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Visual predation by the euphausiid *Meganyctiphanes norvegica*

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ABSTRACT: Experiments showed that *Meganyctiphanes norvegica* are visual predators on copepods. Adult *M. norvegica* were offered a mixture of equal numbers of late stage *Calanus* spp. and *Metridia longa* in total darkness and at a light intensity corresponding to their daytime habitat. Predation rates were 3 times higher in the illuminated containers than in the dark ones (7 vs 2.3 copepods krill⁻¹ 18h⁻¹), and higher on *M. longa* than on *Calanus* spp. in both light (1.3 times) and darkness (2.3 times). Swimming speeds of *M. longa* were about 10 times faster than those of *Calanus* spp., making *M. longa* more susceptible to mechanical detection.

KEY WORDS: Visual predation · *Meganyctiphanes norvegica* · Euphausiid feeding

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While planktivorous fish are normally considered visual predators, vision is rarely considered in the feeding of invertebrate planktivores. However, some invertebrate planktivores do possess highly developed eyes that may be used to detect prey. Both the marine cyclopoid copepod *Coryacaeus anglicus* (Gophen & Harris 1981) and the freshwater mysid *Mysis relicta* (Ramcharan & Sprules 1986), whose eyes are very similar to those of *Meganyctiphanes norvegica* (Hallberg & Nilsson 1983), locate animal prey visually, and several deep-living hyperiids and krill possess tubular eyes, indicating that they search for prey by looking for silhouettes against the dim downwelling light like some meso- and bathypelagic fish (Nilsson 1996).

The euphausiids *Meganyctiphanes norvegica* are a major component of both nearshore and offshore pelagic communities in the north Atlantic (Mauchline & Fisher 1969, Mauchline 1980). They feed on both zooplankton and algae, zooplankton being more important for them than for other euphausiids (Mauchline & Fisher 1969, Mauchline 1980, McClatchie 1985, Beyer 1992, Båmstedt & Karlson 1998, Hjelmseth 1998, Larsen

1998, Onsrud & Kaartvedt 1998). Their behaviour in Norwegian fjords, forming acoustic layers following isolumines throughout the diel cycle (Onsrud & Kaartvedt 1998), closely resembles that of visually hunting mesopelagic fish (Giske et al. 1990, Baliño & Aksnes 1993). Hence, my primary aim was to test if *M. norvegica* are able to act as visual predators, displaying higher feeding rates at low, realistic light intensities than in total darkness. Moreover, if *M. norvegica* is both a visual and a tactile predator, relative conspicuousness of prey with different behaviours may be perception-mode, and hence light-regime, specific. This paper addresses these questions experimentally.

Materials and methods. Capture and treatment of animals: *Meganyctiphanes norvegica* were caught on the 17 and 24 November 1997 with a modified Nansen net (1 m diameter, 500 µm mesh size) with a closed cod end in the inner Oslofjord (bottom depth ca 115 m). Copepods were caught in the outer Oslofjord with vertical hauls from the bottom (200 m) to the surface at the same dates with the same net. Upon capture, animals were immediately transferred to 5 l buckets with ca 4°C 0.03 µm filtered seawater (FSW) collected at ~50 m, where salinity is above ~33 PSU throughout the year. Krill were covered with dark plastic. Both krill and copepods were diluted at the laboratory in 50 l slightly conical, white polypropylene containers, and kept in the dark at 6°C. This temperature was used in all experiments. Animals were used 1 to 4 d after capture, and not fed before the experiments.

Predation experiments: Experiments for comparison of *Meganyctiphanes norvegica* predation in light and in darkness were run simultaneously in 50 l white polypropylene containers on 5 different dates (n = 16). Three krill measuring (from the centre of the eye to the end of the telson) 29.3 ± 1.7 mm (mean ± SD) were transferred to each container filled with 43 l FSW 1.5 to 3.5 h before experiments were started. All containers were illuminated with indirect light from a 5 W, 6 V halogen lamp directed towards the walls and ceiling.

