus* has a lower sensitivity to red compared to the blue and green wavebands. Hence, since the irradiance values used here were integrated over 400-700 nm, the irradiance thresholds for phototactic response may be even lower than those we report, when taking spectral sensitivity into account. Accordingly, corresponding ocean and fjord depths would have increased slightly. Re-calculating our irradiance values based on the assumed highest spectral sensitivity (400-600 nm) reduces the irradiance at each level to about half. However, this is still within the same order of magnitude as the irradiance values we have reported, thus the effect of not correcting for spectral sensitivity is modest and for the depth estimates it is in the range of a few meters. Still, investigating the spectral sensitivity of *C. finmarchicus* is an important topic that deserves attention in future studies.

Most previous studies on phototactic behaviour in plankton have been performed with wild-caught animals, and the representativeness of the cultured animals used in the present study may be questioned. However, to counteract unintended effects of possible selection the current stock of *C. finmarchicus* has been cultured under a light regime simulating light conditions at a representative destination within the distribution area of the species. Also other rearing conditions have been kept as close to natural conditions as possible. As we assume responses to light are highly adaptive and probably well conserved in the species, we therefore expect, at least qualitatively, a high level of agreement between the cultured animals and wild populations.

To enable migration to depths too dark for fish to hunt by vision while using light as a cue for migration, a high sensitivity to light is necessary. The present study confirms such high sensitivity to light in *C. finmarchicus* by showing that CV and adults of *C. finmarchicus* respond with phototaxis to low levels of irradiance in the range of 9.8×10^{-6} - 9.9×10^{-7} µmol photons m^{-2} s^{-1}, for the first time determining irradiance thresholds for phototactic response in this species. Furthermore, these irradiance levels determined in an experimental laboratory setting correspond to the irradiance at depths where *C. finmarchicus* are found both in ocean and fjords. Small differences in sensitivity were found between the sexes and instars investigated in the present study and further research on the younger copepodite stages is needed to determine whether differences in light sensitivity can help explain and predict the stage-specific depth distribution regularly found in field.

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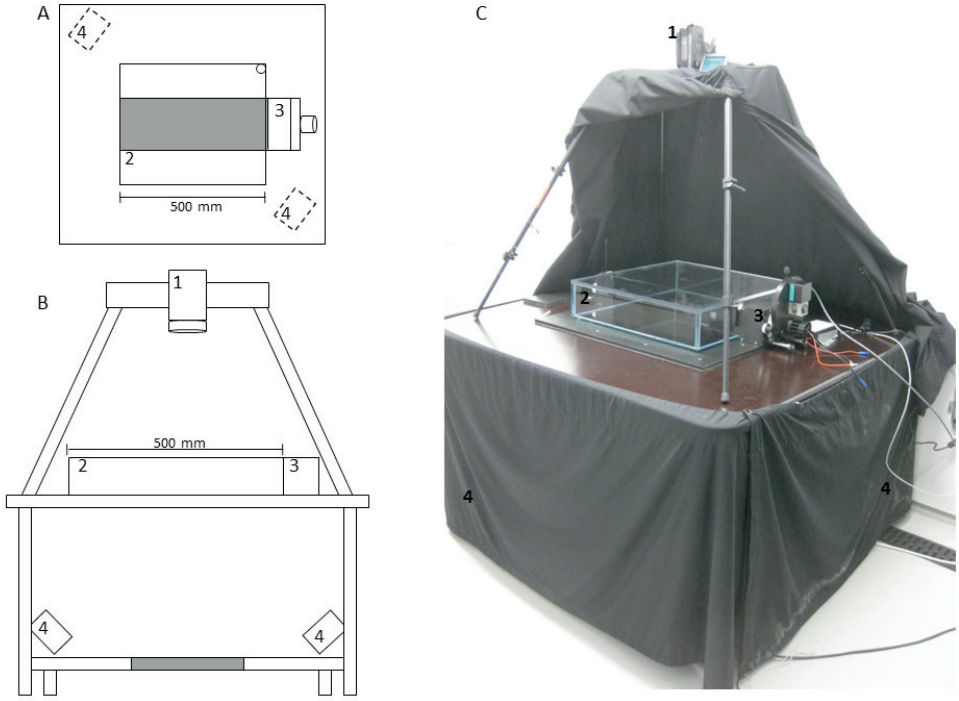

Figure 1. A schematic overview of the experimental setup used to detect phototactic behaviour in *Calanus finmarchicus* from above (A) and the side (B) and a photograph of the experimental setup from the side (C). The experimental setup consisted of a camera (1), an aquarium (2) with a raceway in the middle (shaded area) fitted to the width of the light stimulus (3). A computer controlled filter wheel was fitted to the light stimulus device (3). On the table legs two near-infrared lamps (4) were attached with adjustable brackets.

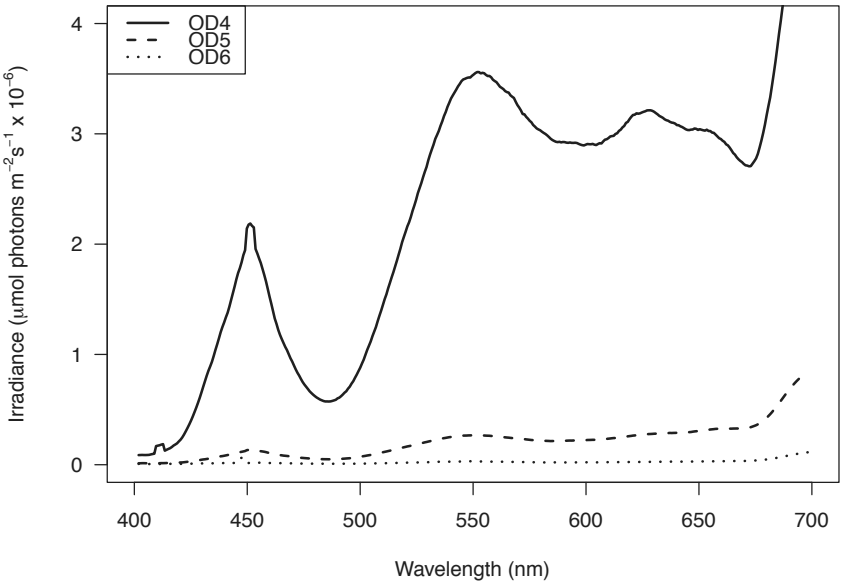

Figure 2. Spectral irradiance for the light stimulus at irradiance level OD4 to OD6 obtained with neutral density filters.

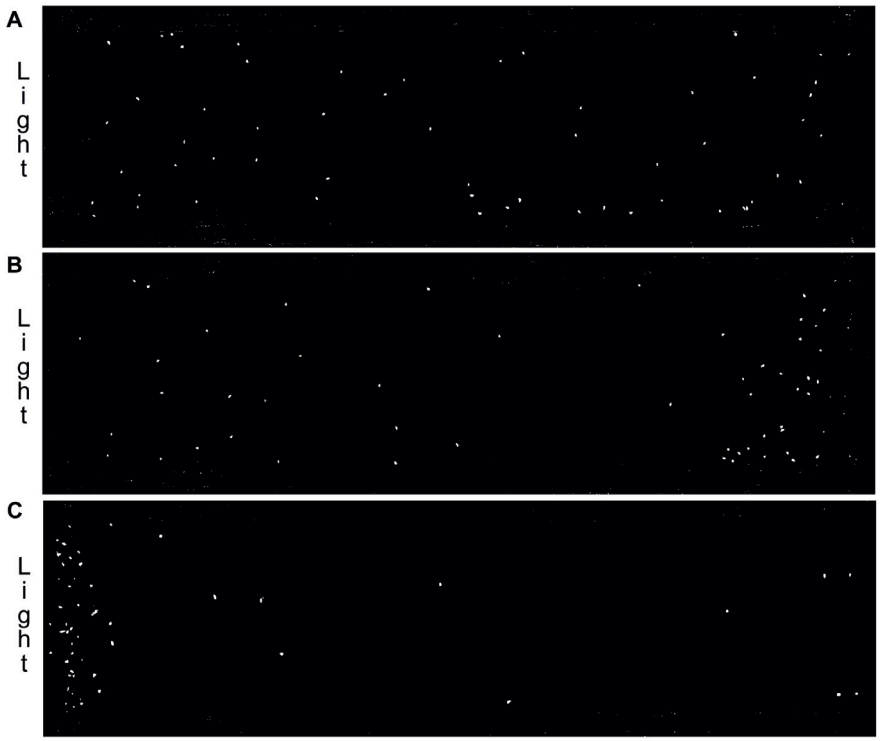

Figure 3. Examples of copepod distribution, viewing the aquarium from above, A) in the initial dark period for CV (random distribution), B) at OD6 for CV (negative phototaxis) and C) at OD6 for CVIm (positive phototaxis).

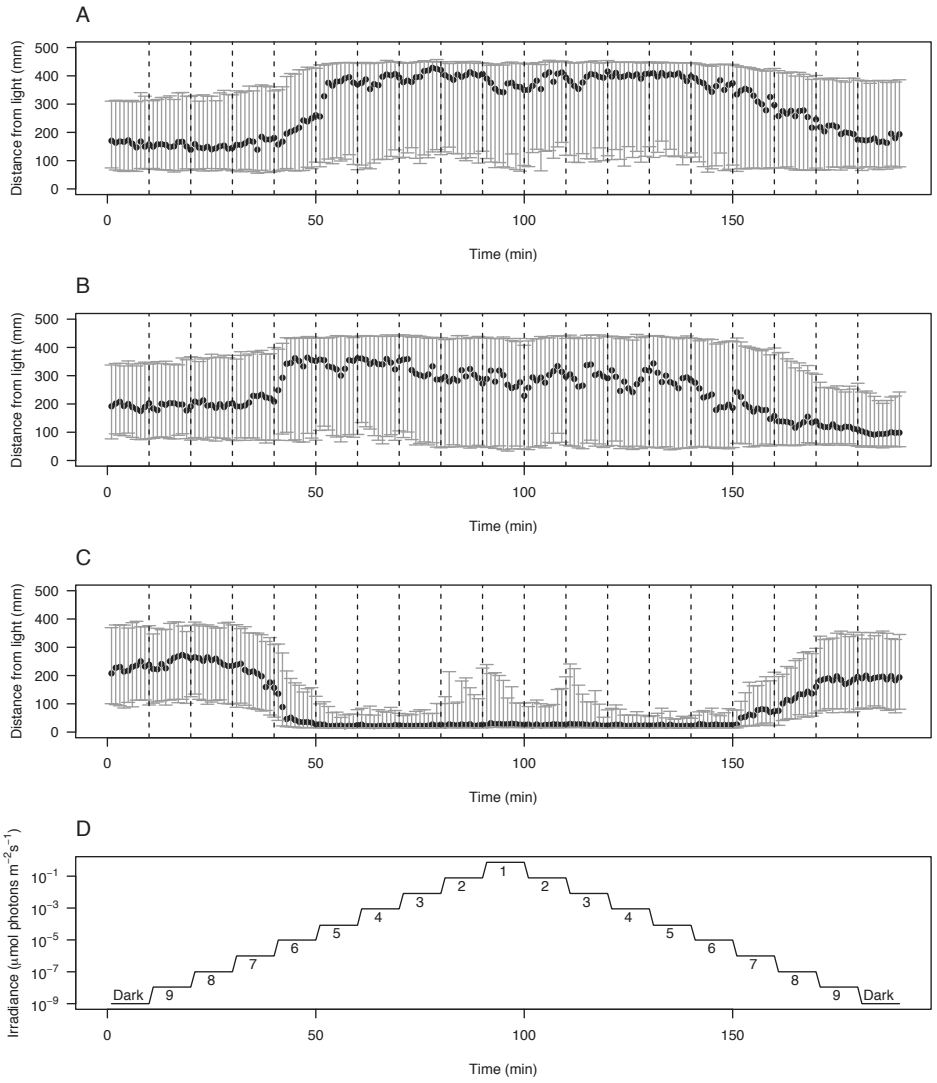

Figure 4. Median distance (±interquartile range; mm) to light source for A) copepodite stage V (CV) B) adult females (copepodite VI; CVIf) and C) adult males (copepodite VI; CVIm) exposed to increasing and decreasing irradiance of white light. Dashed lines indicate change in irradiance level. D) A schematic view of the stepwise changes in irradiance related to OD level.

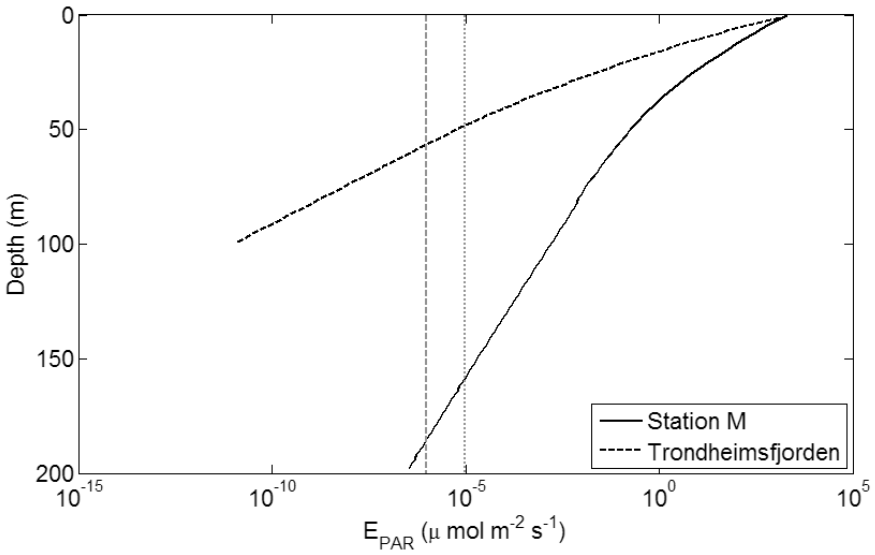

Figure 5. Estimated irradiance (E_{PAR}) plotted against depth for an ocean scenario (Station M, solid line) and a fjord scenario (Trondheimsfjorden, Norway, dashed line) at noon during the spring bloom. Vertical grey lines indicate the irradiance threshold for phototactic response in *C. finmarchicus* in CV and CVIf (dotted line) and CVIm (dashed line). The calculations are representing the situation at noon during the spring algal bloom.

Table 1. Measured (OD4, OD5 and OD6) and extrapolated irradiance at 400-700 nm (µmol photons m^{-2} s^{-1}) for the light stimulus levels used in experiments. . The lowest irradiances eliciting significant phototactic response are shown in bold.

Light stimulus	Irradiance (400-700 nm) (µmol photons m^{-2} s^{-1})
OD1	7.4×10^{-1}
OD2	7.8×10^{-2}
OD3	8.2×10^{-3}
OD4	8.9×10^{-4}
OD5	8.3×10^{-5}
OD6	**9.8×10^{-6}**
OD7	**9.9×10^{-7}**
OD8	1.0×10^{-7}
OD9	1.1×10^{-8}

Table 2. Output from mixed modelling of phototactic response, comparing distance from light source (mm) at each irradiance level to the distance to light source in the initial dark period, for CV, adult females (CVIf) and adult males (CVIm). Position is the median distance from light stimulus (mm) for the initial dark period (Dark) and the change in median distance for the subsequent irradiance levels. P-values indicate significance or irradiance level relative to the initial dark period, and significant P-values are indicated in bold. Likelihood ratio ANOVA tests; CV: F=9.39, P<0.001, CVIf: F=4.04, P<0.001, CVIm: F=43.60, P<0.001.

	CV			**CVIf**			**CVIm**		
	Position	t-value	P-value	Position	t-value	P-value	Position	t-value	P-value
Dark	169	4.45	**<0.001**	186	3.54	**<0.001**	236	14.51	**<0.001**
OD9 increasing	-6	-0.15	0.883	28	0.65	0.517	29	1.61	0.112
OD8 increasing	1	0.01	0.989	34	0.80	0.424	-1	-0.08	0.939
OD7 increasing	15	0.36	0.720	36	0.85	0.399	-87	-4.78	**<0.001**
OD6 increasing	106	2.58	**0.012**	102	2.38	**0.020**	-199	-10.91	**<0.001**
OD5 increasing	205	4.96	**<0.001**	163	3.81	**<0.001**	-205	-11.25	**<0.001**
OD4 increasing	205	4.98	**<0.001**	135	3.17	**0.002**	-206	-11.30	**<0.001**
OD3 increasing	252	6.11	**<0.001**	77	1.81	0.074	-189	-10.34	**<0.001**
OD2 increasing	198	4.81	**<0.001**	79	1.84	0.070	-191	-10.46	**<0.001**
OD1	159	3.86	**<0.001**	45	1.04	0.300	-200	-10.94	**<0.001**
OD2 decreasing	208	5.05	**<0.001**	85	2.00	**0.049**	-170	-9.34	**<0.001**
OD3 decreasing	215	5.21	**<0.001**	85	2.00	**0.050**	-202	-11.05	**<0.001**
OD4 decreasing	209	5.08	**<0.001**	81	1.89	0.062	-199	-10.93	**<0.001**
OD5 decreasing	195	4.73	**<0.001**	75	1.76	0.083	-205	-11.21	**<0.001**
OD6 decreasing	153	3.70	**<0.001**	28	0.66	0.513	-199	-10.93	**<0.001**
OD7 decreasing	103	2.50	**0.015**	26	0.62	0.538	-158	-8.68	**<0.001**
OD8 decreasing	61	1.49	0.142	-23	-0.54	0.589	-76	-4.17	**<0.001**
OD9 decreasing	34	0.83	0.409	-61	-1.42	0.159	-41	-2.22	**0.029**
Dark	42	1.01	0.315	-76	-1.78	0.079	-39	-2.11	**0.038**

Paper V

Orchestrated movements of copepods in the dark conducted by the Moon, Sun, and aurora borealis

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Abstract

Recent studies have shown that the biological activity during the Arctic polar night is higher than previously thought. Zooplankton perform diel vertical migration during the dark period/winter, with the calanoid copepods *Calanus* spp. being one of the main taxa assumed to contribute to the observed diel vertical migration. We investigated the sensitivity of field collected *Calanus* spp. to irradiance by keeping individuals in an aquarium and exposing them to gradually increasing irradiance in white, blue, green, and red wavebands, recording their response with a near-infrared-sensitive video camera. Experiments were performed with the two oldest copepodite stages as well as adult males and females. The copepods were negatively phototactic, and the lowest irradiance eliciting a significant phototactic response was of the order of 10^{-6} μmol photons m^{-2} s^{-1} for white, green and blue wavebands, whereas the comparative irradiance for red wavebands was up to three orders of magnitudes higher.

