

Torsten Fregin · Konrad Wiese

The photophores of *Meganyctiphanes norvegica* (M. Sars) (Euphausiacea): mode of operation

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Abstract The photophores of *Meganyctiphanes* were investigated with regard to the control of light production and with respect to their role in a hitherto unknown communication system using light flashes which became evident from observation of specialised signalling behaviour. To that purpose the light production was recorded during presentation of a range of stimuli delivered to the intact, tethered shrimp. Stimuli used were changes in ambient light, water turbulence, simulated predator approach and light flashes, as well as electric shocks and serotonin injections. Strong negative light gradients, exaggerating the natural sunset signal, reliably elicited light production, the peak of which lasted on average 2 min. In the late phase of this light production, low frequency water oscillations and turbulent flow (assumed intraspecific communication signals at close range) elicited transient increases in light production. Artificial light flashes presented to a group of shrimp evoked a signalling behaviour in which the animal points the light of its photophore beamers (positioned at the ventral side and normally directed downwards) for a fraction of a second at observers within the same depth level. The responses produced by the signalling behaviour indicate a fixed delay with respect to the triggering flash. Electric stimulation of the ventral nerve cord via implanted electrodes resulted in a strong light production with a latency of 160 ms. Injection of serotonin, resulting in haemolymph concentrations of 10^{-5} M and higher, initiated increasingly strong and increasingly long-lasting continuous light production. Implications for the control of the photophores are discussed.

Keywords Euphausiacea · *Meganyctiphanes* · Bioluminescence · Serotonin · Control of photophores

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T. Fregin · K. Wiese (✉)
Zoologisches Institut und Zoologisches Museum der Universität,
Martin-Luther-King-Platz 3, 20146 Hamburg, Germany
e-mail: kwiese@zoologie.uni-hamburg.de
Fax: +49-40-428383937

Introduction

The present study investigates the control of the photophores of the euphausiid *Meganyctiphanes norvegica* (North Atlantic krill; Fig. 1). Our present knowledge of euphausiid photophores (Peterson 1968; for a review, see Herring and Locket 1978) is predominantly based on their morphology, while no information exists on their assumed role in intraspecific communication. In contrast, the lantern organs of luminescent insects stimulated research on structure, control (for a review, see Case and Strauss 1978), and on their role in the corresponding light flash communication system (for a review, see Lloyd 1971). A fairly comprehensive treatise on all aspects of bioluminescence was published by Hastings and Morin (1991).

The lantern organs of the insects *Photuris versicolor* and *Photinus greenii* are innervated by segmental octopaminergic nerve cells (Christensen and Carlson 1982), called DUM (dorsal unpaired medial) neurons. The reported strong effect of serotonin on light production in the photophores of *Meganyctiphanes* (Doyle and Kay 1967) suggests a corresponding aminergic innervation, since serotonin in the crustacean nervous system is commonly assumed to represent the functional analogue of octopamine in the insect nervous system.

Potential candidates for the innervation of the photophores are serotonergic cells such as those identified by serotonin-like immunoreactivity (Beltz and Kravitz 1983; for a review, see Beltz 1999) in the ganglia of lobsters, in the crayfish ventral nerve cord (Real and Czernasty 1990) and in the crayfish brain (Sandeman et al. 1988, 1995), proved that such cells also exist in euphausiids. Serotonin may act as a regular, ionotropic transmitter like glutamate at the neuromuscular synapse of arthropods or it may affect the target cells via a second messenger system (metabotropic) – usually with longer latencies and longer lasting effects (Bermudez et al. 1992; Roeder 1994, 1999). Finally, serotonin was also found to act as a hormone, because it accelerates the heartbeat frequency in *Astacus* at bath-applied doses

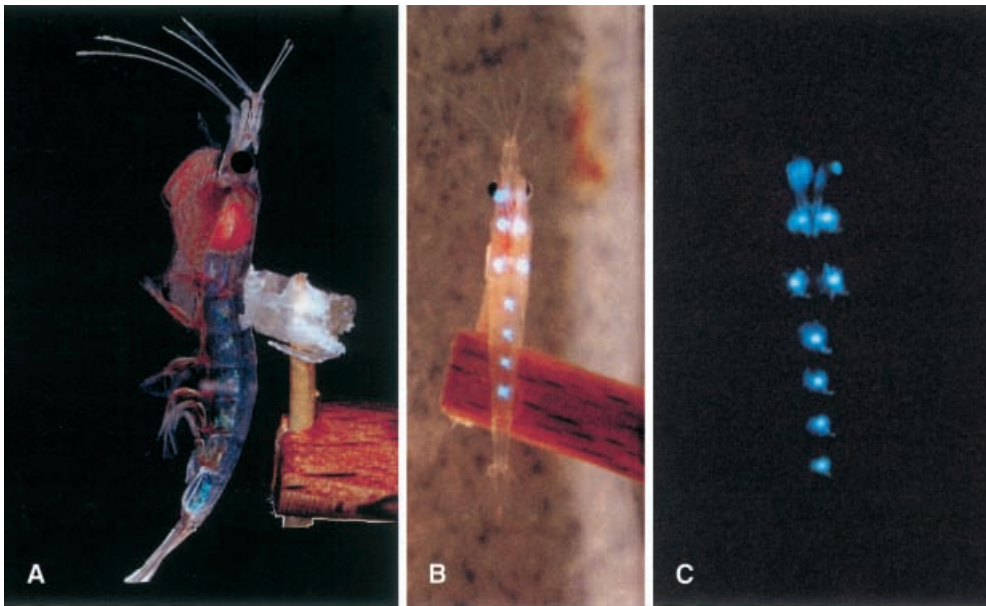


Fig. 1 **A** *Meganyctiphanes norvegica* Sars (Arctic krill), body length about 40 mm. The skeleton is transparent and allows inspection of most internal structures from the outside. The antennular flagella in this specimen are damaged, showing about half the intact length. Note the large eyes, the folded filter basket formed from bristle-lined, double branched pereopods for sifting plankton, and the set of five, continuously and metachronically beating pairs of swimmerets. (Photograph by Torsten Fregin.) **B** *Meganyctiphanes*, in tethered condition, as viewed ventrally after injection of serotonin. Only from this viewing angle is it possible to see that all ten photophores are alight, two in the eyestalks, two near the mouth and two at the posterior end of the thorax; four more photophores are unpaired, positioned directly above the median of the sternites in abdominal segments 1–4. **C** The pattern of light dots photographed in darkness, exposure time 40 s/400 ASA. The natural colour, a narrow band blue of 480 nm wavelength, is visible to the human eye with background irradiation dimmer than 10^{-2} $\mu\text{W}/\text{cm}^2$. Note that parts of the appendages are illuminated

characteristic of hormones – as low as 10^{-8} M (Florey and Rathmayer 1978). Light and TEM microscopy revealed that the photophores of *Meganyctiphanes* are innervated (Peterson 1968; Harvey 1977; Herring and Locket 1978); however, the innervation is inconspicuous and it is not known whether the terminals contain serotonin.

In conclusion, three considerations motivated the present study of the photophores in *Meganyctiphanes*: firstly, the influence of serotonin on the process of light production possibly provides information on the functional role of the amine in the special context; secondly the photophores are part of an as yet uninvestigated system of intraspecific communication using light signals; thirdly, the possibility of measuring light production by sensitive photomultiplier tubes in an intact shrimp may elucidate the origin of commands controlling light production.