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Light intensity within the illuminated containers was about $5 \times 10^{-3} \mu\text{mol m}^{-2} \text{s}^{-1}$, measured from above with a 2π LiCor 190SA quantum sensor connected to a LiCor-1000 data logger. This is comparable to maximum values in the krill layer in the Oslofjord during daytime (Hjelmseth 1998, Onsrud & Kaartvedt 1998, pers. obs.), although the spectral composition may differ significantly. Experiments were started by transferring 40 late stage *Calanus* spp. (97% CV in the controls, average prosome length 1.75 mm) and 40 *Metridia* spp. (96% of the control specimens were adult female *M. longa*, average prosome length 1.90 mm) to each container at random. Random containers were kept dark by covering them with double layers of folded, black plastic. After 18 (± 0.5) h, experiments were terminated by removing the krill. Remaining copepods were collected on a 180 μm sieve and counted immediately. Additionally, 7 controls with copepods only were run (1 or 2 on every date). Mean recovery of copepods in the controls was 99.6% for *Calanus* spp. and 100.4% for *M. longa*. All missing copepods in the krill containers were therefore considered eaten. No obviously injured copepods were recovered, although they were not checked thoroughly for damage. One illuminated and 1 dark container were discarded due to recovery above 100%. All krill and control copepods were fixed in >4% formalin for length measurements and identification of stage.

Video recordings: Eventual differences in feeding rate on species or between treatments may be due to differences in prey behaviour and distribution. In order to evaluate these possible effects, 6 replicate 10 min video recordings were made of both copepod species in the same light regimes as the predation experiments. Copepods were filmed with an IR-sensitive Sony CCD camera and recorded on an S-VHS recorder. Illumination consisted of an array of 880 nm IR-diodes, which probably did not affect the copepods (cf. Forward & Costlow 1974, Bradley & Forward 1984, Cronin & Forward 1988). For each replicate, the first species to be recorded was chosen at random. Ten copepods were transferred to a 600 ml Nunclon™ culture flask filled with FSW and left in the recording room for 30 min before they were recorded. Sequence of light and darkness was decided by flipping a coin, and after 10 min of recording, lights were turned on or off and the animals were recorded for a new 10 min period. Average numbers of copepods in each vertical quartile of the flasks were estimated from 5 counts from the last 5 min of the filming periods. Some copepods were not visible on the screen. Most of these were associated with the bottom. The copepods were assumed to swim equally in both horizontal directions, and swimming speeds were therefore determined as:

$$v = \frac{\sqrt{2 \times \Delta X^2 + \Delta Y^2}}{\Delta t}$$

ΔX and ΔY were determined to the closest mm by measuring horizontal and vertical displacements between each turn (change of vertical or horizontal direction) during an 11 s period. For each replicate recording, the swimming of the copepod closest to the centre of the flask was measured.

Results. The number of copepods eaten (*Calanus* spp., *Metridia longa* and total) krill⁻¹ were log₁₀ transformed for a better fit to the ANOVA assumptions of normal distribution and uniform variance. Total number of copepods eaten krill⁻¹ in the illuminated containers was almost 3 times the number in the dark containers (7.1 vs 2.5; Fig. 1). The difference was statistically significant ($p < 0.0001$, 1-factor ANOVA). Estimated difference in predation rates between treatments on *Calanus* spp. and *M. longa* were statistically significant for both species ($p < 0.0001$, 1-factor ANOVAs) and practically identical in absolute terms (2.3 krill⁻¹ 18h⁻¹ more in the illuminated containers; Fig. 1). The relative difference between treatments, however, was greater for *Calanus* (a factor of 4.3) than for *M. longa* (2.4).

Predation on *Metridia longa* was 2.3 times that on *Calanus* spp. in the dark containers and only 1.3 times in the illuminated ones. The *Calanus* spp. proportion in the diets of the krill was significantly lower than 0.5 in both the dark and the illuminated containers (Fig. 2). The *Calanus* spp. proportion in the illuminated containers was significantly higher statistically than in the dark ones ($p = 0.03$, Mann-Whitney *U*-test).

In the flasks, *Metridia longa* were distributed deeper than *Calanus* spp. (Fig. 3). Average swimming speed was much higher for *M. longa* (7.2 mm s⁻¹ or 3.8 BL [body lengths] s⁻¹) than for *Calanus* spp. (0.6 mm s⁻¹ or 0.3 BL s⁻¹) (Fig. 4). Neither vertical distribution nor swimming speed were found to depend on light regime.