The different copepod developmental stages displayed different sensitivities to irradiance. During the darkest part of the polar night, the lowest irradiance for significant response corresponded to 0.0085-3.4 % of the ambient surface irradiance, and *Calanus* spp. may respond to irradiance from the night sky down to 40-50 m, moonlight to 100-140 m, and aurora borealis down to 60-100 m depth. The high sensitivity to blue and green light may explain the *Calanus*' ability to perform diel vertical migration during the polar night when intensity and diurnal variation of ambient irradiance is low.

Keywords: phototaxis, light response, spectral sensitivity, Arctic

Introduction

The diel vertical migration (DVM) of zooplankton is found in all the world's oceans, and is considered the largest synchronised movement of biomass on the planet (Hays 2003). It is thus an important factor in structuring the pelagic community. The most common type is nocturnal DVM, where the plankton ascend to surface waters at sunset to feed in the darkness, hiding from visual predators, and descend to deeper waters at sunrise. The ultimate cause for DVM is considered to be the optimising of feeding at the same time as minimising the risk of being predated (the predator evasion hypothesis; e.g., Lampert 1989; Hays 2003). The primary proximate cause of DVM is considered to be the use of light as an exogenous cue (irradiance 400-700 nm; henceforth abbreviated as E) (e.g., reviewed in Cohen and Forward 2009). There are three main hypotheses to explain this. The isolume hypothesis states that the zooplankton will follow a preferred E level during migration. The rate-of-change hypothesis describes the relative rate and direction of change in E from the ambient level as the cue for migration, while the absolute intensity threshold hypothesis states that migration is initiated when E increases above or decreases below a certain threshold intensity (Lampert 1989; Ringelberg 1995, 1999; Hays 2003; Ringelberg and Van Gool 2003; Cohen and Forward 2009). The spectral sensitivity of the zooplankton is also of importance, as it influences the E available to the individuals. The peak spectral sensitivity tends to be clustered in the blue-green wavebands (460-530 nm), matching the ambient E at the time of migration, which commonly is twilight (Forward 1988; Cohen and Forward 2009).

Copepods are major contributors to DVM, and may perform diel migrations down to 200-300 meters (e.g., Tande 1988; Dale and Kaartvedt 2000; Fortier et al. 2001; Baumgartner et al. 2003; Yamagutchi et al. 2004; Cottier et al. 2006). Assuming that E is the proximate factor triggering the migration behaviour, copepods must have high sensitivity to light to be able to detect and respond to E at great depths. A few studies have investigated the phototactic response of copepods related to the rate of change and absolute intensity threshold as well as spectral sensitivity. Cohen and Forward (2005) studied responses of *Calanopia americana* to absolute E changes as well as relative rates of change, and found that both factors affected DVM. Stearns and Forward (1984) investigated both E thresholds for phototactic response as well as the spectral sensitivity of *Acartia tonsa*, and found that the peak spectral sensitivity was broad and matched the E available for the copepods during daytime. Cohen and Forward (2002) found that the spectral sensitivities of copepod species varied between species and were closely connected to different patterns of DVM, the peak spectral sensitivity of species performing DVM in coastal waters matching the E during twilight, and that of a non-migrating species being broader and corresponding to a shallower habitat. Miljeteig et al. (submitted) established the absolute E threshold for phototactic response of *Calanus finmarchicus* from a laboratory culture, and concluded that it matched the E available in the depth range reported for natural *C. finmarchicus* populations.

In the Arctic, DVM has mostly been studied during the time of year when there is a distinct photoperiod (daylight), and a clear DVM signal has been described (Fortier et al. 2001; Cottier et al. 2006; Falk-Petersen et al. 2008; Wallace et al. 2010; Rabindranath et al. 2011). Over the last few years, researchers have also taken interest in the dark winter period, the polar night, and recent studies have described biological activity far higher than previously thought during this time of year (Sato et al. 2002; Berge et al. 2009, 2012; Fort et al. 2010). It has been shown that zooplankton perform DVM during the polar night despite the low light conditions (Berge et al. 2009, 2012). The E in the polar night originates from different sources, and has varying periodicity. The night sky and scattered E from the Sun has a 24 hour cycle, and the latter varies with the time of year, the daytime E increasing/decreasing with the solar elevation angle (e.g., Simmons et al. 1996). The moonlight has an approximate 25 hour daily cycle as well as the 29 days lunar cycle. The aurora borealis also has a 24 hour cycle due to the Earth's rotation under the aurora oval, and in Svalbard, the green aurora (emission line 557.7nm) outbreaks are most frequent between 19:00 and 00:00 (e.g., Myrabø 1985; Simmons et al. 1996). In the Arctic, the frequency of active aurora borealis varies

depending on location and the solar activity. Furthermore, all E varies according to cloud cover. Thus, although variable, there is a periodicity in all polar night E, which in theory could influence high-latitude ecosystems.

The calanoid copepod genus *Calanus* is one of the major taxa performing DVM in the Arctic (e.g., Dale and Kaartvedt 2000; Fortier et al. 2001; Cottier et al. 2006; Rabindranath et al. 2011). The genus constitute a major part of the zooplankton biomass in the Arctic shelf seas (e.g., Hassel 1986; Mumm et al. 1998; Blachowiak-Samolyk et al. 2008), and is a highly important food source for amphipods and other zooplankton, as well as fish, seabirds, and whales (e.g., Falk-Petersen et al. 1990; Auel and Werner 2003; Baumgartner and Mate 2003; Karnovsky et al. 2003). *Calanus* spp. are considered to be primarily herbivores, but may also switch to heterotrophic prey (reviews by Falk-Petersen et al. 2009; Vadstein 2009). In the Arctic, the most dominant *Calanus* species are *C. hyperboreus*, which is associated with the deeper parts of the polar ocean, *C. glacialis*, an Arctic shelf species, and *C. finmarchicus*, which is dominant in areas influenced by water masses with Atlantic origin (e.g., Conover 1988; Falk-Petersen et al. 2009). As *C. hyperboreus* mainly is a polar basin species, overwintering at large depths (500-2000 m; Falk-Petersen et al. 2009), *C. glacialis* and *C. finmarchicus* are the dominant species in West Spitsbergen fjords during winter (Arnkværn et al. 2005; Berge et al. 2012). The main overwintering stages of *C. glacialis* and *C. finmarchicus* are copepodite stage IV (CIV) through adults (e.g., Tande 1982; Hirche 1991; Falk-Petersen et al. 2009).

Due to the ecological importance of *Calanus* spp., as well as the reported DVM during polar night (Berge et al. 2009, 2012), the genus was used in this study. The E in the polar night has low intensity, but still a certain periodicity, and given a sufficient sensitivity to E, zooplankton could be influenced by it. To our knowledge, the only study investigating the E threshold for response of *Calanus* spp. was performed with laboratory cultured *C. finmarchicus*, using a white light stimulus (Miljeteig et al. submitted). We aim to investigate the absolute E needed to elicit a phototactic response in an Arctic population of *Calanus* spp. by sampling in field during the polar night, and using a laboratory experimental setup designed to test phototactic response in low-light conditions. We perform experiments with the developmental stages of *Calanus* spp. present in the polar night, investigating the sensitivity to different wavebands of visible light. We also compare the *Calanus* spp. response

and sensitivity to E during daytime and night-time, and finally we relate our findings to the ambient E in the polar night.

Materials and methods

Zooplankton collection

Calanus spp. were collected using a WP3 net (mesh size 500 μm, diameter 1 m) in Adventfjorden, close to Longyearbyen, Svalbard (78.228 N, 15.604 E) through a hole in the ice. Samples were collected the 7^{th}-8^{th}, 11^{th}, and 17^{th} of January 2011. Several net hauls were taken during the 4 sampling days to collect the sufficient amount of zooplankton. The samples were stored in 10-20 L buckets and transported to a seawater laboratory at the University Centre in Svalbard, Longyearbyen. The *Calanus* spp. were immediately sorted by developmental stage; copepodite stages IV and V (CIV and CV), and sex; adult females and males (AF and AM), and incubated according to stage in 3 L buckets with lids at 1-2 °C (20-25 individuals per bucket). Due to sampling in shallow waters, there was some sediment in the samples. During sorting, the *Calanus* spp. were inspected visually for sediment particles and only individuals appearing healthy were selected for experiments. Buckets were covered in 3 layers of black plastic bin liners and stored in the dark seawater laboratory for at least 24 hours to ensure the zooplankton were acclimated to darkness before the experiments.

The experimental setup

An acrylic glass aquarium with 18 cm width, 48 cm length, and 8 cm height (internal dimensions), and 1 cm thick walls, was used to keep the zooplankton (sampled in January 2011) during experiments. Inside the aquarium was a 48×8 cm wall, which was used to adjust the width to fit the light stimulus (13 cm), limiting the projection area available to the copepods to 48×13 cm. The water depth was 6 cm during all experiments. Experiments were performed in the horizontal plane to avoid possible effect of gravitation. A light emitting diode (LED) was fitted to a filter wheel with integrated controller (Tofra, Inc., Palo Alto, California, US). The filter wheel was attached to a 14×10×12 cm light tight box with a Fresnel lens (95×135 mm, optical PVC, 3Dlens.com, Taiwan) in front, making the light path collimated. To adjust the E, the filter wheel contained neutral optical density (OD) filters (CVI Melles Griot, Netherlands) with increasing OD (absorbance, dimensionless). OD is

logarithmic, decreasing the E with 1×10^{-1} for each increasing OD number. Filters with OD from 4 to 9 were used in the experiments, called OD4 to OD9, respectively. The LED and filter wheel assembled in the light tight box made up the light stimulus unit. WheelTool v1.0 software (Tofra Inc., Palo Alto, California, US) controlled the position of the filter wheel. In addition, LabView 8.2.1 software was used to further adjust the E of the LEDs by pulsing the light. It was used to reduce the E at each OD level by 50 % (for simplicity named OD4.5, OD5.5, and so on), providing a higher resolution to the E levels the zooplankton were exposed to. Experiments were performed with white (LXHL-PW01), blue (LXHL-PR03; emission peak at 455 nm), green (LXHL-PM01; peak at 525 nm; called green525), and red (LXHL-PD01; peak at 640 nm) LEDs (Fig. 1). In addition, the white LED was used with a green transmission filter with peak at 550 nm (hereafter called aurora green550), to more closely simulate the green aurora borealis (emission line at 557.7 nm), which is a common light source in the polar night.

To record the responses of the zooplankton, the aquarium was placed on a table with a 48×18 cm hole, and illuminated from below by four inclined near-infrared (N-IR) lamps (IR30, SmartProdukter Norge AS, emission peak at 850 nm). The experiments were recorded from above using a N-IR sensitive video camera (Sony Handycam HDR-XR550) in NightShot mode standing on a quadrapod (Quadrapod Elite Copy Stand, Forensic Imaging, Inc., US). The N-IR lamps were covered with filters to remove the visible part of the spectrum (Kodak Wratten Infrared filters, #87C, Edmund Optics Ltd, York, UK; 0% transmission up to ~790 nm). The experimental setup was covered in black fabric during experiments to avoid possible stray light from entering and to minimise the effect of air currents on the aquarium. See Online Resource 1 for a photograph of the experimental setup.
The experimental setup, apart from the aquarium and the N-IR lamps, was the same as described in Miljeteig et al. (submitted).

A spectroradiometer (ORIEL Fixed Imaging Compact Spectrograph; FICS SN 7743) was used to obtain the spectral E used in experiments. The detector of the instrument was placed in front of the aquarium, on the opposite side of the light stimulus unit, and the highest E levels for all LEDs (OD4 through OD6 for white, blue, green525, and red, and OD3 through OD5.5 for the aurora green550) were measured. The lower E levels were outside the linear response area of the instrument, and were instead calculated, extrapolating from the measured E levels. As the detector was not waterproof, the measurements were done outside of the

aquarium, including both aquarium walls as well as the water. Thus, the E measured was lower than that experienced by the copepods. To correct for this, measurements were also done (white LED, OD5), with only one aquarium wall as well as through both walls of the aquarium without water, and the fraction of E absorbed by one aquarium wall was calculated. This factor was then used to correct the E for all wavebands and OD levels used. The spectroradiometer was calibrated with a Quartz Tungsten Halogen lamp (Oriel Instruments, Model no. 63358, 45 W, 6.5 A) to convert the data from the original output in counts s^{-1} to $\mu W\ m^{-2}\ nm^{-1}$. To convert to photons $m^{-2}\ s^{-1}\ nm^{-1}$, the equation by Baker and Romick (1976) was used:

$$1 \text{ photon/s} = 1.986475(1/\lambda) \times 10^{-19} \text{ W},$$

where λ is wavelength in μm. The output was further converted into μmol photons $m^{-2}\ s^{-1}\ nm^{-1}$.

Light response experiments

All experiments were performed in a temperature controlled seawater laboratory at the University Centre in Svalbard. Room and water temperature was 1-2 °C. To make the laboratory completely dark and prevent stray light, all openings were covered with 3 layers of aluminium foil. The computer controlling the light stimulus was placed outside the laboratory, so that the experiments could be performed without entering the room. Freshly collected *Calanus* spp. (20 individuals for stages CIV and AM, 25 individuals for stages CV and AF; acclimated in dark for at least 24 hours prior to experiments) were transferred from the storing buckets to the aquarium as quickly as possible, using only red light to minimise light exposure (Cohen and Forward 2005). A small touch by a pair of tweezers was used as a simple fitness test; only individuals performing immediate escape response were considered healthy and used in experiments. The *Calanus* spp. were acclimated in the aquarium for at least 1 h in darkness before experiments started. The location of the light stimulus was alternated from one side of the aquarium to the other between replicates to control for room effects, e.g., air currents produced by the cooling system.

24 hour experiments

24 hour experiments (two replicates with different sets of *Calanus* spp. individuals) were performed to test whether the *Calanus* spp. responded differently during daytime than night-

time. The light stimulus was a white LED. A sample of 25 specimens of *Calanus* spp. CV were transferred to the aquarium at 11:00 and dark acclimated, and at 12:00 (noon) the camera was turned on to record the starting distribution (darkness). After 10 min the LED was turned on, starting with OD8 (0.099×10^{-6} μmol photons m^{-2} s^{-1}; Table 1). The E range used in the experiment was determined by preliminary experiments (not shown), to ensure a starting E well below the threshold for phototactic response. Every 10 minutes, the filter wheel was turned so that the OD decreased by 1, thus increasing the E. The highest E used for this experiment was OD4 (860×10^{-6} μmol photons m^{-2} s^{-1}), giving a total of 6 E levels including the dark initial period. The light stimulus was then turned off and the *Calanus* spp. were left in the aquarium. This procedure (trial) was repeated every 3 hours for 24 hours (at 15:00, 18:00, 21:00, 00:00, 03:00, 06:00, 09:00) and then one last time at 12:00; making a total of 9 trials for each replicate.

Threshold value experiments (white, blue, green525, aurora green550, and red wavebands)

A sample of 20 (for stages CIV and AM) or 25 (for stages CV and AF) specimens of *Calanus* spp. were transferred to the aquarium and dark acclimated. The camera was turned on, and the first 10 minute period of the experiment was recorded as distribution in darkness. The light stimulus was then turned on, the starting E level varying from OD7.5 to OD9 depending on the waveband (Table 2; Fig. 1). The E range used for each waveband was determined by preliminary experiments (not shown), to ensure a starting E well below the threshold for phototactic response. Every 10 minutes the E was increased by incrementing the OD by 0.5. The *Calanus* spp. were left in the dark for at least 1h to acclimate, the LED was then changed to a different waveband and a corresponding experiment was performed. The order of the wavebands was randomized. Experiments with the aurora green light stimulus were run with stage CV only.