Materials and methods

Freshly caught shrimp *M. norvegica* (krill) were provided by the crew of the ships of Kristinebergs Marina Forskningsstation, Fiskebäckskil, Gulmarfjord, Sweden, where the experiments were performed. The shrimp, caught during daytime, arrived on shore in a 50-l thermos container at 0–5°C and, to provide optimal conditions, were directly transferred to a 1-m³ tank (fibreglass, painted in light grey, non-reflecting, supplied with flow-through seawater at 8°C) in a constant temperature dark room. If the shrimp were not fed, after about 3 days the photophores could no longer be activated by normally effective triggering signals (see below). As a consequence, homogenised *Mytilus* were suspended in the tank water, which preserved the readiness of the shrimp to light the photophores for another few days. The shrimp had to be handled with extreme care in order to prevent the delicate flagella of the antennules from breaking off, which leaves the shrimp without sensitivity to flow events.

Triggering light production

Depending on the duration of the light period which the shrimp have experienced previously, a negative light gradient (dimming or switching off room lights) resulted in an activation of the photophores with a latency of about 20 s. For measurements individual shrimp were preselected based on their readiness to activate the photophores. The IC-sensor TSL 235 (Texas Instruments) was used to measure irradiance. It has a sensitivity of 0.2 nW/cm² and provides a square-wave frequency at the output, which is proportional to irradiance (1 kHz at the output corresponds to 1 mW/cm²). When room lights were on an irradiance of 60 $\mu\text{W}/\text{cm}^2$ was measured, in the condition with room lights off it was 0.2 nW/cm², the situation in which most photophore light measurements were made. The spectral sensitivity of the eyes of *M. norvegica* is centred around a maximum at 480 nm (Kampa 1955; Frank and Case 1988; for fireflies see Cronin et al. 2000).

Tethering the shrimp for measurement of light production

A cubelet (4×4×4 mm) cut from perspex and fitted with a 1.5 mm hole was glued (cyanoacrylate: Pattex-Sekundenkleber) to the animal's carapace, the hole in parallel with the long axis of the body. During the 30 s required for the glue to harden, the animal had to lie on its side in a Petri dish with only the ventral side and swim-

merets partly immersed in a film of water. The shrimp, immersed in seawater, was then attached to the tip of a toothpick fitted to a wooden stick, the other end of which was clamped above the cuvette. By turning the cubelet around the toothpick, the ventral side of the shrimp with all ten photophores could be turned sideways to face the lens and photomultiplier tube (PMT). The temperature of the water in the experimental dish was kept identical to that in the storage tank to avoid stress to the "stenothermal" organism.

Injections of serotonin

Once the perspex cubicle had been glued to the carapace, freshly prepared solutions, not more than 20 μ l mostly 5 μ l in volume, of serotonin in distilled water were injected by Hamilton syringe into the pleon in a ventrocaudal direction. The volume of haemolymph within the shrimp was determined to be one-third of the water displacement (total body volume) of the shrimp (H. Dirksen, personal communication).

Measurement of light from the photophores

A suitable photomultiplier tube type 1P28 [manufacturer, RCA; distributor, BURLE, Milwaukee, Wis., USA; maximum sensitivity at 350 nm, 50% of maximum sensitivity at 480 nm; the wavelength of 480 nm corresponds to the centre of the spectrum of light emitted by *Meganctiphanes*: Widder et al. (1983)] was fitted into a light-proof housing, which contained a wheel of neutral density filters and a mechanical shutter. The voltage generated across the ends of the resistor (1–100 kohms was used), which connected the anode to ground was amplified by an inverting operational amplifier with variable gain (typically 30 \times). To reduce the high frequency noise of the anode current of the PMT and that of the signal amplifier, a low-pass filter was built by connecting the output of the signal amplifier ($R_i = 80$ ohms) to ground by a capacity of 1 microfarad (μ F). The upper frequency limit under that condition was 2,000 Hz, calculated according to $F_{\text{limit}} = 1/2\pi RC$.

Three arrangements were used to measure light production by the photophores:

1. The PMT fitted with a collimator lens was directed from the side onto a glass aquarium (1–2 m distance) holding a population of swimming shrimp, or from above (1 m distance) onto the shrimp swimming in the 1-m³ tank.
2. A tethered swimming shrimp was rolled sideways so that the set of ten photophores faced the lens and PMT, positioned about 30 cm from the cuvette containing the shrimp.
3. A tethered swimming shrimp inside the experimental cuvette was positioned above the objective (10 mm working distance) of an inverted microscope. The posterior thoracal photophores or the most anterior photophore of the abdominal segments were closest to the attachment of the shrimp and hence moved very little in the visual field of the microscope. An optical beam-splitter allowed us to direct the light from the photophore onto the PMT attached to the microscope.

Water displacements

The shrimp were stimulated with water oscillations at frequencies of 3–150 Hz produced by a dipole source (sphere of 12 mm diameter) oscillating along an axis oriented frontodorsally and orthogonally onto the ventrally directed antennular flagellum. The sphere was pointed at the midpoint of the length of the flagellum. If 12 mm away from the centre of the sphere, this point on the flagellum receives water displacements attenuated by a factor 0.125 of the peak-to-peak amplitude of the sphere (van Bergeijk 1967). The oscillations, set to a uniform level of velocity at 1 mm/s at the flagellum, had controlled rising flanks (200 ms duration), formed by a simple device built from a flashlight bulb and a photoresistor (Wiese et al. 1980). Nearly laminar, as well as characteristically

turbulent flow signals were applied from a jet nozzle 5 cm away from the shrimp, directed frontally onto its head. Turbulence was generated by a piston moving up and down in a side branch of the tube close to the jet nozzle.

Visual stimuli

A light-emitting diode (LED) (470 nm) mounted at the end of a perspex tube of 6 mm diameter was positioned in the centre of the large tank (1 m³ water volume) and driven by square-wave pulses (5 V) to emit light flashes from inside the water body and hence directly from within the population of shrimp. Flash duration was varied between 1 and 10 ms.

Stimulation by electric shock

Electrodes were positioned to the right and left of the shrimp's body in the water of the cuvette and were connected to a 4.5 V battery (zinc-carbon, a fraction of the voltage was used for a protocol of the stimulus). The stimuli were controlled manually by push-button, leading to current flows of approximately 1 s duration. Alternatively, a pair of lacquer-insulated stainless steel wires, the cut ends serving as electrodes, were implanted under microscopic control into a tethered shrimp (*M. norvegica* is almost completely transparent) and positioned near the dorsal surface of the ventral cord within the first two abdominal segments of the shrimp. The stimulus voltage had to be very high (about 50 V) because of the very small electrode surfaces (80 μ m diameter) and thin steel wires, which constitute in-series resistors (25 ohms/10 cm) and cause a voltage drop. Effective stimuli were trains (200 Hz repetition) of monopolar rectangular pulses, 0.5–1.0 ms in duration. Trains were produced by the gating mode of the stimulator.