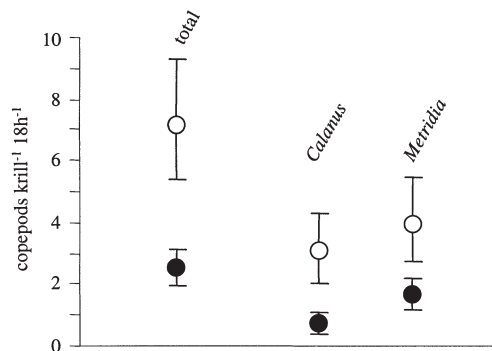


Fig. 1. *Meganyctiphanes norvegica*. Predation rates in dark (●) and illuminated (○) containers. 95% confidence intervals (CI) are shown. Estimates from 1-factor ANOVAs on log₁₀ transformed values (n = 15)

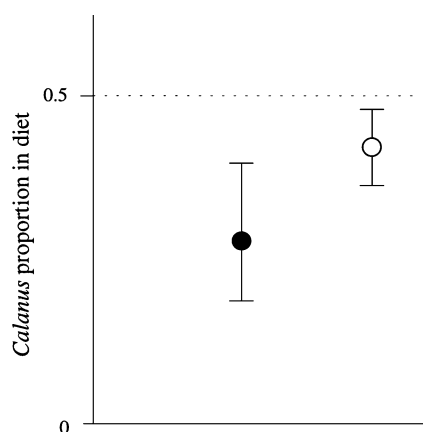


Fig. 2. *Calanus* spp. proportion in the diets of *Meganycitiphanes norvegica* in dark (●) and illuminated (○) containers, estimated from \log_{10} transformed values. 95% CI (independently assessed for each estimate) are shown ($n = 15$)

M. longa were mainly cruising in horizontal loops, while the modest swimming of *Calanus* spp. mainly consisted of vertical 'hop and sink' behaviour.

Discussion. The results provide evidence that *Meganycitiphanes norvegica* is a visual predator, being able to prey more efficiently on copepods at low, realistic light intensities than in total darkness. As the level of activity in the flasks was independent of light regime, higher prey activity is not a plausible explanation for the enhanced predation rates observed in the illuminated containers. Moreover, it is unlikely that a non-visual predator the size of *M. norvegica*, itself being subject to visual predation, should display more predation effort in light than in darkness. The higher proportion of *Calanus* spp. in the diets of *M. norvegica* in the illuminated containers also controverts the possibility of increased predation effort as an explanation for increased predation rates, since this should not affect the relative contribution of prey species in the diet. If, due to possibly deeper krill distribution in the illuminated containers, the higher predation rates in

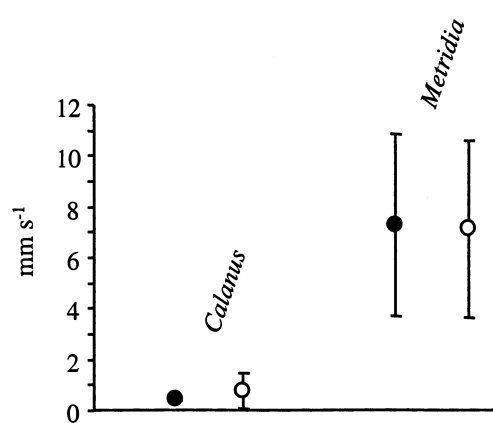


Fig. 4. Average swimming speeds of *Calanus* spp. and *Metridia longa* in the 600 ml flasks in dark (●) and illuminated (○) flasks (\pm 95% CI, $n = 6$)

these was a result of better spatial overlap between krill and the copepods, *Metridia longa* should constitute a larger proportion of the diet in the illuminated containers, as this species showed the higher affinity for the bottom in the flasks. However, the opposite was found with *Calanus* spp. constituting a higher proportion in the illuminated containers.

Since *Calanus* spp. and *Metridia longa* do not differ much in size or contrast, the importance of their difference in motion for visual and non-visual (i.e., hydrodynamic) conspicuousness may be inferred from the relationship between predation rates in the illuminated and dark containers for the 2 species. McClatchie (1985), investigating feeding of *Meganycitiphanes norvegica* on copepods in darkness experimentally, found clearance rate to be almost 20 times the sweeping rate (volume actually swept by the food basket time^{-1}), showing that also non-visual predation on copepods in this species is an active process. The 2.3 times higher feeding rate on *M. longa* than on *Calanus* spp. in darkness found in my experiments suggests that *M. longa* is