Image analysis

Using Picture Motion Browser video software (v 4.2, Sony Corporation) we extracted one still image per minute from the video of the experiments, amounting to ten images representing each E level. Images were analysed in stacks (one stack per replicate), using the image analysing software ImageJ (1.43u; Rasband 1997-2009). The images were cropped and contrast was improved. Using the whole image stack, the median image was calculated and

then subtracted from the stack, removing air bubbles, aquarium edges, and debris (all stationary objects). Colour threshold was adjusted (saturation and brightness) to create binary images for particle analysis. The particle analyses was performed by defining thresholds for minimum size and circularity, and provided the particles' distances from the light stimulus (in cm; the total length of the aquarium was 48 cm), as well as their size (area in square pixels). Due to some floating debris particles in the aquarium, the number of particles was larger than the number of copepods. We assumed that the copepods were the largest particles observed, and used the R environment (R Development Core Team 2012) to extract the position of the 20 or 25 (depending on stage) copepods for further analyses.

Statistical analyses

Statistical modelling of the experimental data was performed using linear mixed-effects modelling, computed with the packages nlme and lme4 in the R environment (Bates et al. 2011; Pinheiro et al. 2012; R Development Core Team 2012).

24 hour experiments:

The trials performed at 18:00, 21:00, 00:00, 03:00, and 06:00 from both replicates (10 trials altogether) were defined as night-time, and the remaining (12:00, 15:00, 09:00, and 12:00 second time; 8 trials altogether) were defined as daytime. The phototactic response was tested with linear mixed-effects modelling, with trial as random factor to account for the repeated measurements nature of the design. Median position (distance from light stimulus) over the duration of an E level (10 minutes) was used in the analysis. Firstly, for night-time, the distribution of copepods at each E level was compared to the distribution of copepods in the initial dark period. Then, the distribution of copepods during daytime trials as a whole was compared to that of night-time. Lastly, the distribution of copepods at each level during daytime was compared to that of each level during night-time, to investigate whether the response was different during day compared to night. The conventional significance level of 0.05 was lowered to 0.01, to reduce the false discovery rate when conducting multiple tests.

Threshold value experiments (white, blue, green525, aurora green550, and red wavebands):

The phototactic response in each experiment (developmental stage and waveband; Table 2) was investigated using linear mixed-effects modelling, with replicate as random factor to account for the repeated measurements nature of the design. Median position (distance from

light stimulus) over the duration of an E level (10 minutes) was used in the analyses. The distribution of copepods at each E level was compared to the distribution of copepods in the initial dark period. The overall significance of effects in the model was tested by the ANOVA F statistic, with the significance level set at 0.05. The significance level was again lowered to 0.01 for testing individual effects, due to the problem of multiple testing.

Irradiance from natural light sources in the polar night

There was no light meter or spectroradiometer available that was sensitive enough to measure ambient polar night E, hence values for background (night sky) E, moonlight, and aurora borealis at sea surface, as well as data on cloud cover, could only be derived from literature (Waterman 1974; Myrabø 1985; Simmons et al. 1996; Jensen et al. 2001; Müller et al. 2011). Neither was there an extinction coefficient available for the water masses on West Spitsbergen during winter, but we assumed that the inherent optical properties of the water and its constituents (Johnsen et al. 2009) resembled those of Arctic water masses at a time of year with low concentrations of chlorophyll a ("winter concentration"), coloured dissolved organic matter and total suspended matter (Case 1 waters; Jerlov 1968). Water masses with these characteristics were sampled in the Barents Sea during August by Hovland et al. (2012), and this extinction coefficient was used to model the E from the different light sources with increasing depth. The E with increasing depth was compared to the lowest E for significant response in *Calanus* spp. to investigate how deep the copepods may be influenced by E during the polar night. The E eliciting a significant response in *Calanus* spp. was also compared (in %) to the surface E from moonlight, night sky and aurora borealis.

Results

24 hour experiments

The median distance to the light stimulus increased with increasing E through the trials, thus, the *Calanus* spp. CV were consistently negatively phototactic throughout the 24 hour period (see Online Resource 2 for figures). The response to the white LED used was significant from 0.94×10^{-6} μmol photons m^{-2} s^{-1} (OD7; Tables 1, 3). There was no overall change in response to the light stimulus during day compared to night ($p = 0.822$; Table 3). Neither were there diel changes in response to the light stimulus at any E level ($0.057 < p < 0.646$; Table 3).

Threshold values experiments

Calanus spp. were negatively phototactic for all wavebands (Fig. 2; Table 4; see Online Resource 2 for viewing the replicates separately). For all stage CV experiments, AF experiments with white, green525, and red, and AM experiments with white, blue, and red LED, there was a phototactic response throughout the experiments, and a threshold value for response was identified. For the experiment with stage CIV white LED, there was a phototactic response over time (ANOVA p=0.026; Table 4), however, no significant threshold value for response was detected. For the remaining experiments we did not detect a significant phototactic response. The threshold E level for response differed depending on waveband as well as copepod developmental stage (summarised in Table 5). For the white waveband, the threshold for significant phototactic response was 0.47-42×10^{-6} μmol photons m^{-2} s^{-1} (Tables 4, 5). For the blue waveband, the threshold for response was 4.3×10^{-6} μmol photons m^{-2} s^{-1}, and for the green525 waveband, the threshold for response was 0.34-2.1×10^{-6} μmol photons m^{-2} s^{-1}. For aurora green550 (experiments performed with stage CV only), the threshold was 0.43×10^{-6} μmol photons m^{-2} s^{-1}, which was lower than the significant response of stage CV to green525 LED (2.1×10^{-6} μmol photons m^{-2} s^{-1}). For the red waveband the threshold for significant response was 310-1800×10^{-6} μmol photons m^{-2} s^{-1}. Thus, the sensitivity to red light was one to three orders of magnitude lower compared to other wavebands. For white and green525 wavebands, AF showed the highest sensitivity to light, while CIV generally were the least sensitive, displaying a significant response to white only. Where a threshold level for phototaxis could be detected for blue and green wavebands, the threshold E corresponded to <0.86% of surface moonlight and 1-43% of surface night sky E (Table 5). The threshold level for phototaxis for green525 and aurora green550 corresponded to <2.1% of surface aurora borealis E. For the red waveband, the threshold level for response corresponded to >20% of the surface moonlight, and >100% of the night sky E.

Discussion

All developmental stages and both sexes of *Calanus* spp. displayed negative phototaxis, and were highly sensitive to E. The negative phototaxis is in accordance with what would be expected for species displaying nocturnal (normal) DVM, which has been documented for *Calanus* spp. (e.g., Nicholls 1933; Huntley and Brooks 1982; Frost 1988; Lampert 1989;

Fortier et al. 2001; Falk-Petersen et al. 2008; Baumgartner et al. 2011). The lowest E eliciting a significant phototactic response in this study were 0.34×10^{-6} μmol photons m^{-2} s^{-1}, displayed by AF (green525 waveband; see Tables 3-5), and 0.43×10^{-6} μmol photons m^{-2} s^{-1}, displayed by CV (aurora green550; simulating aurora borealis emission line). These are ecologically relevant E values, corresponding to <0.09% of the surface moon E, <4% of the night sky E, and <0.4% of the Aurora borealis E (Table 5). This clearly indicates that a phototactic response to ambient E is indeed possible for *Calanus* spp. in the polar night.

When applying an E threshold value of 0.34×10^{-6} μmol photons m^{-2} s^{-1} as well as an attenuation coefficient of light in water assumed to correspond to the ambient (winter) conditions, *Calanus* spp. may respond to E from the clear night sky down to about 40-50 m, from aurora borealis down to 60-100 m, and moonlight to 100-140 m depth (Fig. 3). Berge et al. (2009) found that DVM occurred at a depth range of 30-60 m during the darkest time of the polar night (mid December to early January). This corresponds well to our estimated depth range of night sky E detection of *Calanus* spp. As the solar elevation angle increases after winter solstice, the E (solar background) during midday will increase, as will the depth for E detection. This is reflected in the data of Berge et al. (2009), showing that the depth of DVM increased to around 70 m in late January and beyond 90 m in February. Berge et al. (2012) also detected a DVM signal down to 80-90 m in late January. The E from aurora and moonlight will probably be detected deeper into the water column than night sky/solar background during mid-winter (Table 5; Fig. 2). This is supported by the study of Berge et al. (2009), who found that during the 3 days prior to and after full moon, there was a shift in DVM signal from a 24 hour cycle toward a 25 hour lunar cycle. Zooplankton performing reverse DVM during full moon, the Moon rising during night and setting during day, has also been described in Svalbard in January (Webster et al. unpublished data). The DVM signal has to our knowledge not been investigated in relation to the aurora borealis, but the intensity of auroras is probably high enough for affecting DVM (Fig. 3). The frequency of winter nights with clear or partially clear skies has been reported to be 68 % for Longyearbyen, Svalbard (1986-1995; Simmons et al. 1996). Looking at the frequency of auroras, the average occurrence was approximately 65 % for the same location (varying between 55 and 95 % from 2000 through 2012; Pulkkinen et al. 2011). Thus, the frequency of nights with aurora visible at sea surface level may be about 44 % (0.68 × 0.65 = 0.44). The intensity of the aurora varies, as will the depth it can be perceived by the zooplankton, so the frequency of

44 % may be seen as a maximum estimate. Still, the aurora may, at least in periods, affect the zooplankton during the polar night.

The *Calanus* spp. specimens used in our experiments were probably a mix of *C. glacialis* and *C. finmarchicus*, as these are species described to be common in West Spitsbergen fjords (e.g., Hop et al. 2006, Kwasniewski et al. 2003, Arnkværn et al. 2005, Gabrielsen et al. 2012), and that the third common *Calanus* species, *C. hyperboreus*, would have been recognised by its size as well as morphological traits during sorting. We chose not to attempt identification of the specimens to species, due to that recent investigations have described large rates of misidentification using prosome length, which is the conventional and least time-consuming way of separating *C. glacialis* and *C. finmarchicus* (Parent et al. 2011; Lindeque et al. 2004; Gabrielsen et al. 2012). In addition, these species have recently been found to have a high frequency of hybridisation (Parent et al. 2012). We thus treated our sets of individuals as *Calanus* spp. As the specimens were sampled from the population in Adventfjorden during January, they were ecologically relevant for our study.

The different developmental stages and sexes showed different sensitivities to E. AF were the most sensitive, with thresholds of e.g., 0.47 and 0.34×10^{-6} μmol photons m^{-2} s^{-1} for white and green525 wavebands, respectively (Table 5). The lowest E thresholds for stage CV were 0.43 and 2.1×10^{-6} μmol photons m^{-2} s^{-1} for aurora green550 and green525 wavebands, respectively, while for AM the lowest threshold values were 4.3 and 42×10^{-6} μmol photons m^{-2} s^{-1} for blue and white wavebands, respectively. Stage CIV displayed negative phototaxis to white only, but no threshold value could be identified. Related to DVM, this would correspond to deepest migration depths for AF, followed by CV, AM, and probably shallowest for CIV, which is in accordance with field studies of stage-specific migration depth of *Calanus* spp. copepodite stages and AF. Huntley and Brooks (1982) found that for *C. pacificus*, the amplitude of DVM increased with increasing age/stage, the night depths remaining constant while daytime depths increased. Nicholls (1933) reported that *C. finmarchicus* AF inhabited the deepest parts and that migration depth decreases with stage, and Unstad and Tande (1991) reported the same for both *C. finmarchicus* and *C. glacialis*. During summer in Kongsfjorden, West Spitsbergen, the younger stages (CI-CIV) of *C. finmarchicus* and *C. glacialis* have been reported to inhabit surface and intermediate water layers, while older stages stayed in bottom layers, however, the latter had probably descended for overwintering (Kwasniewski et al. 2003). An explanation to the deeper migration of larger stages may be that larger and more pigmented

individuals are more susceptible to predators, and must thus, according to the predator evasion hypothesis, migrate deeper to get the same protection (Hays 2003). The need of high sensitivity to light is thus expected to be more pronounced in larger and older individuals, which is generally supported in this study. Larger individuals also tend to have larger lipid reserves, which decreases the need of migrating to surface waters to feed (e.g., Hays et al. 2001; Hays 2003). This may be part of the explanation to the deeper distribution and higher light sensitivity of older individuals. In this study, AM displayed lower sensitivity to light than AF and CV, as well as higher variability in response (Fig. 2; Table 4; Online Resource 2), and did thus not follow the general rule of higher sensitivity to light in older stages. Copepod AM generally display higher swimming activity than AF and CV, spend little time feeding, and are mainly focused on mate-finding, (e.g., Irigoien et al. 2000; Kiørboe and Bagøien 2005), which may lead to the weaker and less uniform response to E. In contrast to this study, Miljeteig et al. (submitted) found that *C. finmarchicus* AM from a laboratory culture had a strong, uniform positive phototaxis. The reason for these differences is not known, but the cultured animals may be acclimated differently both regarding nutritional and mating status compared to the polar night acclimated, field collected specimens.

The threshold E values we found for *Calanus* spp. are highly comparable to those of other zooplankton. For Crustacea in general, the threshold was stated to be about 5×10^{-5} μW cm^{-2} (Waterman 1974), corresponding to about 2.3×10^{-6} μmol photons m^{-2} s^{-1}, which is approximately one order of magnitude higher than the lowest threshold detected in this study. Cohen and Forward (2005) found that using the blue-green waveband, the copepod *C. americana* responded to E > 1×10^{11} to 1×10^{14} photons m^{-2} s^{-1} during day and night, respectively, which corresponds to 0.17-170×10^{-6} μmol photons m^{-2} s^{-1}. The copepod *A. tonsa* displayed positive phototaxis, and responded to E down to 2.8×10^{11} photons m^{-2} s^{-1}, corresponding to 0.46×10^{-6} μmol photons m^{-2} s^{-1} (Stearns and Forward 1984). For *Calanus* spp., a few studies have looked at the response to ultraviolet radiation stress and PAR in *C. finmarchicus* (Aarseth and Schram 1999; Wold and Norrbin 2004), but the E levels used in these studies were relatively high (14-75 μmol photons m^{-2} s^{-1}) and thus not relevant for detecting a threshold level for response. Miljeteig et al. (submitted) detected threshold levels of 0.99-9.8×10^{-6} μmol photons m^{-2} s^{-1} (white waveband) for *C. finmarchicus* CV, AM, and AF from a laboratory culture. The threshold E for response of field collected *Calanus* spp. in this study to the white waveband was slightly lower for CV and AF, but higher for AM.

The E needed to elicit a significant phototactic response was lowest in the green wavebands (0.34-2.1×10^{-6} μmol photons m^{-2} s^{-1}; Table 2), slightly higher in the blue waveband (4.3×10^{-6} μmol photons m^{-2} s^{-1}), and more variable in white (0.47-42×10^{-6} μmol photons m^{-2} s^{-1}). For stage CV, the E for significant response was lower in aurora green550 (0.43×10^{-6} μmol photons m^{-2} s^{-1}) compared to green525 (2.1×10^{-6} μmol photons m^{-2} s^{-1}). The *Calanus* spp. were about 1 to 3 orders of magnitude less sensitive to red (310-1800×10^{-6} μmol photons m^{-2} s^{-1}), depending on developmental stage and sex. The low sensitivity to red is probably related to the ecology of these copepods. The extinction coefficient of light in water is higher in the red waveband (600-700 nm) than in the rest of the visible spectrum (Sakshaug et al. 2009), and the blue or green light penetrates deepest depending on the constituents of the water (blue in Case I water, green in Case II water; Jerlov 1968; Sakshaug et al. 2009). *C. finmarchicus* and *C. glacialis* are pelagic species, inhabiting depths down to hundreds of meters (e.g., Tande 1988; Fortier et al. 2001; Cottier et al. 2006; Falk-Petersen et al. 2009; Bergvik et al. 2012), and benefit from being more sensitive to the predominant blue-green wavebands than to red. This pattern has also been confirmed by hyperspectral imaging of *Calanus* spp. eyes, showing high reflectance and thus low absorbance in the red waveband, and lower reflectance/higher absorption in blue and green wavebands (Båtnes et al. unpublished data). Cohen and Forward (2002) investigated the spectral sensitivities of four copepod species displaying different migration patterns, and found that the species *Centropages typicus* and *C. americana*, both performing nocturnal DVM, had spectral sensitivity peaks from 480 to 520 nm, which is in the range of the blue and green wavebands used in this study. Species inhabiting shallow/estuarine waters with broad spectral E have broader spectral sensitivities, e.g., *A. tonsa* (Stearns and Forward 1984) and *Labidocera aestiva* (Cohen and Forward 2002).

The phototactic response of *Calanus* spp. was not significantly different during day compared to night (Table 3). In contrast, the copepod *C. americana* had an E threshold of response three orders of magnitude lower during day than during night (Cohen and Forward 2005). *C. americana* undergoes twilight DVM, which involves a descent after sunset (the "midnight sink") and an ascent before sunrise (the "early morning rise") in addition to the sunset ascent and sunrise descent also involved in nocturnal DVM. The additional descent and ascent is under endogenous control, and the endogenous rhythms of *C. americana* were thought to suppress the phototactic response during night (Cohen and Forward 2005). *Calanus* spp. is

known to perform nocturnal DVM, which may explain the uniform phototactic response over 24 hours.