Recording of data

Data were recorded using a notebook computer (Highscreen LeBook) fitted with A/D converter card and in connection with the program LabView (National Instruments, Houston, Tex., USA). Data were collected at a rate of 250 samples per second; only in experiments requiring very long periods of recording was the rate of sampling reduced to 80 samples per second. The displays on the screen of the computer were edited based on the requirements of the particular measurements and were then printed.

Results

Control of the photophores as deduced from behaviour

Meganctiphanes is obviously negatively phototactic. This statement is based on the observation that the shrimp occupy all of the water volume in the aquarium in darkness, while in light they instantaneously let themselves sink to the bottom, expecting to drift into protective darkness. All photophores, except those inside the eyestalk, are arranged close to and so as to shine their light through the transparent ventral body surface (Fig. 1B, C). The photophores are beamers (Herring and Locket 1978) with refined optics, emitting a parallel beam. Except for the outlet of light, the beamers are well sealed by screening pigments with the result that the light is visible only to observers located on the extension of the optical axis of the beamer. To complicate matters, the photophores are always pointed away from down-

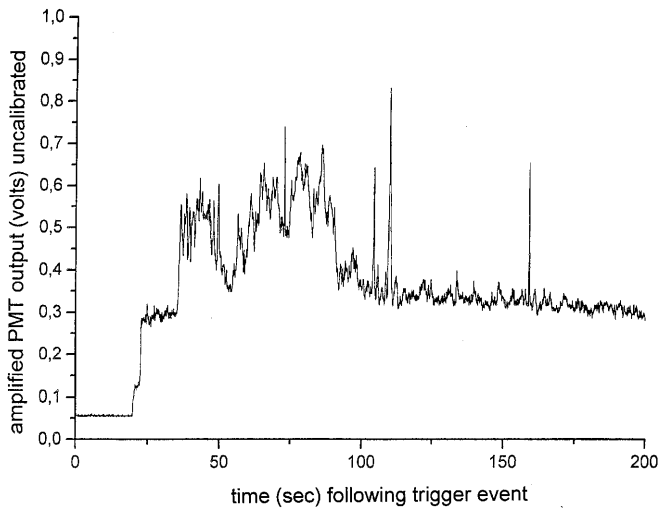


Fig. 2 Protocol of light flashing emerging from about 100 *Meganyctiphanes* inside an aquarium 35×35×60 cm in size. The photomultiplier tube (PMT) fitted with a collimator lens records light events within the aquarium from 2 m distance. After the triggering event for light production in the photophores (switching off room lights), the recording is started (0 s), then the PMT power supply and signal amplifier are switched on and lastly a mechanical shutter is opened. The recording trace jumps up and shows noise. Flashes represented by small needle type peaks in the recording are generated by the signalling behaviour of the shrimp (see text) distorted here by the small size of the aquarium. The numerous shrimp with activated photophores generate a continuous glow in the aquarium, which elevates the DC-level of the recording. The three sharp peaks between 105 and 170 s of the recording are light signals of a light-emitting diode (LED) used in an attempt to calibrate the light recorded

welling light by the posture control system (Land 1980) which detects a maximum of irradiation in the water to establish top and bottom (Lythgoe 1988). To summarise, the light of photophores is not visible unless the shrimp presents its ventral side to the observer.

In all our experiments the photophores were activated by strong, negative light gradients as observed by Mauchline (1960). The earliest light emissions in the 40-l aquarium became visible about 20 s after the onset of darkness, and lasted for 50–120 s. Essentially, a sequence of light emissions (Fig. 2), each of about 1 s duration, were produced by some individuals of the population, which swim conspicuously in a fast and slightly curved trajectory. Others rested at the bottom of the aquarium and occasionally presented the light of their photophores for 10 or more seconds continuously. This behaviour raised the level of recorded light production significantly (see Fig. 2 with two phases of increased light level).

A large tank of 1×1 m floor size (used in the recordings shown in the Figures) obviously provided the necessary space for a normal signalling behaviour of the shrimp. Either spontaneously or in response to a light signal received, a first shrimp started to swim forward in a curved trajectory of about 1 m length, at maximum speed, while simultaneously rolling around its longitudi-

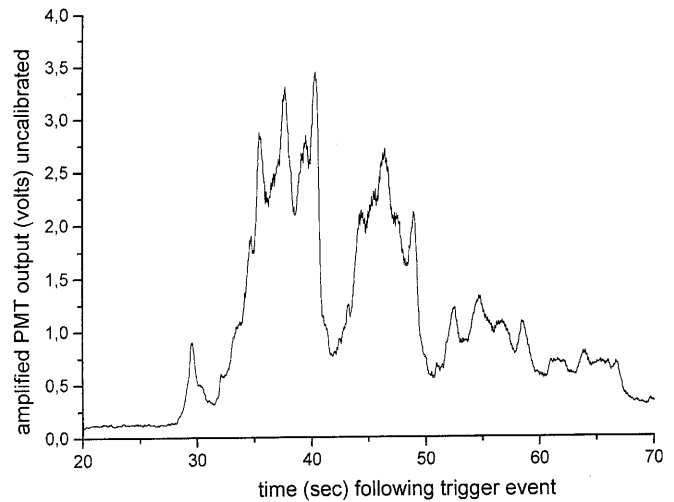


Fig. 3 Continuous light production in all ten photophores of a single specimen during 70 s following the triggering event (room lights off). The shrimp is tethered with its ventral side turned sideways (compare Fig. 1B) to point the photophores towards the PMT at 30 cm distance. Note the distinct delay of the onset of a continuous light production (compare Fig. 2). A strong modulation of light amplitude at times 31, 41 and 50 s of the recording is displayed, resulting from the struggling of the shrimp to return to its normal body posture, thus changing the optical axes of the photophores with respect to the PMT

nal body axis, thereby briefly presenting the ventral side and the light of the photophores to the observer. At the end of the trajectory, the shrimp engaged in a dodging sideways movement and then stopped. Only during presentation, that is for less than a second, did the observer experience the impression of a flash; before and after this the light of the photophores was concealed. Since every signalling triggers a response from more than one conspecific, a sequence of “flashing” occurs which finally subsides after about 2 min if no other signals are provided.

The flash seen by the observer was the result of a fast sweep of focused and continuously active light beams through the respective direction. Continuous light production during the triggered period of activity is shown in Fig. 3.

The shrimp was tethered in a cuvette, with the ventral side and photophores turned towards the PMT, which was about 30 cm away. During the measurement, the shrimp periodically flexed its abdomen somewhat. The movement shifted the optical axis of the photophores away from the PMT simultaneously, which resulted in strong amplitude modulation of the light recorded. Both shifts in pointing of photophores by the posture control system and by movements of the body need to be subtracted before changes in amplitude of light recorded can be attributed to the process of light production.

Single light flashes not produced by the rolling behaviour, but instead probably following neural command only, is assumed to occur, because the recording of flashing activity in the big tank showed more flashes than

could be attributed to individuals which were seen displaying the signalling behaviour. An appropriately designed experimental arrangement is required in order to prove this hypothesis.

The number of shrimps producing flash events was small compared with the total number of shrimps in the tank. However, a longer lights-on period before the triggering lights-off signal tended to increase the number of animals activating their photophores.

The light produced by the photophores during the normal, continuous mode of operation became invisible to human eyes if a background light stronger than 10^{-2} $\mu\text{W}/\text{cm}^2$ was maintained.