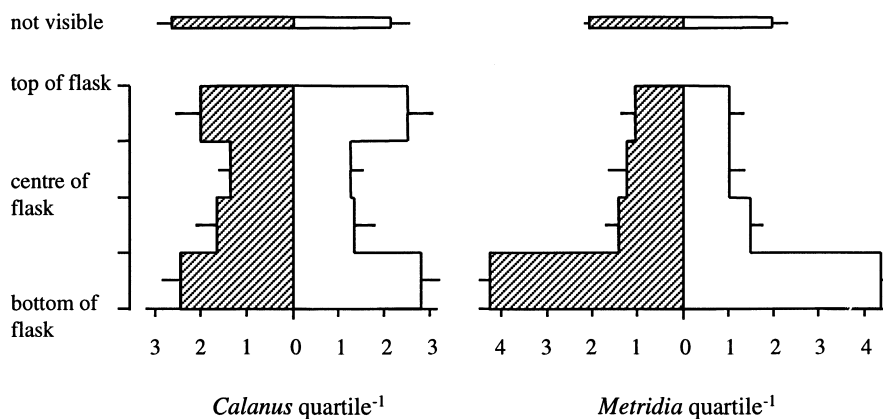


Fig. 3. Vertical distribution of *Calanus* spp. and *Metridia longa* in the 600 ml flasks, in dark (filled) and illuminated (open) flasks. 1 SD is indicated ($n = 6$)

more easily perceived mechanically than the less active *Calanus* spp. (cf. Feigenbaum & Reeve 1977, Gerritsen & Strickler 1977, Greene 1983, Tiselius et al. 1997).

The values from the illuminated containers may be interpreted in 2 ways, depending on assumptions of the perceptive world of *Meganyctiphanes norvegica*. If the visual reactive field does not overlap with the reactive field for mechanical perception, or at least one of the reactive fields is a large one in which probability of perception is low, visual and non-visual predation rates will be additive. Interpreting my results within this model, estimated visual conspicuousness to *M. norvegica* for the 2 species is identical, 1.3 and 3.3 times higher than mechanical conspicuousness for *Metridia longa* and *Calanus* spp. respectively. If, however, the smaller, mechanical perceptive field is confined within the visual one, all prey in the illuminated containers were seen before they entered the mechanical perceptive field, and the predation rates in the illuminated containers represent exclusively visual predation rates, implying a slightly higher visual conspicuousness for *M. longa*. It should be kept in mind that differences in catchability between the 2 species may well mask or falsely suggest differences in conspicuousness.

Several authors have reported that motion increases visual conspicuousness of zooplankton (Ware 1973, Kislalioglu & Gibson 1976, Janssen 1982, Wright & O'Brien 1982, 1984, Dodson et al. 1995, Brewer & Coughlin 1996, O'Keefe et al. 1998). The littoral fishes used as predators in these investigations make use of a saltatory search, alternating between swimming short distances and looking for moving prey while remaining stationary (O'Brien et al. 1986, 1989, 1990, Evans & O'Brien 1988). However, Janssen (1982) showed that opposed to littoral, facultative planktivores, the obligate, pelagic plantivore blueback herring did not detect moving prey more easily than non-moving prey. Due to the featureless visual pelagic world (see Nilsson 1996), pelagic visual predators may not be able to distinguish the moderate motion of their prey from their own, nor do they have the need to discriminate between prey and non-moving, inedible surroundings. Bollens et al. (1993) found no experimental or field evidence of higher visual conspicuousness of *Metridia lucens* than of the less active *Calanus pacificus*. However, other behavioural differences between *Calanus* spp. and *Metridia* spp. are relevant for their visual conspicuousness to pelagic visual predators. The irradiance in open water is 2 to 3 orders of magnitude higher from above than from below, also at great depths (Jerlov 1968, Nilsson 1996). *Calanus* spp., with its upright position, exposes its smallest area (tentatively estimated to $\frac{1}{3}$ of its dorsoventral or lateral area) to predators looking for their silhouette against the dim

downwelling light, while *Metridia* spp. does the opposite by cruising around in horizontal loops. Both my experiments and those conducted by Bollens et al. (1993), using herring as predators, provided light from all angles, thus depriving *Calanus* spp. of its forte. These results therefore probably exaggerate the visual risk of predation of *Calanus* spp. relative to that of *Metridia* spp.

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