For the CIV white waveband experiment, there was a significant phototactic response, but no particular threshold could be detected (Table 4), and for many of the experiments, the response seems to be gradual, ranging over at least three E levels (Fig. 2). This may indicate variability within the group of copepods, some of the individuals starting the response earlier than others, and some not responding at all. As we did not track the position of the individuals, only of the group, we could not detect this in detail. The group of individuals in each replicate was probably composed of at least two different species (*C. glacialis* and *C. finmarchicus*), and of individuals with different nutritional status as well as different age/development within the stage (Nicholls 1933), and this may affect the DVM behaviour (e.g., Huntley and Brooks 1982; Hays et al. 2001; Bergvik et al. 2012) and the underlying light responses. In addition, due to sampling difficulties the number of replicates (2-3 replicates with 20-25 individuals in each) was low, which makes the analyses vulnerable to variability between replicates. The variability between replicates may appear because of "room effects" (air currents from the cooling system and other, unidentified causes), in addition to that some of the *Calanus* spp. may have been in poor condition after sampling and storage in buckets over time (24 hours to 18 days). Particularly AM are vulnerable to handling and keeping in small containers, (D. Altin, personal comment), which is reflected in highly variable results with replicates 2 and 3 (Online Resource 2). The variability between replicates may also partly explain the lack of significant results in some of the experiments (e.g., CIV and AF blue waveband), even though the results as shown in a figure (Fig. 2) may be interpreted as a clear phototactic response.

Knowledge about the spectral sensitivities as well as the E levels triggering phototactic response is crucial to understanding the migrations of *Calanus* spp. and their role in the polar night ecosystem. In this study, we show that both developmental stages and both sexes (CIV, CV, AF, and AM) responded with negative phototaxis to at least one of the wavebands used in the experiments. The lowest E eliciting a significant response (0.34×10^{-6} μmol photons m^{-2} s^{-1}) corresponds to 0.0085-3.4 % of the polar night surface E. Modelling the E from different light sources with depth, the *Calanus* spp. may respond down to approximately 40-50 m depth to clear night sky E, 100-140 m to moonlight, and 60-100 m to aurora borealis. This supports that the ambient E, including the aurora borealis, may be a proximate cue for DVM

also during the polar night. Further investigations on the rhythmicity of migrations in relation to ambient E, as well as the ultimate reasons for undergoing diel migrations in "complete darkness", would further increase the understanding of marine pelagic ecosystem in the polar night.

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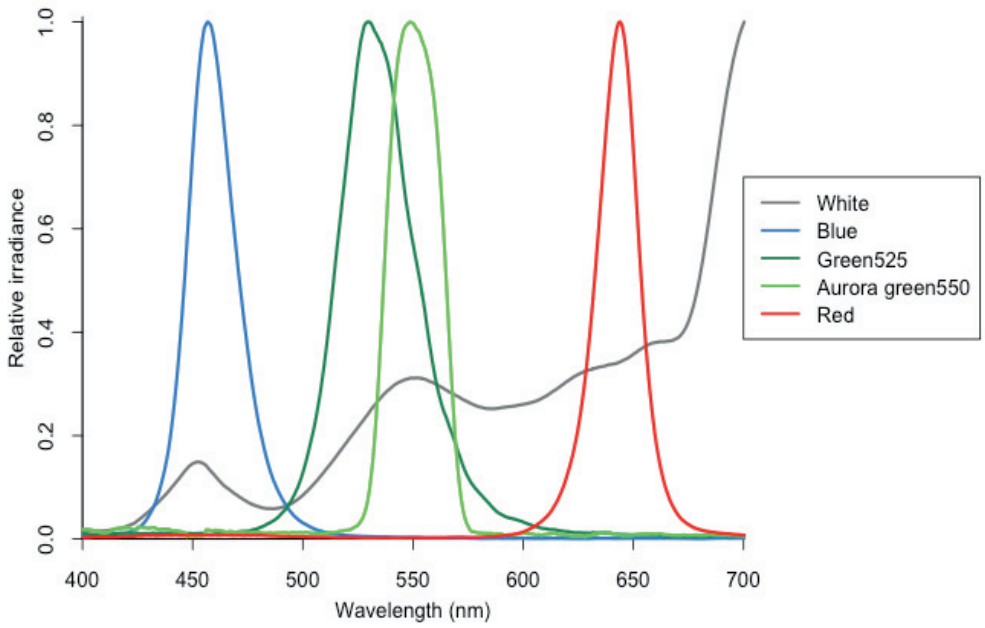

Fig.1 Relative spectral irradiance (E) for the different wavebands used in experiments. Based on the measurements of OD5 for all wavebands

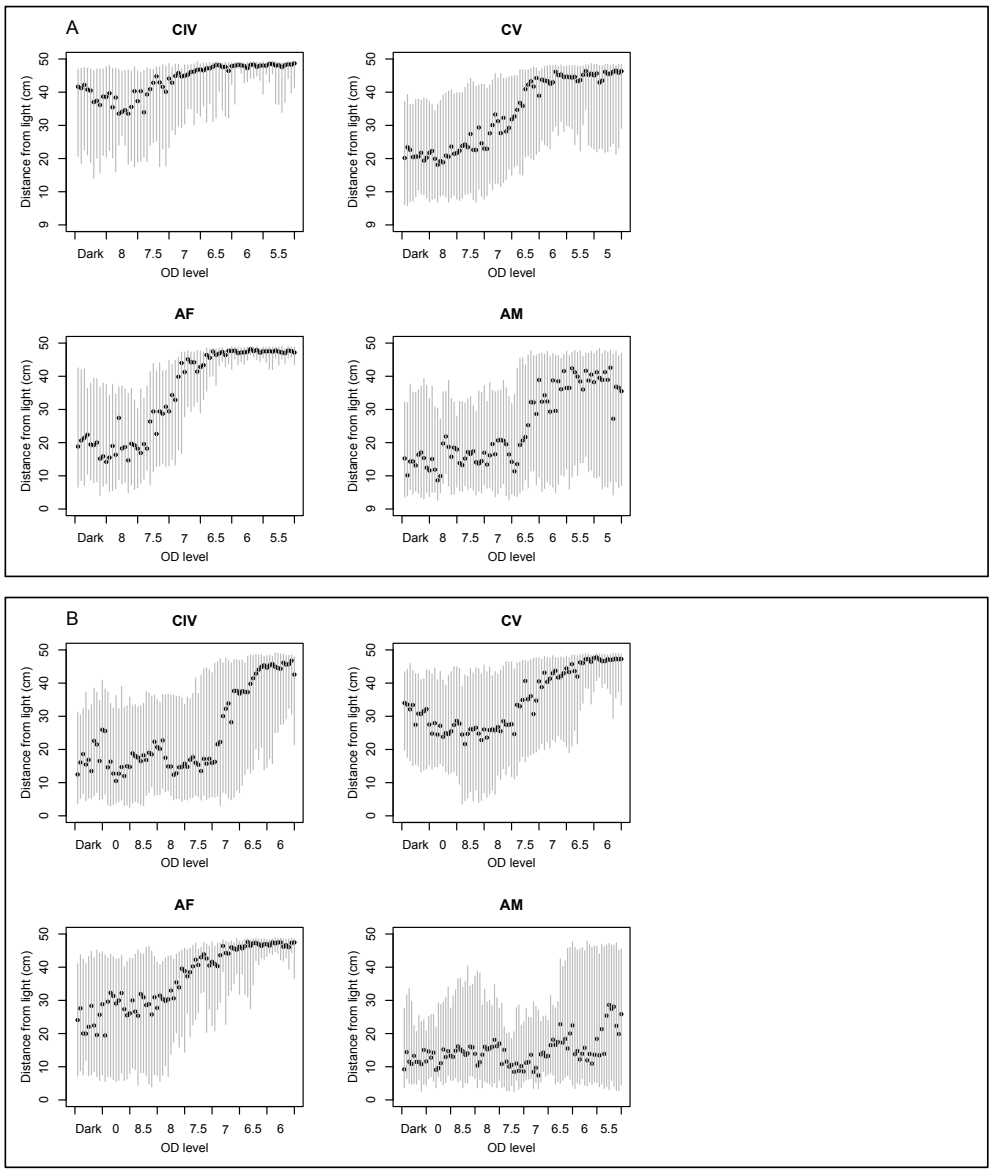

Fig. 2 Median distance from light (cm; each black dot representing one minute) with interquartile range (grey bars) over the duration of each experiment (2-3 replicates per experiment, see Table 2) for A) white, B) blue, C) green525 and aurora green550 (the latter only for stage CV), and D) red wavebands. Developmental stage/sex is indicated above each panel. Each irradiance level lasted 10 minutes. Dark is the initial dark period; subsequent OD levels are indicated (see Table 1 for the irradiance range used in each experiment).

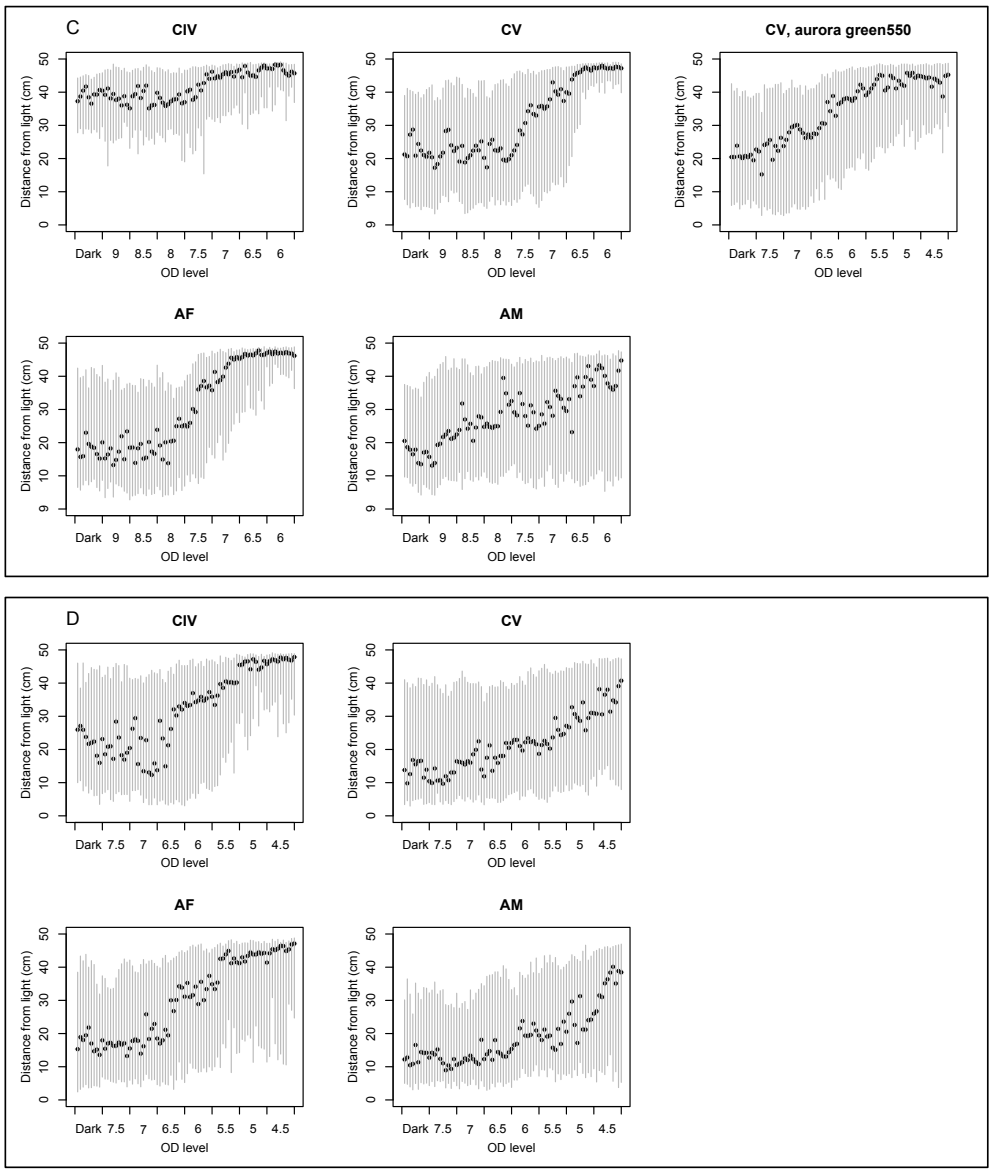
C
CIV
CV
CV, aurora green550
AF
AM
Distance from light (cm)
OD level
Dark 9 8.5 8 7.5 7 6.5 6
Dark 7.5 7 6.5 6 5.5 5 4.5
D
CIV
CV
AF
AM

Fig. 2 Cont.

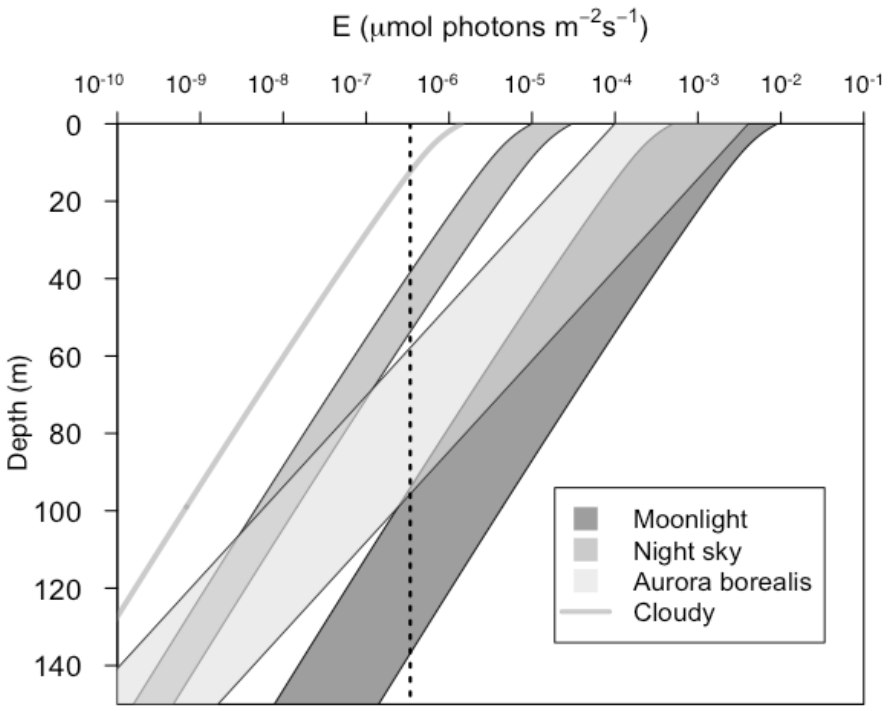

Fig. 3 Irradiance in the polar night from the Moon, night sky, and aurora borealis with depth. The vertical dotted line (0.34×10^{-6} μmol photons m^{-2} s^{-1}) represents the lowest E value for phototactic response in *Calanus* spp.

Table 1 Irradiance (E; 400-700 nm) for the different wavebands and OD levels used in experiments. Values are in μmol photons m^{-2} s^{-1} $\times 10^{-6}$.

	White	Blue	Green525	Aurora green550	Red
OD4	860	-	-	-	-
OD4.5	-	-	-	52	1800
OD5	79	-	-	8.1	310
OD5.5	42	39	-	4.6	150
OD6	9.4	8.7	4.3	0.85	28
OD6.5	4.7	4.3	2.1	0.43	14
OD7	0.94	0.62	0.34	0.083	2.6
OD7.5	0.47	0.31	0.17	0.041	1.3
OD8	0.099	0.050	0.030	-	-
OD8.5	-	0.025	0.015	-	-
OD9	-	0.0040	0.0026	-	-

Table 2 Overview of threshold value experiments performed with different *Calanus* spp. developmental stages and sexes. Number of replicates, number of individuals per replicate, the range of light intensities (range of optical densities; OD), and duration of experiments (minutes) for each waveband. White, blue, green525, and red are LEDs, aurora green550 is the white LED with a green transmission filter, emission peak 550 nm.

Stage/sex	CIV 2 replicates, 20 ind. OD range (duration)	CV 3 replicates, 25 ind. OD range (duration)	AF 2 replicates, 25 ind. OD range (duration)	AM 3 replicates, 20 ind. OD range (duration)
White	5.5-8 (70)	5-8 (80)	5.5-8 (70)	5-8 (80)
Blue	6-9 (80)	6-9 (80)	6-9 (80)	5.5-9 (90)
Green525	6-9 (80)	6-9 (80)	6-9 (80)	6-9 (80)
Aurora green550		4.5-7.5 (80)		
Red	4.5-7.5 (80)	4.5-7.5 (80)	4.5-7.5 (80)	4.5-7.5 (80)

Table 3 Output from mixed modelling of phototactic response in 24 hour experiment, comparing the distance from the light source at each irradiance level to the to the distance from light source in the initial dark period. "Distance" is the median distance from the light stimulus (cm) for the initial dark period (Dark) and change in median distance for the subsequent E levels. Dark through OD4 represent the results from night-time trials. Day is daytime; the effect needed to add to the results from night-time to get those of daytime. OD8:Day through OD4:Day represent the effects needed to add to the effects from night-time, level by level, to get the results of daytime trials.

	Distance	p-value
Dark	19.5	<0.001
OD8	0.2	0.871
OD7	3.2	<0.001
OD6	13.7	<0.001
OD5	20.8	<0.001
OD4	22.5	<0.001
Day	-0.2	0.822
OD8:Day	-2.7	0.057
OD7:Day	-1.4	0.309
OD6:Day	-1.7	0.218
OD5:Day	-0.6	0.646
OD4:Day	0.8	0.557

Table 4. Output from mixed modelling of phototactic response in threshold value experiments for all *Calanus* spp. stages and wavebands, comparing distance from the light source at each irradiance level to the distance from light source in the initial dark period. The ANOVA F statistic was used as an overall test of the models (significant values in bold, using a significance level of 0.05). "Distance" is the median distance from the light stimulus (cm) for the initial dark period (Dark), and change in median distance for the subsequent light levels (OD4.5-9) (significant values in bold, using a stricter significance level of 0.01).