Experimental analysis of photophore control

Signals of water displacement stimulate light production

Meganctiphanes continuously uses the swimmerets at an average 6 Hz beat frequency to generate lift and propulsion. In this functional context it generates a strong and characteristically modulated propulsion jet (Wiese and Ebina 1995; Markl 1983). *Meganctiphanes*, adapted to a life in continuous darkness, presumably recognises the characteristic turbulent flow produced by conspecifics. These considerations led us to test whether quantified 6 Hz water vibrations, applied to the antennules, would have an effect on the light production of the photophores.

A 6 Hz water vibration of calculated 27 μm at the antennular flagellum of *M. norvegica* evoked increases in light production correlated with stimulus presentation with a latency of 0.5–1.0 s (Fig. 4). The figure also shows responses to two more water displacement and flow signals, which also led to activation of the photophores: water flow from a jet nozzle (modulated at 6 Hz and directed head-on to the antennules of a tethered shrimp) and a strong propeller (5 cm diameter) generated turbulence. Each of the tests was made following a transition from light to darkness – towards the end of the triggered photophore activity. The consistently observed increases in light production in response to low frequency water vibration depended on intact antennular flagella.

Visual stimuli increase light production

The specific pattern of ten photophores. The peculiar and characteristic pattern of the ten photophores on the ventral body surface of *Meganctiphanes* (Fig. 1B, C) is resolved by arthropod eyes only from a few centimetres distance (see also Discussion).

Response to a model of an approaching predator. An increase in the size of a black square in the visual field of the tethered shrimp, mimicking the approach of a predator, stopped the spontaneous pointing movements of the

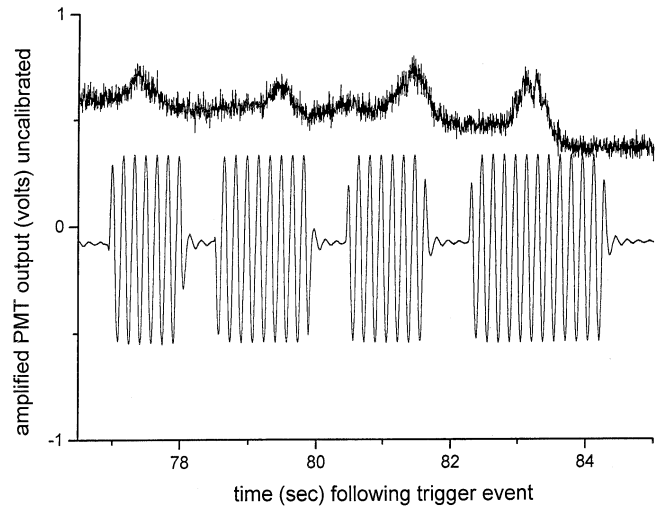


Fig. 4 Light production in the photophores in response to signals of low frequency water turbulence of 6 Hz and of a calculated 27 μm (peak to peak displacement at a point at half the length of the antennular flagellum). The stimulus record (*lower trace*) uses the electric signal driving the dipole source (see Methods). Light production increases transiently (*upper trace*) whenever the 6 Hz signal is presented

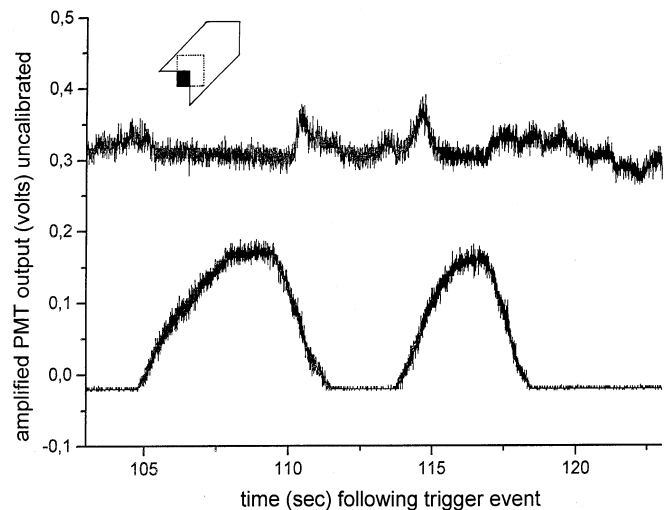


Fig. 5 A model of an approaching predator (see Methods) inhibits fluctuations in pointing of the photophores. The black cardboard square (see *small inset at top left*) was gradually exposed (*the lower trace*, which writes the stimulus, moves upward; noise is due to a bad potentiometer) and covered again to mimic the approach and retreat of a large predator. After a very short delay, the observed fluctuations of recorded light freeze to a relatively constant level upon approach and are resumed as soon as the model mimics retreat of the predator

photophores, which were resumed once the size of the black square was decreased again (Fig. 5). This reaction is tentatively interpreted as an attempt by the shrimp to hide the light of its photophores from the approaching enemy.

Response of the photophores to natural and artificial light flashes. The PMT fitted with a collimator lens was

pointed at an angle of 45° downwards into the centre of the 1-m³ tank with non-reflecting walls. About 70 shrimp inside the tank were adapted to light for 30 min before the room was darkened completely (see Methods).

Figure 6A shows a PMT recording of light events in the tank at high temporal resolution and a sufficient signal-to-noise ratio. A shrimp resting on the bottom of the tank with all photophores activated and pointing toward the PMT was probably responsible for the baseline shift in the light recording (Fig. 6A, right side). The recording showed a large number of peaks in the light protocol. Although the observation of the shrimps in the tank suggests that each flash stimulates flashes from other shrimps, call and response are impossible to discriminate in this constellation of recording. Differences in the amplitude of the flashes recorded resulted from changes in the actual alignment of the photophore optics with the orientation of the PMT, as the shrimps presented their photophores at different locations in the tank.

In several cases, individual flash events seemed to be followed by flashes which often showed delays of between 0.5 and 2.5 s. Attempts to correlate peaks in the recording with observed events in the tank tentatively led to the hypothesis that it is flashes produced by the signalling behaviour in response to flashes observed previously which generates the trailing peaks in the recording.

In Fig. 6B another scene of flashing is shown at low gain of the light recording. Nevertheless, the record shows at least four peaks (flashes, arrows) which are trailed by another (asterisks) at a delay of 1.5–2 s. A large number of shrimps with photophores alight were in the tank during this recording, raising the general light level considerably.

Figure 7A, B shows sample records of artificial and natural dialogue situations from the 1 m³ tank holding about 70 shrimps. Monopolar square pulses (5 V/1–10 ms) were used to drive an LED (470 nm) which was positioned in midwater. Single and repeated artificial flashes were produced, identifiable in the recording by their sharply rising flank (indicated by arrows) in contrast to the response flashes produced by the shrimps, which have distinctly slower rise times. Again, in several cases the artificial flashes as well as the natural flashes are followed by small or large flash events produced by some of the shrimps in the tank. This was most obvious if the LED flashes were given only every 6 s and in the late phase of the 2-min photophore activity period (Fig. 7B). Under the condition of reduced dialogue activity, the reply of one or two shrimps directly in response to LED flashes was elicited. Again, the timing of the flash responses showed a delay of 0.5–2.5 s after the leading flash.