White	CIV		CV		AF		AM	
ANOVA	F=5.73, p=**0.026**		F=12.56, p<**0.001**		F=31.99, p<**0.001**		F=3.02, p=**0.037**	
	Distance	p-value	Distance	p-value	Distance	p-value	Distance	p-value
Dark	38.0	**<0.001**	20.5	**<0.001**	12.3	**0.002**	13.9	0.073
OD8	-5.1	0.118	-1.9	0.652	4.4	0.255	2.1	0.719
OD7.5	0.9	0.756	-2.0	0.630	15.1	**0.005**	3.8	0.520
OD7	5.7	0.088	9.3	0.039	27.3	**<0.001**	2.1	0.720
OD6.5	6.6	0.055	17.5	**<0.001**	32.0	**<0.001**	16.7	0.011
OD6	6.9	0.049	21.1	**<0.001**	31.9	**<0.001**	12.3	0.049
OD5.5	7.5	0.037	18.6	**<0.001**	31.6	**<0.001**	17.5	**0.008**
OD5	-	-	19.6	**<0.001**	-	-	11.1	0.074

Blue	CIV		CV		AF		AM	
ANOVA	F=2.54, p=0.121		F=6.17, p=**0.002**		F=2.32, p=0.145		F=2.93, p=**0.032**	
	Distance	p-value	Distance	p-value	Distance	p-value	Distance	p-value
Dark	18.3	0.095	25.1	**<0.001**	24.5	0.031	11.9	0.030
OD9	-1.6	0.851	0.3	0.949	-0.6	0.947	1.4	0.751
OD8.5	-0.7	0.934	-4.8	0.371	-1.2	0.893	5.6	0.223
OD8	-2.9	0.731	-1.1	0.833	9.2	0.306	4.7	0.298
OD7.5	0.4	0.962	8.4	0.123	11.5	0.211	-3.8	0.406
OD7	6.3	0.471	13.0	0.024	16.9	0.082	3.5	0.432
OD6.5	17.6	0.070	18.1	**0.004**	19.2	0.055	13.4	**0.008**
OD6	21.0	0.038	17.8	**0.004**	19.8	0.050	8.6	0.068
OD5.5	-	-	-	-	-	-	10.2	0.035

Green525	CIV		CV		AF		AM		**Aurora green550**	CV	
ANOVA	F=1.04, p=0.481		F=6.73, p<**0.001**		F=9.17, p=**0.005**		F=0.60, p=0.748			F=7.72, p<**0.001**	
	Distance	p-value	Distance	p-value	Distance	p-value	Distance	p-value		Distance	p-value
Dark	36.9	<0.001	19.5	0.011	19.2	0.033	23.6	0.005	Dark	19.3	**<0.001**
OD9	-2.3	0.666	3.1	0.612	-4.2	0.489	1.4	0.839	OD7.5	2.5	0.602
OD8.5	-2.0	0.702	-0.7	0.906	-2.7	0.657	2.0	0.775	OD7	4.8	0.323
OD8	-1.9	0.711	-2.0	0.751	3.0	0.619	6.4	0.354	OD6.5	16.1	**0.004**
OD7.5	0.3	0.951	0.7	0.913	8.3	0.187	5.8	0.404	OD6	15.7	**0.005**
OD7	2.8	0.591	9.0	0.159	22.0	**0.006**	3.8	0.580	OD5.5	22.4	**<0.001**
OD6.5	6.9	0.215	24.4	**0.001**	24.4	**0.004**	8.2	0.238	OD5	19.6	**<0.001**
OD6	6.0	0.273	24.7	**0.001**	23.6	**0.004**	10.7	0.133	OD4.5	22.8	**<0.001**

Red	CIV		CV		AF		AM	
ANOVA	F=3.13, p=0.078		F=5.23, p=**0.040**		F=4.02, p=**0.043**		F=3.98, p=**0.013**	
	Distance	p-value	Distance	p-value	Distance	p-value	Distance	p-value
Dark	22.9	0.043	13.7	**0.009**	19.2	0.094	13.7	0.099
OD7.5	-4.6	0.579	1.2	0.823	1.4	0.832	2.3	0.556
OD7	0.1	0.992	-2.8	0.611	0.9	0.893	0.7	0.866
OD6.5	2.4	0.771	3.7	0.507	7.7	0.246	4.0	0.301
OD6	7.7	0.360	4.5	0.427	10.7	0.121	6.5	0.107
OD5.5	17.1	0.067	12.1	0.042	16.9	0.028	6.7	0.098
OD5	18.1	0.055	15.7	0.012	19.1	0.017	11.8	**0.007**
OD4.5	21.3	0.030	22.6	**0.001**	21.3	**0.010**	14.9	**0.001**

Table 5. Modelling summary (ANOVA; + or -) and threshold value (where significant; μmol photons m^{-2} s^{-1}) is given for all developmental stages and wavebands, as well as the fraction (%) of surface irradiance for each light source for the specific threshold value.

		White	Blue	Green525	Aurora green550	Red
CIV	**Model**	+	-	-		-
	Threshold	-				
	Moon					
	Night sky					
	Aurora borealis					
CV	**Model**	+	+	+	+	+
	Threshold	**4.7×10^{-6}**	**4.3×10^{-6}**	**2.1×10^{-6}**	**0.43×10^{-6}**	**1800×10^{-6}**
	Moon	0.052-0.94 %	0.048-0.86 %	0.023-0.42 %	0.0048-0.086 %	>20 %
	Night sky	15-47 %	14-43 %	7-21 %	1.4-4.3 %	>100 %
	Aurora borealis	0.12-4.7 %	0.11-4.3 %	0.053-2.1 %	0.011-0.43 %	>45 %
AF	**Model**	+	-	+		+
	Threshold	**0.47×10^{-6}**		**0.34×10^{-6}**		**1800×10^{-6}**
	Moon	0.0052-0.094 %		0.0038-0.068 %		>20 %
	Night sky	1.6-4.7 %		1.1-3.4 %		>100 %
	Aurora borealis	0.012-0.47 %		0.0085-0.34 %		>45 %
AM	**Model**	+	+	-		+
	Threshold	**42×10^{-6}**	**4.3×10^{-6}**			**310×10^{-6}**
	Moon	0.46-8.4 %	0.048-0.86 %			3.4-62 %
	Night sky	>100 %	14-43 %			>100 %
	Aurora borealis	1.0-42 %	0.11-4.3 %			>7.8 %

Orchestrated movements in the dark conducted by the Moon, Sun, and aurora borealis

Polar Biology

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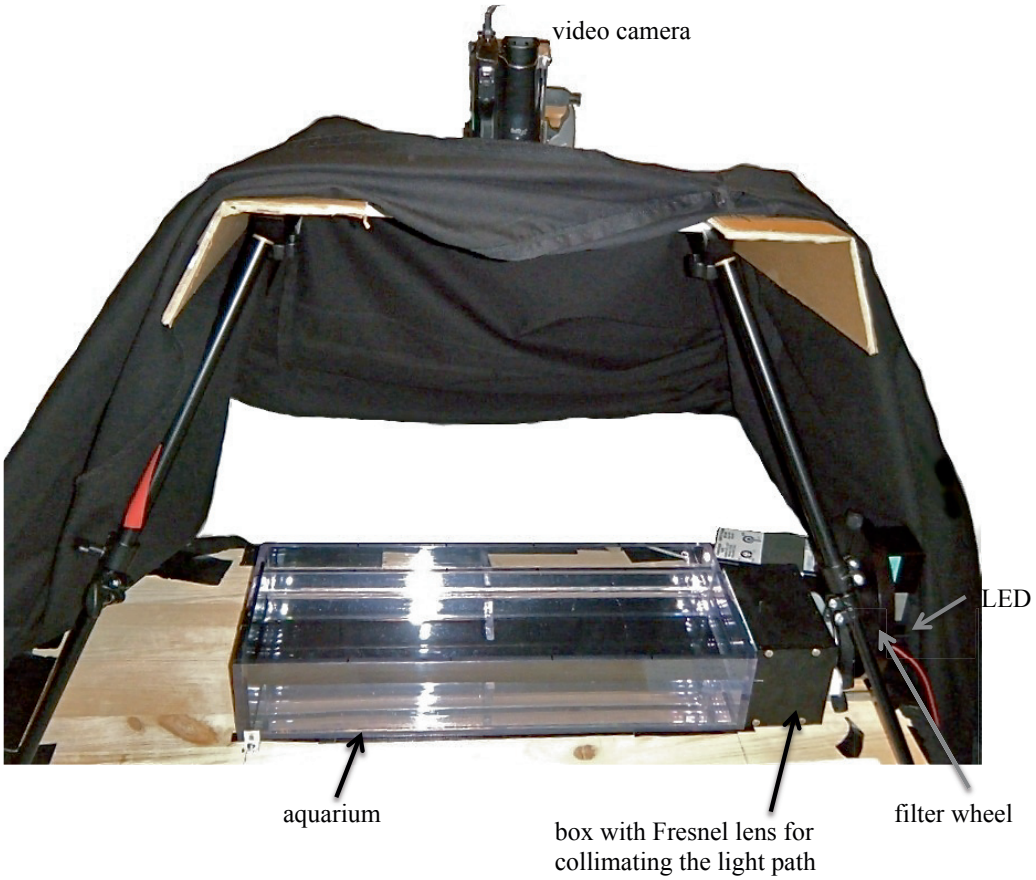
Online Resource 1



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Polar Biology

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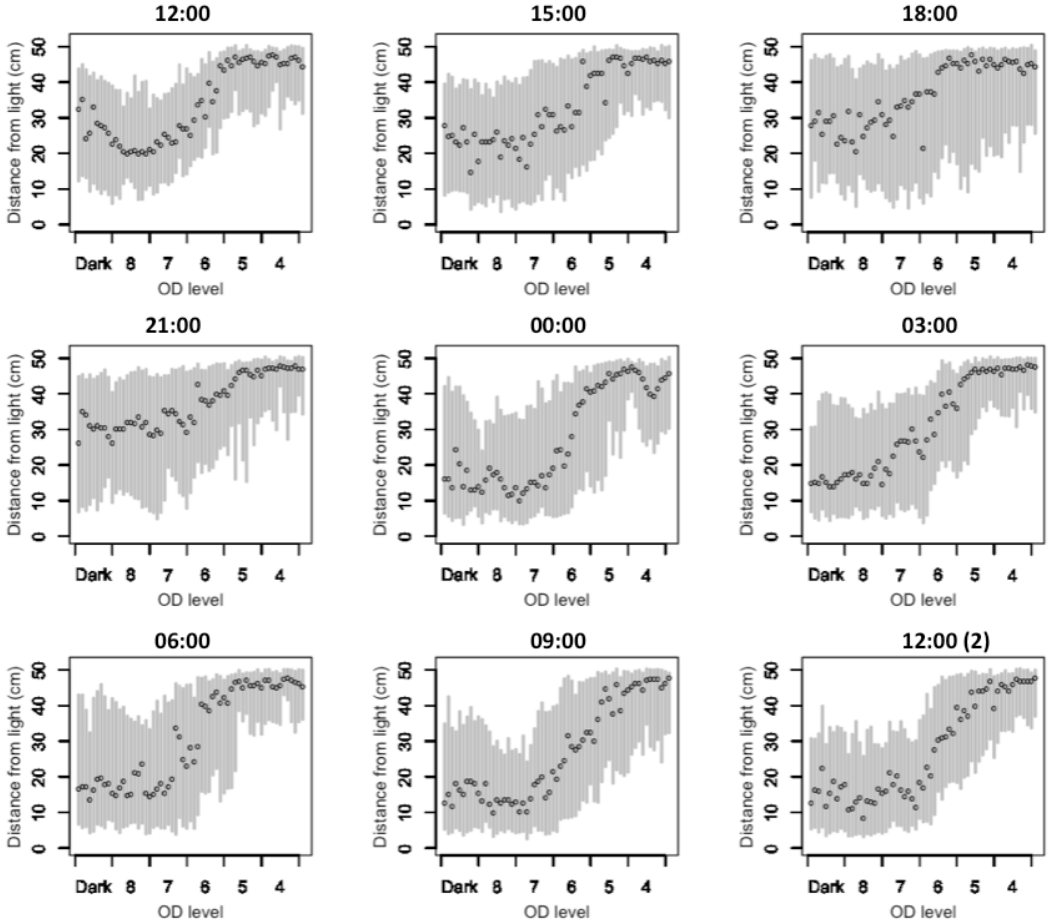
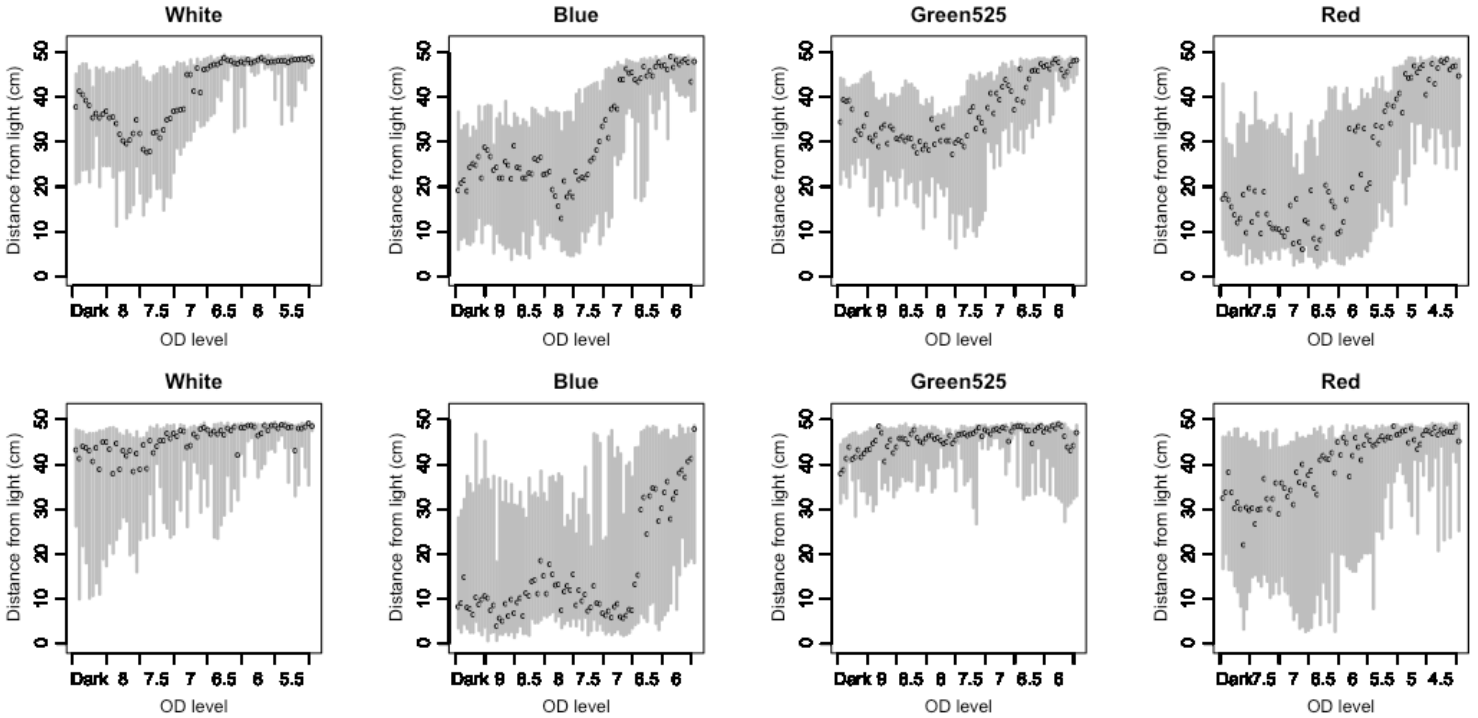
Online Resource 2

All figures show the median distance from light (dots), with interquartile range (bars), over the time of the experiment. Each OD level (irradiance level) lasts for 10 minutes.
For the 24 h experiment, all trials are presented, each with both replicates combined. For the threshold value experiments, all replicates are presented separately.