Response of photophores to electric stimulation

Stimulation of the entire animal. Wire electrodes were positioned in the water to the right and left of the thorax

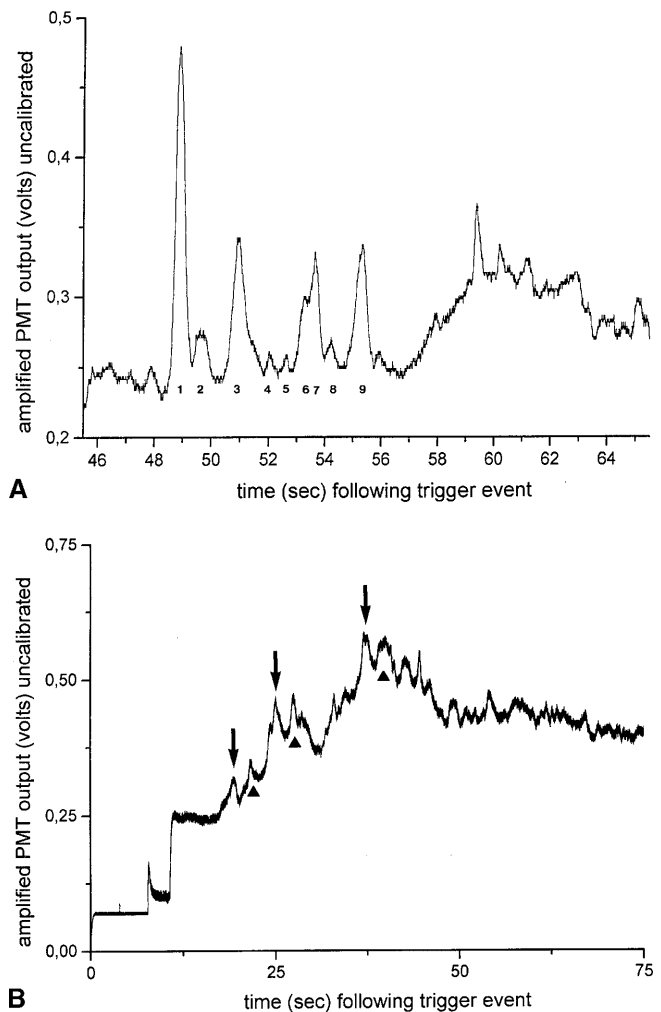


Fig. 6A, B Recording of light flash activity within a population of *Meganycitiphanes* started by the triggering event. About 70 *Meganycitiphanes* populate a large 1-m³ rectangular tank with non-reflecting walls. The PMT fitted with a collimator lens is tilted at an angle of 45° downwards towards the water. **A** Record of signalling going on in the tank. Flashes are produced by shrimps which for a fraction of a second have been pointing their photophores towards the PMT. The different amplitudes result from different orientations and distances of the photophores relative to the recording optics. Nearly all major light peaks seen in the recording seem to be trailed by smaller peaks about 1 s delayed (see also Fig. 7B). Peaks considered to be flashes have been numbered in a section of the recording. **B** Record of flashing activity in the tank displayed at a slightly extended (cf. Fig. 2) timescale. Flash dialogues (pairs of peaks, *arrow and triangle*) are obvious during the rising phase of light production in the tank because individual shrimps do not produce double flashes. Again, the large number of photophores active illuminate the tank to some extent, thus elevating the baseline of light recording

of the shrimp. Contact to a 4.5 V battery was made by a hand-operated pushbutton.

The recording shown in Fig. 8A indicates that the first shock produced a baseline shift in the light recording (Fig. 8A), interpreted as a shift in the photophore position relative to the optics of microscope and PMT. The shift was probably produced by a tail flip. After a latency

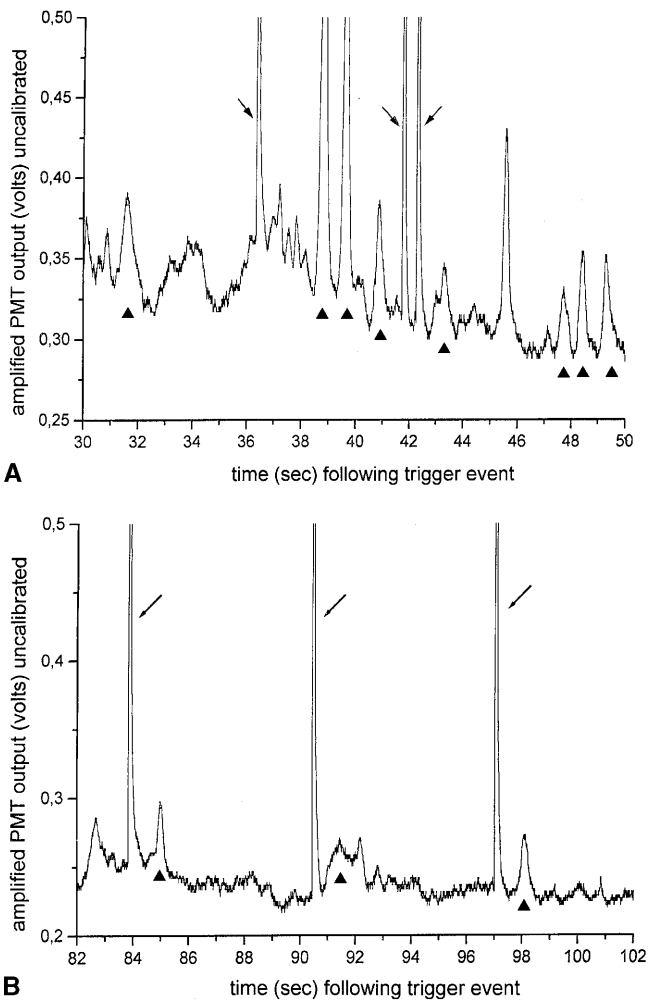


Fig. 7A, B Light-flash responses of *Meganyctiphanes* following artificial flashes produced by a blue LED (see Methods). The artificial flashes (*arrows*) differ from the biogenic flashes by their shorter rise time. **A** An episode from an early phase of trigger-induced signaling, with three artificial flashes (*thin arrows*) interspersed. Note especially the two shrimp-made intense flashes at 38–40 s after start of the recording. It is likely that the second constitutes the response to the first flash. The larger of the flashes produced by the shrimps are marked by *triangles*. **B** An episode from a late phase of trigger-induced signalling, showing that three artificial flashes (*thin arrows*, spaced 6 s apart) each evoke a flash response (marked by *triangles*) from one or two shrimp at 1–2 s of delay

of 1 s, a light production with slowly rising flank is observed. The irregular intervals and durations of the stimulus pulses reveal that the addressed “slow” light responses are triggered by the onset and not by the end of the current pulse. The latency of the slow response changes from about 1 s for the first response to approximately 0.5 s for the fifth response, indicating response sensitisation.

It is remarkable that for the second through to fifth stimulation a fast response – right at the onset of the current pulses – is observed in addition to the slow response. The latency of these fast responses amounts to about 20 ms. However, close examination has identified

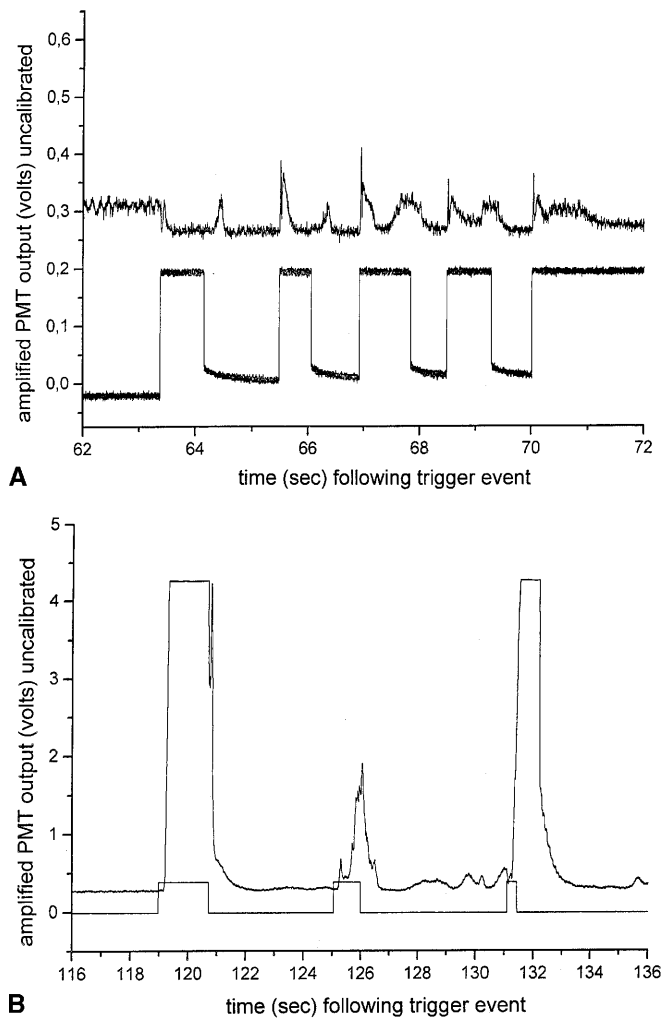
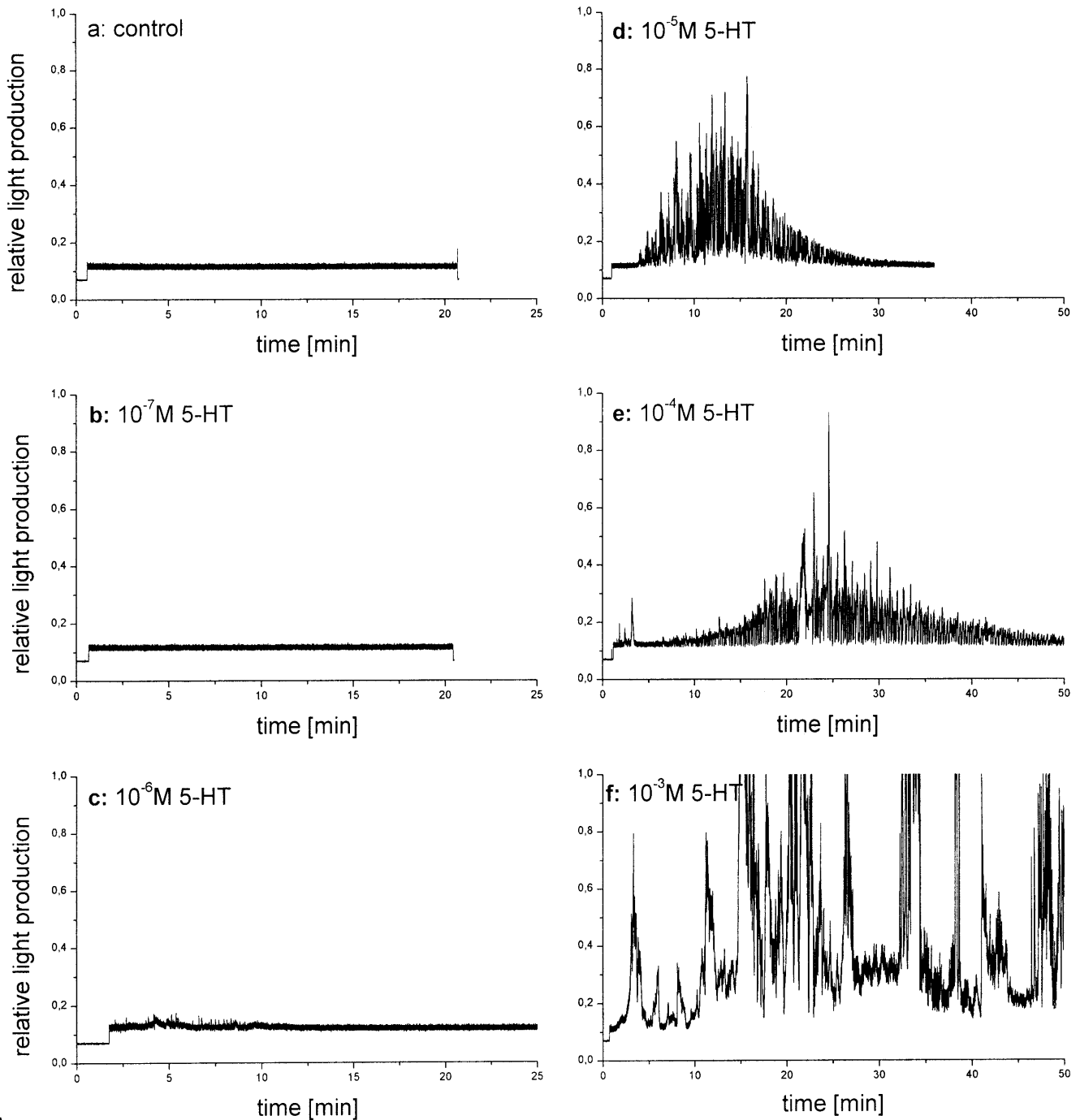


Fig. 8 Fast and slow response in an individual photophore to electric stimulation via the water surrounding the shrimp (**A**) and flash responses of all ten photophores to selective electric stimulation of the ventral nerve cord (**B**). **A** The light recording stems from a single posterothoracal photophore. Electrodes are positioned to the right and left of the thorax of the tethered shrimp. The response to the first current pulse (tail flip) displaced the photophore slightly relative to the objective of the microscope. In the following stimulations only the peaks of light production, not baseline luminescence, were recorded. In response to the applied current pulses, a light signal of fast rise time and of short latency (interpreted as a movement artefact) as also a light signal of slow rise time and of longer latency, both linked to the onset of the current pulse, are observed. The latency of the slow response decreases from 1.5 s for the first stimulus to 0.7 s for the third and fourth stimulations, indicating sensitisation. **B** Response of all ten photophores to electric stimulation of the ventral nerve cord via a pair of implanted wire electrodes. The stimulus, marked by its envelope, is a 200 Hz train of monopolar pulses (6 V/1.0 ms). The latency of the light-response is about 160 ms in all three cases. Though the duration of the stimulus is gradually shortened to 250 ms, the duration of the generated flash remains long (about 1 s). Upper frequency limit of the lowpass filter used is 200 Hz

this fast response as due to a jerk in the muscular system positioning the photophore.