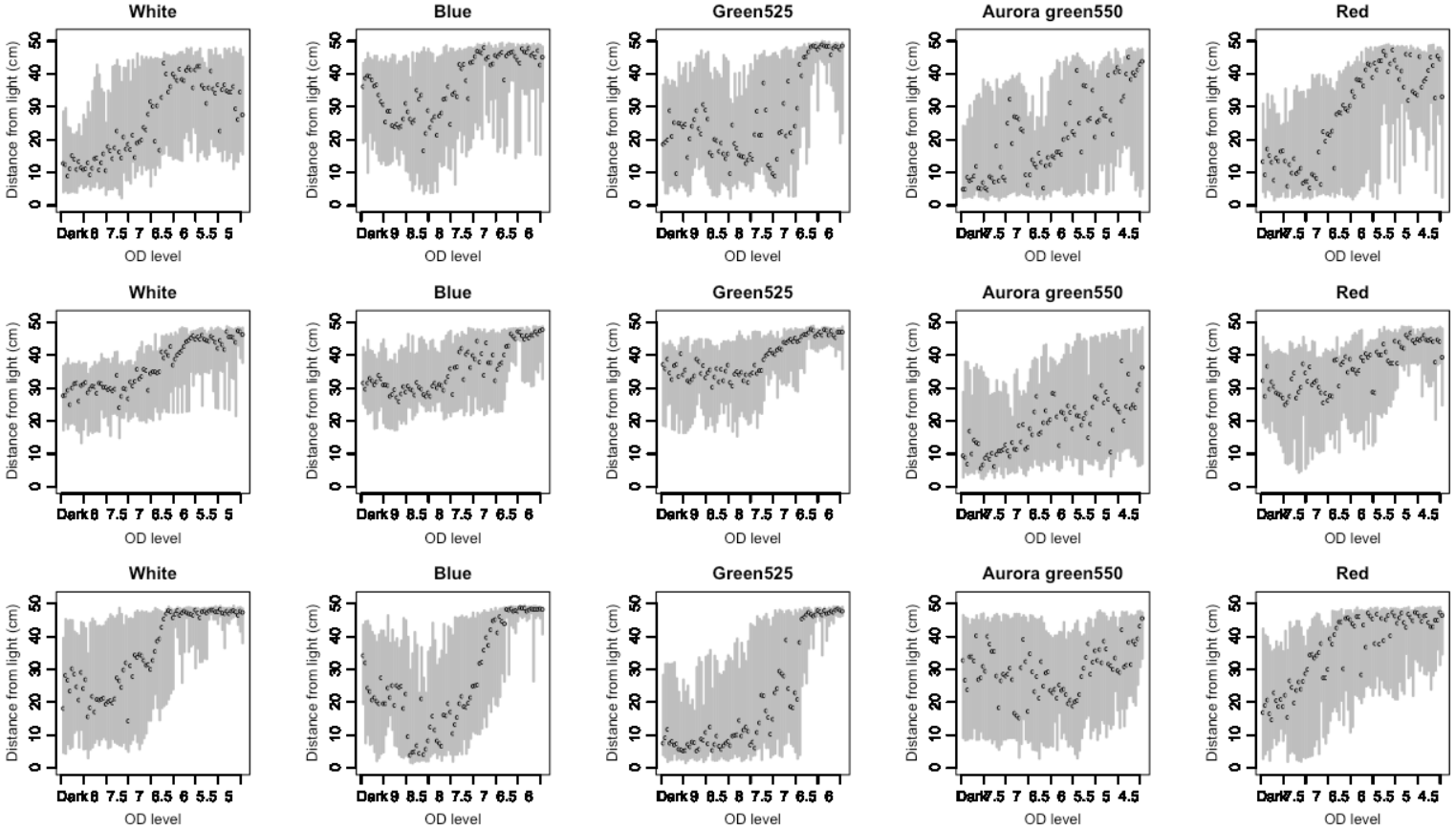


24 h experiment results. All trials are presented, each with both replicates combined.

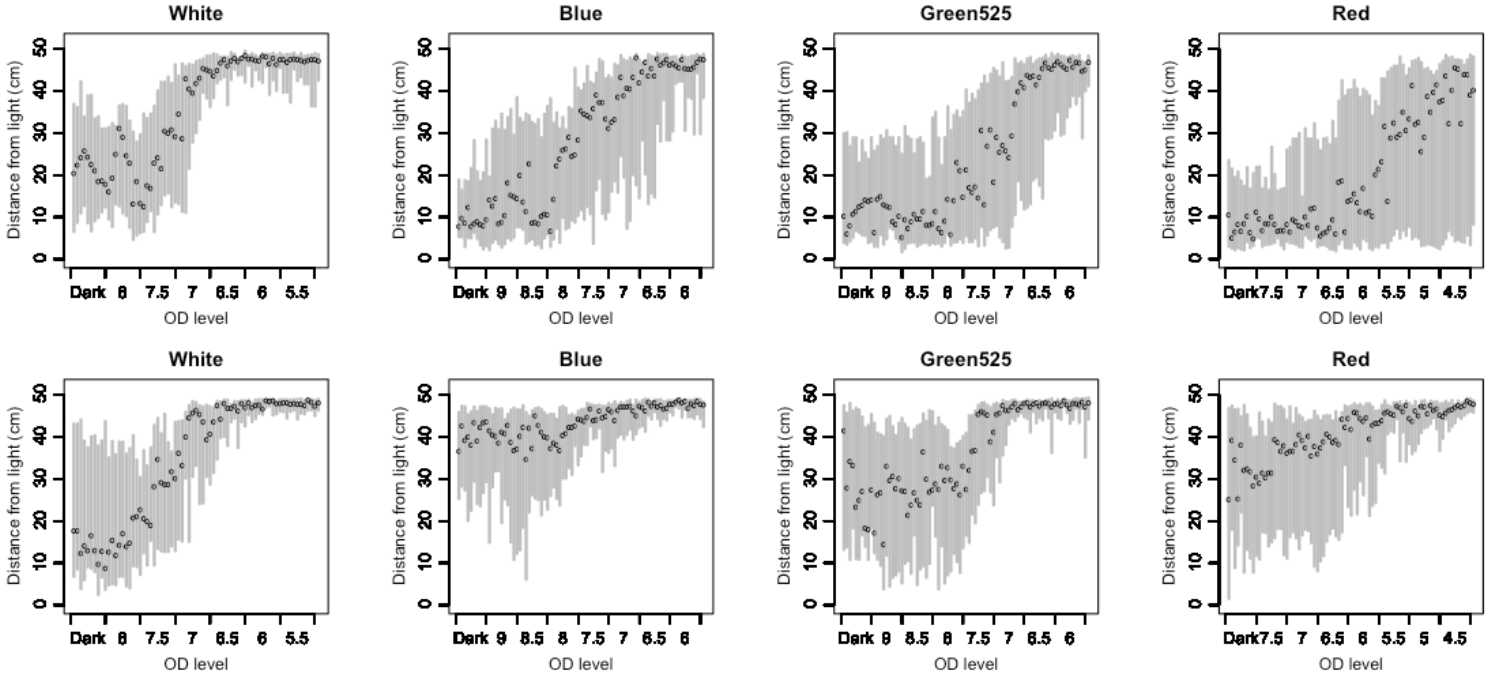
Threshold value experiments:



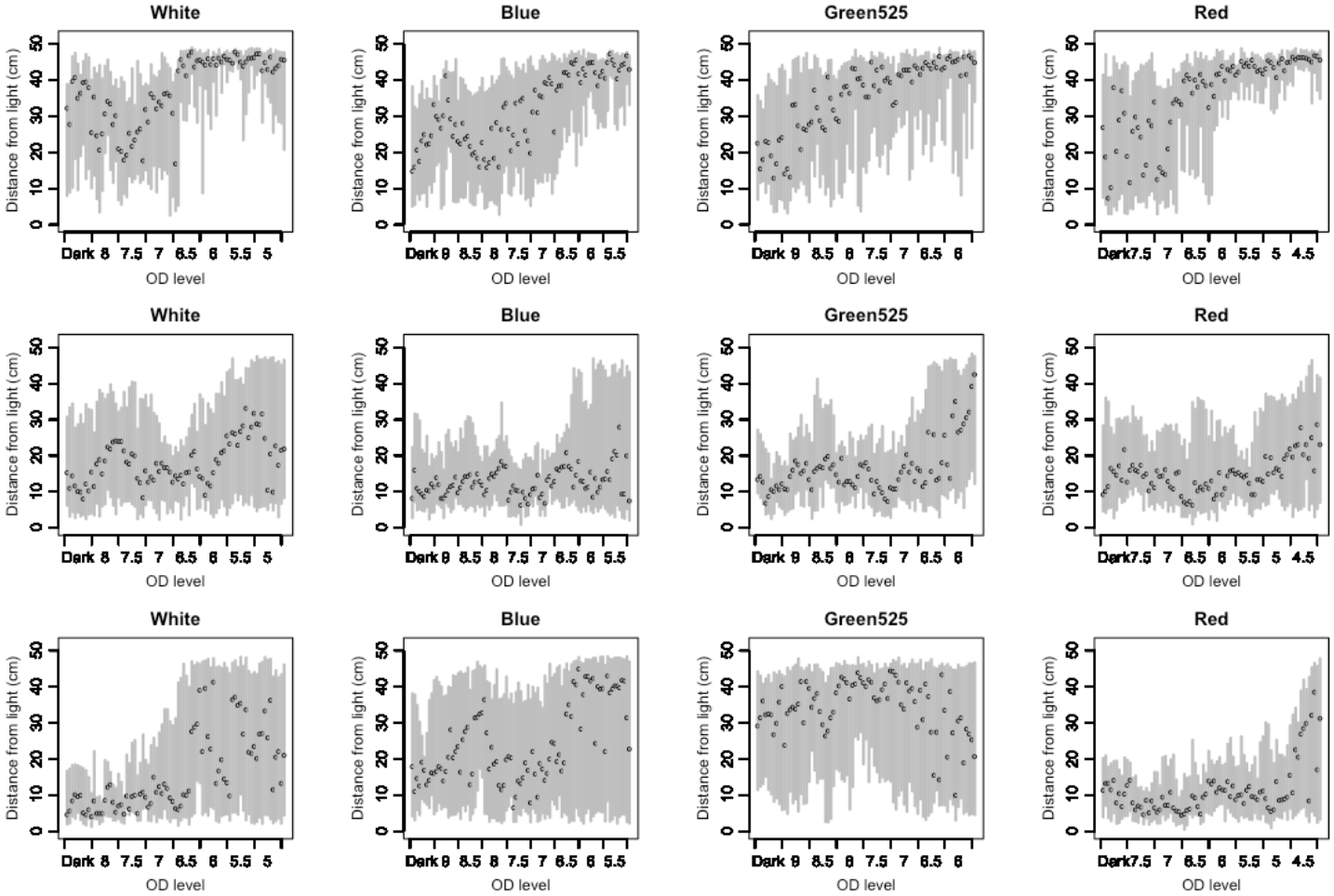
Results from threshold value experiments with CIV. Top panel is replicate 1, bottom panel is replicate 2.



Results from threshold value experiments with CV. Top panel is replicate 1, middle panel is replicate 2, and bottom panel is replicate 3.



Results from threshold value experiments with AF. Top panel is replicate 1, bottom panel is replicate 2.



Results from threshold value experiments with AM. Top panel is replicate 1, middle panel is replicate 2, and bottom panel is replicate 3.

Doctoral theses in Biology
Norwegian University of Science and Technology
Department of Biology

Year	Name	Degree	Title
1974	Tor-Henning Iversen	Dr. philos Botany	The roles of statholiths, auxin transport, and auxin metabolism in root gravitropism
1978	Tore Slagsvold	Dr. philos Zoology	Breeding events of birds in relation to spring temperature and environmental phenology
1978	Egil Sakshaug	Dr.philos Botany	"The influence of environmental factors on the chemical composition of cultivated and natural populations of marine phytoplankton"
1980	Arnfinn Langeland	Dr. philos Zoology	Interaction between fish and zooplankton populations and their effects on the material utilization in a freshwater lake
1980	Helge Reinertsen	Dr. philos Botany	The effect of lake fertilization on the dynamics and stability of a limnetic ecosystem with special reference to the phytoplankton
1982	Gunn Mari Olsen	Dr. scient Botany	Gravitropism in roots of *Pisum sativum* and *Arabidopsis thaliana*
1982	Dag Dolmen	Dr. philos Zoology	Life aspects of two sympartic species of newts (*Triturus, Amphibia*) in Norway, with special emphasis on their ecological niche segregation
1984	Eivin Røskaft	Dr. philos Zoology	Sociobiological studies of the rook *Corvus frugilegus*
1984	Anne Margrethe Cameron	Dr. scient Botany	Effects of alcohol inhalation on levels of circulating testosterone, follicle stimulating hormone and luteinzing hormone in male mature rats
1984	Asbjørn Magne Nilsen	Dr. scient Botany	Alveolar macrophages from expectorates – Biological monitoring of workers exosed to occupational air pollution. An evaluation of the AM-test
1985	Jarle Mork	Dr. philos Zoology	Biochemical genetic studies in fish
1985	John Solem	Dr. philos Zoology	Taxonomy, distribution and ecology of caddisflies (*Trichoptera*) in the Dovrefjell mountains
1985	Randi E. Reinertsen	Dr. philos Zoology	Energy strategies in the cold: Metabolic and thermoregulatory adaptations in small northern birds
1986	Bernt-Erik Sæther	Dr. philos Zoology	Ecological and evolutionary basis for variation in reproductive traits of some vertebrates: A comparative approach
1986	Torleif Holthe	Dr. philos Zoology	Evolution, systematics, nomenclature, and zoogeography in the polychaete orders *Oweniimorpha* and *Terebellomorpha*, with special reference to the Arctic and Scandinavian fauna
1987	Helene Lampe	Dr. scient Zoology	The function of bird song in mate attraction and territorial defence, and the importance of song repertoires

1987	Olav Hogstad	Dr. philos Zoology	Winter survival strategies of the Willow tit *Parus montanus*
1987	Jarle Inge Holten	Dr. philos Botany	Autecological investigations along a coust-inland transect at Nord-Møre, Central Norway
1987	Rita Kumar	Dr. scient Botany	Somaclonal variation in plants regenerated from cell cultures of *Nicotiana sanderae* and *Chrysanthemum morifolium*
1987	Bjørn Åge Tømmerås	Dr. scient. Zoolog	Olfaction in bark beetle communities: Interspecific interactions in regulation of colonization density, predator - prey relationship and host attraction
1988	Hans Christian Pedersen	Dr. philos Zoology	Reproductive behaviour in willow ptarmigan with special emphasis on territoriality and parental care
1988	Tor G. Heggberget	Dr. philos Zoology	Reproduction in Atlantic Salmon (*Salmo salar*): Aspects of spawning, incubation, early life history and population structure
1988	Marianne V. Nielsen	Dr. scient Zoology	The effects of selected environmental factors on carbon allocation/growth of larval and juvenile mussels (*Mytilus edulis*)
1988	Ole Kristian Berg	Dr. scient Zoology	The formation of landlocked Atlantic salmon (*Salmo salar* L.)
1989	John W. Jensen	Dr. philos Zoology	Crustacean plankton and fish during the first decade of the manmade Nesjø reservoir, with special emphasis on the effects of gill nets and salmonid growth
1989	Helga J. Vivås	Dr. scient Zoology	Theoretical models of activity pattern and optimal foraging: Predictions for the Moose *Alces alces*
1989	Reidar Andersen	Dr. scient Zoology	Interactions between a generalist herbivore, the moose *Alces alces*, and its winter food resources: a study of behavioural variation
1989	Kurt Ingar Draget	Dr. scient Botany	Alginate gel media for plant tissue culture
1990	Bengt Finstad	Dr. scient Zoology	Osmotic and ionic regulation in Atlantic salmon, rainbow trout and Arctic charr: Effect of temperature, salinity and season
1990	Hege Johannesen	Dr. scient Zoology	Respiration and temperature regulation in birds with special emphasis on the oxygen extraction by the lung
1990	Åse Krøkje	Dr. scient Botany	The mutagenic load from air pollution at two work-places with PAH-exposure measured with Ames Salmonella/microsome test
1990	Arne Johan Jensen	Dr. philos Zoology	Effects of water temperature on early life history, juvenile growth and prespawning migrations of Atlantic salmion (*Salmo salar*) and brown trout (*Salmo trutta*): A summary of studies in Norwegian streams
1990	Tor Jørgen Almaas	Dr. scient Zoology	Pheromone reception in moths: Response characteristics of olfactory receptor neurons to intra- and interspecific chemical cues
1990	Magne Husby	Dr. scient Zoology	Breeding strategies in birds: Experiments with the Magpie *Pica pica*
1991	Tor Kvam	Dr. scient Zoology	Population biology of the European lynx (*Lynx lynx*) in Norway
1991	Jan Henning L'Abêe Lund	Dr. philos Zoology	Reproductive biology in freshwater fish, brown trout *Salmo trutta* and roach *Rutilus rutilus* in particular