Selective stimulation of the ventral nerve cord. A pair of insulated wire electrodes (steel wire, 80 μ m diameter)



A

Fig. 9 A Photophore light production following injection of serotonin into the haemolymph of the shrimp. Control (a): injection of 5 μ l seawater; recordings b through f: injection of μ l of serotonin dissolved in seawater calculated to produce the indicated concentrations of serotonin (5-HT) in the haemolymph. Depending on the applied dosage, the duration (2 min to several hours) as well as the intensity (relative units: 1–20) of light production increase. Modulations of recorded light are due to changes in the alignment of photophores and PMT optics, caused by movements of the shrimp and the photophores. **B** Statistics of several trials: increasing concentrations of 5-HT in the haemolymph of *Meganctiphanes* increase the duration of continuous activity of the photophore. Note that 5-HT doses lower than 10^{-6} M are not effective and that concentrations of 10^{-6} M or more are required

were implanted into the tethered shrimp and due to the transparency of *M. norvegica* were easily positioned next to the dorsal surface of the ventral nerve cord. A train of monopolar electric pulses of 1 ms duration, repeated at 200 Hz (designed to produce a strong stimulus) and of estimated 6 V net amplitude at the nerve (see Methods) regularly evoked flash events following the onset of the stimulus with a latency of 160–200 ms (Fig. 8B). The response to the second stimulus (applied only 6 s after the first) is strongly attenuated, whereas the third stimulus (again only 6 s after the second) nevertheless elicited a strong flash of 0.7 s duration. Please note that the third

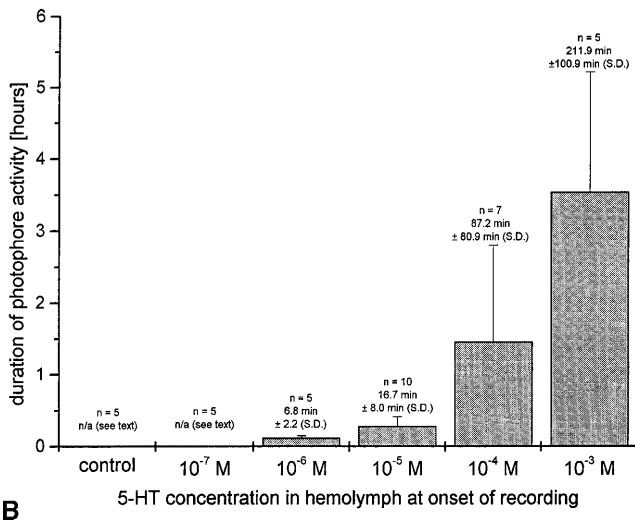


Fig. 9 (continued)

stimulus is very short, the elicited flash, however, has a distinctly longer duration (compare Figs. 8B and 7A).

Effect of injected serotonin on light production by the photophores

Figure 9A, B shows the effects of different amounts of serotonin injected into the haemolymph of *Meganyctiphanes*, which in this experiment were in normal posture and pointed the light of all photophores at the PMT positioned below the cuvette from a distance of just 5 cm. Strong effects of the injected serotonin on the duration of light production as well as on the intensity of the light produced were observed if the concentration of the agent in the haemolymph was 10^{-5} M or more. No interpretation is as yet available of the rise and decay functions of light production during one experiment (Fig. 9Ad,e,f). The strong modulations of the light measured result from body movements, slight and total flexion of the abdomen and corresponding shifts of the optical axis of the photophores with respect to the PMT. The body movements become more and more erratic as the concentration of injected serotonin increases.

Following an injection – as a rule – all ten photophores of the shrimp started to produce light more or less simultaneously. In only two cases, where the injection needle was driven postrad into the abdominal musculature, the photophores of the eyestalks were activated first, followed by a slow progression of activation from the frontal photophores to the last ones in the pleon, this process taking an estimated 2 min to completion.

Discussion

The experiments reported here were aimed at investigating the control of light production in the photophores of

Meganyctiphanes and to explore the recently observed elaborate signalling behaviour shown by *Meganyctiphanes* when stimulated by a preceding light flash. Although we are only at the beginning of understanding this communication, the flashing of *Meganyctiphanes* is not a stress signal or produced to frighten predators, as seen in some copepods when they are caught in a net.

It was found that strong negative gradients of illumination start a phase of light production which lasts on average for 100 s. During this time, light signals produced by conspecifics as well as artificial light flashes evoke a distinct signalling behaviour during which a light-flash response is produced. With respect to the triggering flash, this light response is delayed by 1–2 s. The signalling includes protective measures to evade signal-intercepting predators. Ongoing submaximal light production was found to increase whenever stimuli similar to presumed conspecific communication signals (e.g. 6 Hz modulated turbulent water flow and light signals) were applied. Light flashes can be evoked by neural command, experimentally either by repetitive electric stimulation of the entire animal or by direct stimulation of the giant fibres and the ventral nerve cord. The shortest latencies of flashes generated were at 160 ms. Serotonin, highly effective in starting and maintaining light production, is only effective at haemolymph concentrations 10^{-5} M or more, indicating focused release at the site of action. The results of the study have encouraged us to investigate the function of serotonin in the control of light production in more detail.

On the biology of *Meganyctiphanes*

M. norvegica undergoes extended diel vertical migrations (Firth of Clyde: Mauchline 1960; Mauchline and Fisher 1969; Kattegat: Boysen and Buchholz 1984; Gulf of Maine: Frank and Widder 1997; Oslo Fjord: Onsrud and Kaartvedt 1998; Gulmarsfjord: Bergström and Strömberg 1997; Mediterranean Sea: Tarling et al. 1998), most commonly interpreted as attempts to evade visually hunting predators (Poulsen 1926). Most obvious during bright days, the shrimp assemble in the darkness of such deep waters (>100 m below the surface) that visually hunting fish presumably stay above the shrimp in order to remain oriented. At night, the shrimp prefer to re-ascend to graze on plankton in the most productive water layer (about 20 m below the surface), which is characterised by a strong temperature gradient (Bergström and Strömberg 1997). The response of *Meganyctiphanes* to low oxygen, temperatures higher than 5°C, often changes in salinity, and changes in light conditions have been described (Tarling et al. 1999; van den Thillart et al. 1999; Spicer et al. 1999).

The facts that the individuals of *Meganyctiphanes* have to be assumed to often swim dispersedly, spend their life in continued darkness, and the considerable distances covered during diel migration, require a system of intraspecific communication to make themselves noticed

and at least occasionally to detect the position of conspecifics in the surrounding water. The characteristically turbulent propulsion jet, about 10 cm/s at the start, produced by the shrimp for locomotion (Wiese and Marschall 1990; Wiese and Ebina 1995; Ebina and Miki 1995/1996) is a suitable and specific signal, however, it attenuates realistically to the sensory threshold (range 5 – 40 Hz: 100 $\mu\text{m/s}$; M.P. Partria, unpublished) within a range of 1 m (Schlichting 1982). Light flashes, on the other hand, are assumed to carry through 10 or more metres of clear water.

Signalling by light in a dark environment invariably attracts predators, i.e. fish, which need some light to see their prey. The shrimp, on the other hand, are likely to hide below the fish, because they are oriented to darkness for better protection. Due to continuous life in the dark they are likely to be better adapted to low light levels. The fact that the photophores are pointed downwards (Land 1980), if no signalling is intended, indicates that the light of photophores is hidden from predators lurking above the shrimp.