1991	Asbjørn Moen	Dr. philos Botany	The plant cover of the boreal uplands of Central Norway. I. Vegetation ecology of Sølendet nature reserve; haymaking fens and birch woodlands
1991	Else Marie Løbersli	Dr. scient Botany	Soil acidification and metal uptake in plants
1991	Trond Nordtug	Dr. scient Zoology	Reflctometric studies of photomechanical adaptation in superposition eyes of arthropods
1991	Thyra Solem	Dr. scient Botany	Age, origin and development of blanket mires in Central Norway
1991	Odd Terje Sandlund	Dr. philos Zoology	The dynamics of habitat use in the salmonid genera *Coregonus* and *Salvelinus*: Ontogenic niche shifts and polymorphism
1991	Nina Jonsson	Dr. philos	Aspects of migration and spawning in salmonids
1991	Atle Bones	Dr. scient Botany	Compartmentation and molecular properties of thioglucoside glucohydrolase (myrosinase)
1992	Torgrim Breiehagen	Dr. scient Zoology	Mating behaviour and evolutionary aspects of the breeding system of two bird species: the Temminck's stint and the Pied flycatcher
1992	Anne Kjersti Bakken	Dr. scient Botany	The influence of photoperiod on nitrate assimilation and nitrogen status in timothy (*Phleum pratense* L.)
1992	Tycho Anker-Nilssen	Dr. scient Zoology	Food supply as a determinant of reproduction and population development in Norwegian Puffins *Fratercula arctica*
1992	Bjørn Munro Jenssen	Dr. philos Zoology	Thermoregulation in aquatic birds in air and water: With special emphasis on the effects of crude oil, chemically treated oil and cleaning on the thermal balance of ducks
1992	Arne Vollan Aarset	Dr. philos Zoology	The ecophysiology of under-ice fauna: Osmotic regulation, low temperature tolerance and metabolism in polar crustaceans.
1993	Geir Slupphaug	Dr. scient Botany	Regulation and expression of uracil-DNA glycosylase and O^6-methylguanine-DNA methyltransferase in mammalian cells
1993	Tor Fredrik Næsje	Dr. scient Zoology	Habitat shifts in coregonids.
1993	Yngvar Asbjørn Olsen	Dr. scient Zoology	Cortisol dynamics in Atlantic salmon, *Salmo salar* L.: Basal and stressor-induced variations in plasma levels ans some secondary effects.
1993	Bård Pedersen	Dr. scient Botany	Theoretical studies of life history evolution in modular and clonal organisms
1993	Ole Petter Thangstad	Dr. scient Botany	Molecular studies of myrosinase in Brassicaceae
1993	Thrine L. M. Heggberget	Dr. scient Zoology	Reproductive strategy and feeding ecology of the Eurasian otter *Lutra lutra*.
1993	Kjetil Bevanger	Dr. scient. Zoology	Avian interactions with utility structures, a biological approach.
1993	Kåre Haugan	Dr. scient Bothany	Mutations in the replication control gene trfA of the broad host-range plasmid RK2
1994	Peder Fiske	Dr. scient. Zoology	Sexual selection in the lekking great snipe (*Gallinago media*): Male mating success and female behaviour at the lek
1994	Kjell Inge Reitan	Dr. scient Botany	Nutritional effects of algae in first-feeding of marine fish larvae
1994	Nils Røv	Dr. scient	Breeding distribution, population status and regulation

		Zoology	of breeding numbers in the northeast-Atlantic Great Cormorant *Phalacrocorax carbo carbo*
1994	Annette-Susanne Hoepfner	Dr. scient Botany	Tissue culture techniques in propagation and breeding of Red Raspberry (*Rubus idaeus* L.)
1994	Inga Elise Bruteig	Dr. scient Bothany	Distribution, ecology and biomonitoring studies of epiphytic lichens on conifers
1994	Geir Johnsen	Dr. scient Botany	Light harvesting and utilization in marine phytoplankton: Species-specific and photoadaptive responses
1994	Morten Bakken	Dr. scient Zoology	Infanticidal behaviour and reproductive performance in relation to competition capacity among farmed silver fox vixens, *Vulpes vulpes*
1994	Arne Moksnes	Dr. philos Zoology	Host adaptations towards brood parasitism by the Cockoo
1994	Solveig Bakken	Dr. scient Bothany	Growth and nitrogen status in the moss *Dicranum majus* Sm. as influenced by nitrogen supply
1994	Torbjørn Forseth	Dr. scient Zoology	Bioenergetics in ecological and life history studies of fishes.
1995	Olav Vadstein	Dr. philos Botany	The role of heterotrophic planktonic bacteria in the cycling of phosphorus in lakes: Phosphorus requirement, competitive ability and food web interactions
1995	Hanne Christensen	Dr. scient Zoology	Determinants of Otter *Lutra lutra* distribution in Norway: Effects of harvest, polychlorinated biphenyls (PCBs), human population density and competition with mink *Mustela vision*
1995	Svein Håkon Lorentsen	Dr. scient Zoology	Reproductive effort in the Antarctic Petrel *Thalassoica antarctica*; the effect of parental body size and condition
1995	Chris Jørgen Jensen	Dr. scient Zoology	The surface electromyographic (EMG) amplitude as an estimate of upper trapezius muscle activity
1995	Martha Kold Bakkevig	Dr. scient Zoology	The impact of clothing textiles and construction in a clothing system on thermoregulatory responses, sweat accumulation and heat transport
1995	Vidar Moen	Dr. scient Zoology	Distribution patterns and adaptations to light in newly introduced populations of *Mysis relicta* and constraints on Cladoceran and Char populations
1995	Hans Haavardsholm Blom	Dr. philos Bothany	A revision of the *Schistidium apocarpum* complex in Norway and Sweden
1996	Jorun Skjærmo	Dr. scient Botany	Microbial ecology of early stages of cultivated marine fish; inpact fish-bacterial interactions on growth and survival of larvae
1996	Ola Ugedal	Dr. scient Zoology	Radiocesium turnover in freshwater fishes
1996	Ingibjørg Einarsdottir	Dr. scient Zoology	Production of Atlantic salmon (*Salmo salar*) and Arctic charr (*Salvelinus alpinus*): A study of some physiological and immunological responses to rearing routines
1996	Christina M. S. Pereira	Dr. scient Zoology	Glucose metabolism in salmonids: Dietary effects and hormonal regulation
1996	Jan Fredrik Børseth	Dr. scient Zoology	The sodium energy gradients in muscle cells of *Mytilus edulis* and the effects of organic xenobiotics
1996	Gunnar Henriksen	Dr. scient Zoology	Status of Grey seal *Halichoerus grypus* and Harbour seal *Phoca vitulina* in the Barents sea region

1997	Gunvor Øie	Dr. scient Bothany	Eevalution of rotifer *Brachionus plicatilis* quality in early first feeding of turbot *Scophtalmus maximus* L. larvae
1997	Håkon Holien	Dr. scient Botany	Studies of lichens in spurce forest of Central Norway. Diversity, old growth species and the relationship to site and stand parameters
1997	Ole Reitan	Dr. scient. Zoology	Responses of birds to habitat disturbance due to damming
1997	Jon Arne Grøttum	Dr. scient. Zoology	Physiological effects of reduced water quality on fish in aquaculture
1997	Per Gustav Thingstad	Dr. scient. Zoology	Birds as indicators for studying natural and human-induced variations in the environment, with special emphasis on the suitability of the Pied Flycatcher
1997	Torgeir Nygård	Dr. scient Zoology	Temporal and spatial trends of pollutants in birds in Norway: Birds of prey and Willow Grouse used as Biomonitors
1997	Signe Nybø	Dr. scient. Zoology	Impacts of long-range transported air pollution on birds with particular reference to the dipper *Cinclus cinclus* in southern Norway
1997	Atle Wibe	Dr. scient. Zoology	Identification of conifer volatiles detected by receptor neurons in the pine weevil (*Hylobius abietis*), analysed by gas chromatography linked to electrophysiology and to mass spectrometry
1997	Rolv Lundheim	Dr. scient Zoology	Adaptive and incidental biological ice nucleators
1997	Arild Magne Landa	Dr. scient Zoology	Wolverines in Scandinavia: ecology, sheep depredation and conservation
1997	Kåre Magne Nielsen	Dr. scient Botany	An evolution of possible horizontal gene transfer from plants to sail bacteria by studies of natural transformation in *Acinetobacter calcoacetius*
1997	Jarle Tufto	Dr. scient Zoology	Gene flow and genetic drift in geographically structured populations: Ecological, population genetic, and statistical models
1997	Trygve Hesthagen	Dr. philos Zoology	Population responces of Arctic charr (*Salvelinus alpinus* (L.)) and brown trout (*Salmo trutta* L.) to acidification in Norwegian inland waters
1997	Trygve Sigholt	Dr. philos Zoology	Control of Parr-smolt transformation and seawater tolerance in farmed Atlantic Salmon (*Salmo salar*) Effects of photoperiod, temperature, gradual seawater acclimation, NaCl and betaine in the diet
1997	Jan Østnes	Dr. scient Zoology	Cold sensation in adult and neonate birds
1998	Seethaledsumy Visvalingam	Dr. scient Botany	Influence of environmental factors on myrosinases and myrosinase-binding proteins
1998	Thor Harald Ringsby	Dr. scient Zoology	Variation in space and time: The biology of a House sparrow metapopulation
1998	Erling Johan Solberg	Dr. scient. Zoology	Variation in population dynamics and life history in a Norwegian moose (*Alces alces*) population: consequences of harvesting in a variable environment
1998	Sigurd Mjøen Saastad	Dr. scient Botany	Species delimitation and phylogenetic relationships between the Sphagnum recurvum complex (Bryophyta): genetic variation and phenotypic plasticity
1998	Bjarte Mortensen	Dr. scient	Metabolism of volatile organic chemicals (VOCs) in a

		Botany	head liver S9 vial equilibration system in vitro
1998	Gunnar Austrheim	Dr. scient Botany	Plant biodiversity and land use in subalpine grasslands. – A conservtaion biological approach
1998	Bente Gunnveig Berg	Dr. scient Zoology	Encoding of pheromone information in two related moth species
1999	Kristian Overskaug	Dr. scient Zoology	Behavioural and morphological characteristics in Northern Tawny Owls *Strix aluco*: An intra- and interspecific comparative approach
1999	Hans Kristen Stenøien	Dr. scient Bothany	Genetic studies of evolutionary processes in various populations of nonvascular plants (mosses, liverworts and hornworts)
1999	Trond Arnesen	Dr. scient Botany	Vegetation dynamics following trampling and burning in the outlying haylands at Sølendet, Central Norway
1999	Ingvar Stenberg	Dr. scient Zoology	Habitat selection, reproduction and survival in the White-backed Woodpecker *Dendrocopos leucotos*
1999	Stein Olle Johansen	Dr. scient Botany	A study of driftwood dispersal to the Nordic Seas by dendrochronology and wood anatomical analysis
1999	Trina Falck Galloway	Dr. scient Zoology	Muscle development and growth in early life stages of the Atlantic cod (*Gadus morhua* L.) and Halibut (*Hippoglossus hippoglossus* L.)
1999	Marianne Giæver	Dr. scient Zoology	Population genetic studies in three gadoid species: blue whiting (*Micromisistius poutassou*), haddock (*Melanogrammus aeglefinus*) and cod (*Gradus morhua*) in the North-East Atlantic
1999	Hans Martin Hanslin	Dr. scient Botany	The impact of environmental conditions of density dependent performance in the boreal forest bryophytes *Dicranum majus*, *Hylocomium splendens*, *Plagiochila asplenigides*, *Ptilium crista-castrensis* and *Rhytidiadelphus lokeus*
1999	Ingrid Bysveen Mjølnerød	Dr. scient Zoology	Aspects of population genetics, behaviour and performance of wild and farmed Atlantic salmon (*Salmo salar*) revealed by molecular genetic techniques
1999	Else Berit Skagen	Dr. scient Botany	The early regeneration process in protoplasts from *Brassica napus* hypocotyls cultivated under various g-forces
1999	Stein-Are Sæther	Dr. philos Zoology	Mate choice, competition for mates, and conflicts of interest in the Lekking Great Snipe
1999	Katrine Wangen Rustad	Dr. scient Zoology	Modulation of glutamatergic neurotransmission related to cognitive dysfunctions and Alzheimer's disease
1999	Per Terje Smiseth	Dr. scient Zoology	Social evolution in monogamous families: mate choice and conflicts over parental care in the Bluethroat (*Luscinia s. svecica*)
1999	Gunnbjørn Bremset	Dr. scient Zoology	Young Atlantic salmon (*Salmo salar* L.) and Brown trout (*Salmo trutta* L.) inhabiting the deep pool habitat, with special reference to their habitat use, habitat preferences and competitive interactions
1999	Frode Ødegaard	Dr. scient Zoology	Host spesificity as parameter in estimates of arhrophod species richness
1999	Sonja Andersen	Dr. scient Bothany	Expressional and functional analyses of human, secretory phospholipase A2
2000	Ingrid Salvesen	Dr. scient Botany	Microbial ecology in early stages of marine fish: Development and evaluation of methods for microbial management in intensive larviculture

2000	Ingar Jostein Øien	Dr. scient Zoology	The Cuckoo (*Cuculus canorus*) and its host: adaptions and counteradaptions in a coevolutionary arms race
2000	Pavlos Makridis	Dr. scient Botany	Methods for the microbial econtrol of live food used for the rearing of marine fish larvae
2000	Sigbjørn Stokke	Dr. scient Zoology	Sexual segregation in the African elephant (*Loxodonta africana*)
2000	Odd A. Gulseth	Dr. philos Zoology	Seawater tolerance, migratory behaviour and growth of Charr, (*Salvelinus alpinus*), with emphasis on the high Arctic Dieset charr on Spitsbergen, Svalbard
2000	Pål A. Olsvik	Dr. scient Zoology	Biochemical impacts of Cd, Cu and Zn on brown trout (*Salmo trutta*) in two mining-contaminated rivers in Central Norway
2000	Sigurd Einum	Dr. scient Zoology	Maternal effects in fish: Implications for the evolution of breeding time and egg size
2001	Jan Ove Evjemo	Dr. scient Zoology	Production and nutritional adaptation of the brine shrimp *Artemia* sp. as live food organism for larvae of marine cold water fish species
2001	Olga Hilmo	Dr. scient Botany	Lichen response to environmental changes in the managed boreal forset systems
2001	Ingebrigt Uglem	Dr. scient Zoology	Male dimorphism and reproductive biology in corkwing wrasse (*Symphodus melops* L.)
2001	Bård Gunnar Stokke	Dr. scient Zoology	Coevolutionary adaptations in avian brood parasites and their hosts
2002	Ronny Aanes	Dr. scient	Spatio-temporal dynamics in Svalbard reindeer (*Rangifer tarandus platyrhynchus*)
2002	Mariann Sandsund	Dr. scient Zoology	Exercise- and cold-induced asthma. Respiratory and thermoregulatory responses
2002	Dag-Inge Øien	Dr. scient Botany	Dynamics of plant communities and populations in boreal vegetation influenced by scything at Sølendet, Central Norway
2002	Frank Rosell	Dr. scient Zoology	The function of scent marking in beaver (*Castor fiber*)
2002	Janne Østvang	Dr. scient Botany	The Role and Regulation of Phospholipase A_2 in Monocytes During Atherosclerosis Development
2002	Terje Thun	Dr.philos Biology	Dendrochronological constructions of Norwegian conifer chronologies providing dating of historical material
2002	Birgit Hafjeld Borgen	Dr. scient Biology	Functional analysis of plant idioblasts (Myrosin cells) and their role in defense, development and growth
2002	Bård Øyvind Solberg	Dr. scient Biology	Effects of climatic change on the growth of dominating tree species along major environmental gradients
2002	Per Winge	Dr. scient Biology	The evolution of small GTP binding proteins in cellular organisms. Studies of RAC GTPases in *Arabidopsis thaliana* and the Ral GTPase from *Drosophila melanogaster*
2002	Henrik Jensen	Dr. scient Biology	Causes and consequenses of individual variation in fitness-related traits in house sparrows
2003	Jens Rohloff	Dr. philos Biology	Cultivation of herbs and medicinal plants in Norway – Essential oil production and quality control
2003	Åsa Maria O. Espmark Wibe	Dr. scient Biology	Behavioural effects of environmental pollution in threespine stickleback *Gasterosteus aculeatur* L.
2003	Dagmar Hagen	Dr. scient Biology	Assisted recovery of disturbed arctic and alpine vegetation – an integrated approach
2003	Bjørn Dahle	Dr. scient	Reproductive strategies in Scandinavian brown bears

		Biology	
2003	Cyril Lebogang Taolo	Dr. scient Biology	Population ecology, seasonal movement and habitat use of the African buffalo (*Syncerus caffer*) in Chobe National Park, Botswana
2003	Marit Stranden	Dr.scient Biology	Olfactory receptor neurones specified for the same odorants in three related Heliothine species (*Helicoverpa armigera, Helicoverpa assulta* and *Heliothis virescens*)
2003	Kristian Hassel	Dr.scient Biology	Life history characteristics and genetic variation in an expanding species, *Pogonatum dentatum*
2003	David Alexander Rae	Dr.scient Biology	Plant- and invertebrate-community responses to species interaction and microclimatic gradients in alpine and Artic environments
2003	Åsa A Borg	Dr.scient Biology	Sex roles and reproductive behaviour in gobies and guppies: a female perspective
2003	Eldar Åsgard Bendiksen	Dr.scient Biology	Environmental effects on lipid nutrition of farmed Atlantic salmon (*Salmo Salar* L.) parr and smolt
2004	Torkild Bakken	Dr.scient Biology	A revision of Nereidinae (Polychaeta, Nereididae)
2004	Ingar Pareliussen	Dr.scient Biology	Natural and Experimental Tree Establishment in a Fragmented Forest, Ambohitantely Forest Reserve, Madagascar
2004	Tore Brembu	Dr.scient Biology	Genetic, molecular and functional studies of RAC GTPases and the WAVE-like regulatory protein complex in *Arabidopsis thaliana*
2004	Liv S. Nilsen	Dr.scient Biology	Coastal heath vegetation on central Norway; recent past, present state and future possibilities
2004	Hanne T. Skiri	Dr.scient Biology	Olfactory coding and olfactory learning of plant odours in heliothine moths. An anatomical, physiological and behavioural study of three related species (*Heliothis virescens, Helicoverpa armigera* and *Helicoverpa assulta*)
2004	Lene Østby	Dr.scient Biology	Cytochrome P4501A (CYP1A) induction and DNA adducts as biomarkers for organic pollution in the natural environment
2004	Emmanuel J. Gerreta	Dr. philos Biology	The Importance of Water Quality and Quantity in the Tropical Ecosystems, Tanzania
2004	Linda Dalen	Dr.scient Biology	Dynamics of Mountain Birch Treelines in the Scandes Mountain Chain, and Effects of Climate Warming
2004	Lisbeth Mehli	Dr.scient Biology	Polygalacturonase-inhibiting protein (PGIP) in cultivated strawberry (*Fragaria* x *ananassa*): characterisation and induction of the gene following fruit infection by *Botrytis cinerea*
2004	Børge Moe	Dr.scient Biology	Energy-Allocation in Avian Nestlings Facing Short-Term Food Shortage
2005	Matilde Skogen Chauton	Dr.scient Biology	Metabolic profiling and species discrimination from High-Resolution Magic Angle Spinning NMR analysis of whole-cell samples
2005	Sten Karlsson	Dr.scient Biology	Dynamics of Genetic Polymorphisms
2005	Terje Bongard	Dr.scient Biology	Life History strategies, mate choice, and parental investment among Norwegians over a 300-year period
2005	Tonette Røstelien	ph.d Biology	Functional characterisation of olfactory receptor neurone types in heliothine moths