The behaviour of *Euphausia superba*, the Antarctic krill, which feed even during the day in the thermocline layer (Everson and Bone 1986a, b), is exceptional because it is the result of an advanced social behaviour, swimming in formation, in which the individual has lost the normal measures to protect itself. This exceptional behaviour has led to the hypothesis that photophores are arranged ventrally and point away from the light to reduce the shadow (by supplying light of the required quality), which the animal's body produces against the lighter water surface if a predator looks at it from below ("countershading", Clarke et al 1962; Warner et al 1979; Grinell et al 1988).

Specific signals of water movement increase light production in the photophores

Numerous interneurons of the ventral nerve cord of a crustacean are activated by water movement (Wiersma 1958). In addition to being directionally selective (headward/tailward: Wilkens and Larimer 1972; Wiese et al. 1976), the respective interneurons are tuned to respond to two frequency bands of water vibration (low pass 1–40 Hz and high pass 40–400 Hz), complemented by some interneurons activated by signals of both frequency ranges (Plummer et al. 1986). Low pass and high pass interneurons were found by these authors to be distinguished by inhibitory contrast enhancement. Such inhibitory circuitry indicates that significant discriminations are made for the respective signal parameter (Wiese 1988). Bleckmann et al. (1991) and Bleckmann (1994) have pointed out that most spectra of biogenic water displacements do not contain frequencies higher than 40 Hz. In *Meganctiphanes*, water vibrations and turbulent flow of a frequency content of 5–40 Hz, not only 6 Hz as shown in Fig. 4, were observed to increase the light production, whereas vibration above 40 Hz tended

to result in decreases. Detailed measurements are needed to prove and to characterise a corresponding selectivity of response.

The medial (MG) and lateral giant (LG) neurons of the crustacean ventral nerve cord are well known to be collectors of mechanosensory input to the nervous system. Action potentials only, not graded potentials, of the giant fibres equivalent to commands for escape behaviour, are able to activate the serotonergic nerve cells of the ventral nerve cord of lobsters (Hörner et al. 1997). As the photophores are activated by mechanosensory input not only in escape situations, the stores of serotonin in charge of controlling the photophores are likely to have connection to mechanosensory interneurons independent from giant fibres. Water turbulence was similarly found to elicit bioluminescence in a copepod (Hartline et al. 1999).

The optics of the eyes of *M. norvegica* (Land et al. 1979) resolve the species pattern of photophores (Fig. 1B, C) which is identical in both sexes (Rickert, unpublished results) from not more than 12 cm distance (Kirschfeld, personal communication). Presentation of patterns made of blue LEDs indicate an effect on the simultaneously recorded light production of the photophores. Experiments are required in order to test responses to changed patterns shown at close range.

Black objects in the visual field induced *Euphausia superba* to keep a large distance away from these (Strand and Hamner 1990). Presentation of a model of an approaching predator was used in this study (Fig. 5). In response to a black square, which was made to increase in size, the tethered shrimp instantaneously arrested the ongoing pointing movement of photophores, a corollary of the animal's attempts to correct position in space, which is in disarray due to the tethering. The "freeze" reaction of the photophore movement is interpreted as an attempt of the shrimp not to betray its position to the approaching predator by the movement of, and perhaps resulting traces of light from, the photophores.

The behaviour of the shrimp in response to natural and artificial light flashes leaves no doubt that the apparent flash is produced by a sweeping movement of the photophores through the direction towards the observer.

A direct neural command for flashing needs to be investigated in more detail. Perhaps such neural command is exclusively established in the photophores of the eye stalk, which differ from the other photophores by their construction, by their colour shade of the screening pigment and by their larger diameter.

A direct neural command for flashing is definitively established in the flash beetle (Case and Strauss 1978). The published work on the physiology of visual interneurons in the crayfish (Glantz 1977; Kondrashev 1993) does not include measurements of their response to light flashes and of the projections of these interneurons into the abdominal ventral nerve cord.

The mechanism of flash recognition in the light communication of the firefly *Luciola mingrelica* (Landa et al. 1993) reveals that a sex-specific delay of the response to

flashes (short delay of response is characteristic for males, longer delay of the response is characteristic for females) is one known method by which the flasher identifies him- or herself.

On the motor side, a delay of 1–2 s in the responses with respect to the triggering flash requires that *Meganyc-tiphanes* is capable of an instantaneous fast start and high speed of swimming and rolling at about 40 cm/s, as has been reported in *Euphausia superba* (Kils 1982).

The control of photophores

Strong negative light gradients are the most reliable triggers of light production in the photophores of *Meganyc-tiphanes*. However, imitations of the naturally occurring slower light gradients at dusk (Gulf of Maine, around sunset: 0.1–0.3% /s reduction of irradiation, Frank and Widder 1997) did not work as triggers. Tentatively, we suggest that 12 h of continuous daylight (and corresponding hours of darkness) may be required to render slow light gradients sufficiently strong to activate the photophores or – in another context – to generate Zeitgeber trigger signals in specialised parts of the visual pathway so as to set the internal clocks of the organism (Fleissner and Fleissner 1993).

Hormones (for hormonal control systems in crustaceans see Cooke and Sullivan 1983; Keller 1996), for example those released from the X-organ/sinus-gland complex (Mangerich et al. 1988; Dirksen 1992) in the eyestalk of the shrimp, were at first assumed to control photophore activity. Red pigment concentrating hormone (RPCH), pigment dispersing hormone (PDH) and crustacean cardioactive peptide (CCAP) were tentatively injected; however, they had no consistent effect on the photophores.

Light production in *M. norvegica* usually started 20 s after the light gradient and lasted for about 2 min. It is striking that transmembrane currents, elicited by micro-jet-applied serotonin in isolated motoneuron somata of the locust have a similar temporal contour (Bermudez et al. 1992).

Injections of serotonin into *Meganyc-tiphanes* had at threshold to produce haemolymph concentrations 10^{-5} to 10^{-3} M to start and maintain light production in the photophores. This fact indicates at a focused release from nerve endings close to the photocytes or similarly allocated cellular stores of serotonin in the control of photophores. Concentrations typical for hormonal control (e.g. of the salivary gland of *Calliphora*: 3–30 nM serotonin; Zimmermann and Walz 1999) are not effective.

Upon electric stimulation of the entire shrimp, a strongly sensitising, distinctly delayed response of slow-rising light production is observed (Fig. 8A). Stimulation of the giant fibres of the ventral nerve cord produced a light flash of about 1 s duration at a latency of 160 ms. The electric stimulations used thus far were not specific enough and need to be replaced in future experiments by more selective and lower amplitude stimuli. In particular, direct application of an electric stimulus to the photo-

phore cells or, better, the photocytes would help to compare effects with the situation described in the lantern organs of the insects *Photuris* und *Photinus* by Buck and Case (1961). If there is an analogy between both systems of luminescence, then we are led to hypothesise that neural commands of unidentified interneurons in the ventral nerve cord stimulate already active light production to higher levels in a fashion similar to the tetanising effect of repeated electric stimuli on the contraction of skeletal muscles (lantern control in fireflies: Buck et al. 1963).

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