2005	Erlend Kristiansen	Dr.scient Biology	Studies on antifreeze proteins
2005	Eugen G. Sørmo	Dr.scient Biology	Organochlorine pollutants in grey seal (*Halichoerus grypus*) pups and their impact on plasma thyrid hormone and vitamin A concentrations
2005	Christian Westad	Dr.scient Biology	Motor control of the upper trapezius
2005	Lasse Mork Olsen	ph.d Biology	Interactions between marine osmo- and phagotrophs in different physicochemical environments
2005	Åslaug Viken	ph.d Biology	Implications of mate choice for the management of small populations
2005	Ariaya Hymete Sahle Dingle	ph.d Biology	Investigation of the biological activities and chemical constituents of selected *Echinops* spp. growing in Ethiopia
2005	Anders Gravbrøt Finstad	ph.d Biology	Salmonid fishes in a changing climate: The winter challenge
2005	Shimane Washington Makabu	ph.d Biology	Interactions between woody plants, elephants and other browsers in the Chobe Riverfront, Botswana
2005	Kjartan Østbye	Dr.scient Biology	The European whitefish *Coregonus lavaretus* (L.) species complex: historical contingency and adaptive radiation
2006	Kari Mette Murvoll	ph.d Biology	Levels and effects of persistent organic pollutans (POPs) in seabirds Retinoids and α-tocopherol – potential biomakers of POPs in birds?
2006	Ivar Herfindal	Dr.scient Biology	Life history consequences of environmental variation along ecological gradients in northern ungulates
2006	Nils Egil Tokle	ph.d Biology	Are the ubiquitous marine copepods limited by food or predation? Experimental and field-based studies with main focus on *Calanus finmarchicus*
2006	Jan Ove Gjershaug	Dr.philos Biology	Taxonomy and conservation status of some booted eagles in south-east Asia
2006	Jon Kristian Skei	Dr.scient Biology	Conservation biology and acidification problems in the breeding habitat of amphibians in Norway
2006	Johanna Järnegren	ph.d Biology	Acesta Oophaga and Acesta Excavata – a study of hidden biodiversity
2006	Bjørn Henrik Hansen	ph.d Biology	Metal-mediated oxidative stress responses in brown trout (*Salmo trutta*) from mining contaminated rivers in Central Norway
2006	Vidar Grøtan	ph.d Biology	Temporal and spatial effects of climate fluctuations on population dynamics of vertebrates
2006	Jafari R Kideghesho	ph.d Biology	Wildlife conservation and local land use conflicts in western Serengeti, Corridor Tanzania
2006	Anna Maria Billing	ph.d Biology	Reproductive decisions in the sex role reversed pipefish *Syngnathus typhle*: when and how to invest in reproduction
2006	Henrik Pärn	ph.d Biology	Female ornaments and reproductive biology in the bluethroat
2006	Anders J. Fjellheim	ph.d Biology	Selection and administration of probiotic bacteria to marine fish larvae
2006	P. Andreas Svensson	ph.d Biology	Female coloration, egg carotenoids and reproductive success: gobies as a model system
2007	Sindre A. Pedersen	ph.d Biology	Metal binding proteins and antifreeze proteins in the beetle *Tenebrio molitor* - a study on possible competition for the semi-essential amino acid cysteine

2007	Kasper Hancke	ph.d Biology	Photosynthetic responses as a function of light and temperature: Field and laboratory studies on marine microalgae
2007	Tomas Holmern	ph.d Biology	Bushmeat hunting in the western Serengeti: Implications for community-based conservation
2007	Kari Jørgensen	ph.d Biology	Functional tracing of gustatory receptor neurons in the CNS and chemosensory learning in the moth *Heliothis virescens*
2007	Stig Ulland	ph.d Biology	Functional Characterisation of Olfactory Receptor Neurons in the Cabbage Moth, (*Mamestra brassicae* L.) (Lepidoptera, Noctuidae). Gas Chromatography Linked to Single Cell Recordings and Mass Spectrometry
2007	Snorre Henriksen	ph.d Biology	Spatial and temporal variation in herbivore resources at northern latitudes
2007	Roelof Frans May	ph.d Biology	Spatial Ecology of Wolverines in Scandinavia
2007	Vedasto Gabriel Ndibalema	ph.d Biology	Demographic variation, distribution and habitat use between wildebeest sub-populations in the Serengeti National Park, Tanzania
2007	Julius William Nyahongo	ph.d Biology	Depredation of Livestock by wild Carnivores and Illegal Utilization of Natural Resources by Humans in the Western Serengeti, Tanzania
2007	Shombe Ntaraluka Hassan	ph.d Biology	Effects of fire on large herbivores and their forage resources in Serengeti, Tanzania
2007	Per-Arvid Wold	ph.d Biology	Functional development and response to dietary treatment in larval Atlantic cod *(Gadus morhua* L.) Focus on formulated diets and early weaning
2007	Anne Skjetne Mortensen	ph.d Biology	Toxicogenomics of Aryl Hydrocarbon- and Estrogen Receptor Interactions in Fish: Mechanisms and Profiling of Gene Expression Patterns in Chemical Mixture Exposure Scenarios
2008	Brage Bremset Hansen	ph.d Biology	The Svalbard reindeer (*Rangifer tarandus platyrhynchus*) and its food base: plant-herbivore interactions in a high-arctic ecosystem
2008	Jiska van Dijk	ph.d Biology	Wolverine foraging strategies in a multiple-use landscape
2008	Flora John Magige	ph.d Biology	The ecology and behaviour of the Masai Ostrich (Struthio camelus massaicus) in the Serengeti Ecosystem, Tanzania
2008	Bernt Rønning	ph.d Biology	Sources of inter- and intra-individual variation in basal metabolic rate in the zebra finch, (*Taeniopygia guttata*)
2008	Sølvi Wehn	ph.d Biology	Biodiversity dynamics in semi-natural mountain landscapes. - A study of consequences of changed agricultural practices in Eastern Jotunheimen
2008	Trond Moxness Kortner	ph.d Biology	"The Role of Androgens on previtellogenic oocyte growth in Atlantic cod (*Gadus morhua*): Identification and patterns of differentially expressed genes in relation to Stereological Evaluations"
2008	Katarina Mariann Jørgensen	Dr.Scient Biology	The role of platelet activating factor in activation of growth arrested keratinocytes and re-epithelialisation
2008	Tommy Jørstad	ph.d	Statistical Modelling of Gene Expression

		Biology	Data
2008	Anna Kusnierczyk	ph.d Bilogy	*Arabidopsis thaliana* Responses to Aphid Infestation
2008	Jussi Evertsen	ph.d Biology	Herbivore sacoglossans with photosynthetic chloroplasts
2008	John Eilif Hermansen	ph.d Biology	Mediating ecological interests between locals and globals by means of indicators. A study attributed to the asymmetry between stakeholders of tropical forest at Mt. Kilimanjaro, Tanzania
2008	Ragnhild Lyngved	ph.d Biology	Somatic embryogenesis in *Cyclamen persicum*. Biological investigations and educational aspects of cloning
2008	Line Elisabeth Sundt-Hansen	ph.d Biology	Cost of rapid growth in salmonid fishes
2008	Line Johansen	ph.d Biology	Exploring factors underlying fluctuations in white clover populations – clonal growth, population structure and spatial distribution
2009	Astrid Jullumstrø Feuerherm	ph.d Biology	Elucidation of molecular mechanisms for pro-inflammatory phospholipase A2 in chronic disease
2009	Pål Kvello	ph.d Biology	Neurons forming the network involved in gustatory coding and learning in the moth *Heliothis virescens:* Physiological and morphological characterisation, and integration into a standard brain atlas
2009	Trygve Devold Kjellsen	ph.d Biology	Extreme Frost Tolerance in Boreal Conifers
2009	Johan Reinert Vikan	ph.d Biology	Coevolutionary interactions between common cuckoos *Cuculus canorus* and *Fringilla* finches
2009	Zsolt Volent	ph.d Biology	Remote sensing of marine environment: Applied surveillance with focus on optical properties of phytoplankton, coloured organic matter and suspended matter
2009	Lester Rocha	ph.d Biology	Functional responses of perennial grasses to simulated grazing and resource availability
2009	Dennis Ikanda	ph.d Biology	Dimensions of a Human-lion conflict: Ecology of human predation and persecution of African lions (*Panthera leo*) in Tanzania
2010	Huy Quang Nguyen	ph.d Biology	Egg characteristics and development of larval digestive function of cobia (*Rachycentron canadum*) in response to dietary treatments -Focus on formulated diets
2010	Eli Kvingedal	ph.d Biology	Intraspecific competition in stream salmonids: the impact of environment and phenotype
2010	Sverre Lundemo	ph.d Biology	Molecular studies of genetic structuring and demography in *Arabidopsis* from Northern Europe
2010	Iddi Mihijai Mfunda	ph.d Biology	Wildlife Conservation and People's livelihoods: Lessons Learnt and Considerations for Improvements. Tha Case of Serengeti Ecosystem, Tanzania
2010	Anton Tinchov Antonov	ph.d Biology	Why do cuckoos lay strong-shelled eggs? Tests of the puncture resistance hypothesis
2010	Anders Lyngstad	ph.d Biology	Population Ecology of *Eriophorum latifolium*, a Clonal Species in Rich Fen Vegetation
2010	Hilde Færevik	ph.d Biology	Impact of protective clothing on thermal and cognitive responses
2010	Ingerid Brænne Arbo	ph.d Medical	Nutritional lifestyle changes – effects of dietary carbohydrate restriction in healthy obese and

		technology	overweight humans
2010	Yngvild Vindenes	ph.d Biology	Stochastic modeling of finite populations with individual heterogeneity in vital parameters
2010	Hans-Richard Brattbakk	ph.d Medical technology	The effect of macronutrient composition, insulin stimulation, and genetic variation on leukocyte gene expression and possible health benefits
2011	Geir Hysing Bolstad	ph.d Biology	Evolution of Signals: Genetic Architecture, Natural Selection and Adaptive Accuracy
2011	Karen de Jong	ph.d Biology	Operational sex ratio and reproductive behaviour in the two-spotted goby (*Gobiusculus flavescens*)
2011	Ann-Iren Kittang	ph.d Biology	*Arabidopsis thaliana* L. adaptation mechanisms to microgravity through the EMCS MULTIGEN-2 experiment on the ISS:– The science of space experiment integration and adaptation to simulated microgravity
2011	Aline Magdalena Lee	ph.d Biology	Stochastic modeling of mating systems and their effect on population dynamics and genetics
2011	Christopher Gravningen Sørmo	ph.d Biology	Rho GTPases in Plants: Structural analysis of ROP GTPases; genetic and functional studies of MIRO GTPases in *Arabidopsis thaliana*
2011	Grethe Robertsen	ph.d Biology	Relative performance of salmonid phenotypes across environments and competitive intensities
2011	Line-Kristin Larsen	ph.d Biology	Life-history trait dynamics in experimental populations of guppy (*Poecilia reticulata*): the role of breeding regime and captive environment
2011	Maxim A. K. Teichert	ph.d Biology	Regulation in Atlantic salmon (*Salmo salar*): The interaction between habitat and density
2011	Torunn Beate Hancke	ph.d Biology	Use of Pulse Amplitude Modulated (PAM) Fluorescence and Bio-optics for Assessing Microalgal Photosynthesis and Physiology
2011	Sajeda Begum	ph.d Biology	Brood Parasitism in Asian Cuckoos: Different Aspects of Interactions between Cuckoos and their Hosts in Bangladesh
2011	Kari J. K. Attramadal	ph.d Biology	Water treatment as an approach to increase microbial control in the culture of cold water marine larvae
2011	Camilla Kalvatn Egset	ph.d Biology	The Evolvability of Static Allometry: A Case Study
2011	AHM Raihan Sarker	ph.d Biology	Conflict over the conservation of the Asian elephant (*Elephas maximus*) in Bangladesh
2011	Gro Dehli Villanger	ph.d Biology	Effects of complex organohalogen contaminant mixtures on thyroid hormone homeostasis in selected arctic marine mammals
2011	Kari Bjørneraas	ph.d Biology	Spatiotemporal variation in resource utilisation by a large herbivore, the moose
2011	John Odden	ph.d Biology	The ecology of a conflict: Eurasian lynx depredation on domestic sheep
2011	Simen Pedersen	ph.d Biology	Effects of native and introduced cervids on small mammals and birds
2011	Mohsen Falahati-Anbaran	ph.d Biology	Evolutionary consequences of seed banks and seed dispersal in *Arabidopsis*
2012	Jakob Hønborg Hansen	ph.d Biology	Shift work in the offshore vessel fleet: circadian rhythms and cognitive performance
2012	Elin Noreen	ph.d Biology	Consequences of diet quality and age on life-history traits in a small passerine bird

2012	Irja Ida Ratikainen	ph.d Biology	Theoretical and empirical approaches to studying foraging decisions: the past and future of behavioural ecology
2012	Aleksander Handå	ph.d Biology	Cultivation of mussels (*Mytilus edulis):*Feed requirements, storage and integration with salmon (*Salmo salar*) farming
2012	Morten Kraabøl	ph.d Biology	Reproductive and migratory challenges inflicted on migrant brown trour (*Salmo trutta* L) in a heavily modified river
2012	Jisca Huisman	ph.d Biology	Gene flow and natural selection in Atlantic salmon
2012	Maria Bergvik	ph.d Biology	Lipid and astaxanthin contents and biochemical post-harvest stability in *Calanus finmarchicus*
2012	Bjarte Bye Løfaldli	ph.d Biology	Functional and morphological characterization of central olfactory neurons in the model insect *Heliothis virescens*.
2012	Karen Marie Hammer	ph.d Biology.	Acid-base regulation and metabolite responses in shallow- and deep-living marine invertebrates during environmental hypercapnia
2012	Øystein Nordrum Wiggen	ph.d Biology	Optimal performance in the cold
2012	Robert Dominikus Fyumagwa	Dr. Philos.	Anthropogenic and natural influence on disease prevalence at the human –livestock-wildlife interface in the Serengeti ecosystem, Tanzania
2012	Jenny Bytingsvik	ph.d Biology	Organohalogenated contaminants (OHCs) in polar bear mother-cub pairs from Svalbard, Norway Maternal transfer, exposure assessment and thyroid hormone disruptive effects in polar bear cubs
2012	Christer Moe Rolandsen	ph.d Biology	The ecological significance of space use and movement patterns of moose in a variable environment
2012	Erlend Kjeldsberg Hovland	ph.d Biology	Bio-optics and Ecology in *Emiliania huxleyi* Blooms: Field and Remote Sensing Studies in Norwegian Waters
2012	Lise Cats Myhre	ph.d Biology	Effects of the social and physical environment on mating behaviour in a marine fish
2012	Tonje Aronsen	ph.d Biology	Demographic, environmental and evolutionary aspects of sexual selection
2012	Bin Liu	ph.d Biology	Molecular genetic investigation of cell separation and cell death regulation in *Arabidopsis thaliana*
2013	Jørgen Rosvold	ph.d Biology	Ungulates in a dynamic and increasingly human dominated landscape – A millennia-scale perspective
2013	Pankaj Barah	ph.d Biology	Integrated Systems Approaches to Study Plant Stress Responses
2013	Marit Linnerud	ph.d Biology	Patterns in spatial and temporal variation in population abundances of vertebrates
2013	Xinxin Wang	ph.d Biology	Integrated multi-trophic aquaculture driven by nutrient wastes released from Atlantic salmon (*Salmo salar*) farming
2013	Ingrid Ertshus Mathisen	ph.d Biology	Structure, dynamics, and regeneration capacity at the sub-arctic forest-tundra ecotone of northern Norway and Kola Peninsula, NW Russia
2013	Anders Foldvik	ph.d Biology	Spatial distributions and productivity in salmonid populations
2013	Anna Marie Holand	ph.d Biology	Statistical methods for estimating intra- and inter-population variation in genetic diversity

2013	Anna Solvang Båtnes	ph.d Biology	Light in the dark – the role of irradiance in the high Arctic marine ecosystem during polar night