# Light-Induced Color Change in the Sapphirinid Copepods: Tunable Photonic Crystals

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**Light-induced tunable photonic systems are rare in nature, and generally beyond the state-of-the-art in artificial systems. Sapphirinid male copepods produce some of the most spectacular colors in nature. The male coloration, used for communication purposes, is structural and is produced from ordered layers of guanine crystals separated by cytoplasm. It is generally accepted that the colors of the males are related to their location in the epipelagic zone. By combining correlative reflectance and cryoelectron microscopy image analyses, together with optical time lapse recording and transfer matrix modeling, it is shown that male sapphirinids have the remarkable ability to change their reflectance spectrum in response to changes in the light conditions. It is also shown that this color change is achieved by a change in the thickness of the cytoplasm layers that separate the guanine crystals. This change is reversible, and is both intensity and wavelength dependent. This capability provides the male with the ability to efficiently reflect light under certain conditions, while remaining transparent and hence camouflaged under other conditions. These copepods can thus provide inspiration for producing synthetic tunable photonic arrays.**

## 1. Introduction

In recent years there has been a major effort to produce and assemble artificial nanomaterials into periodic arrangements to achieve photonic band gap phenomena.[1] This kind of arrangement is already incorporated in a variety of devices, including optical fibers, sensors, glasses, optical mirrors, switches, and display devices. Spectrally tunable structural color systems are a lot less common.[2] Evidently this is due to the fact that in addition to the major challenges of producing photonic nanomaterials, i.e., the design of their nanostructures and their complicated layer by layer assembly, it is even more difficult to actively and dynamically control the periodicity within the structure.

More than 515 million years of evolution have endowed organisms with the ability not only of spectrally tuning photonic structures, but also of triggering the spectral modulation with light. Such light-induced tunable photonic crystals are by and large still of out of reach in artificial devices and systems. Light-induced triggers of structural color change might conceivably provide remote controlled, simple photonic crystals exhibiting reversible modulation. Here we report that certain small marine crustacean copepods evolved exactly this type of light-induced tunable photonic structures, which provides them with the ability to change their color when they vertically migrate below the sea surface.

Color change in animals is used mainly for communication, camouflage, and radiation protection.[3–5] The majority of these systems involve the dispersion or aggregation of pigments that primarily modify the skin shade.[6] Rapid (within minutes) tuning of color hue is much less common in nature and often involves reflectance from structured materials rather than selective absorption by pigments.[3,7,8] Such structures consisting of alternating layers of transparent materials can function as a reflector when the optical thickness $nd$ (the product of the physical thickness $d$ and the refractive index $n$) of the layers is comparable to the wavelength of light. A change in the optical thickness of the layers promotes a color change. Such systems have been described in only a handful of species, such as the chameleon,[4,9] certain species of fish,[8,10] squid,[7] and beetles.[11] Within the tunable structural color systems, light-induced color change has to the best of our knowledge, so far been described only in vertebrates.[12]

The sapphirinid copepods are a family of small marine planktonic crustaceans, in which the males produce a variety of brilliant colors.[13] The male coloration is mainly structural and is produced from layers of hexagonally shaped guanine crystals separated by cytoplasm.[13–15] Members of the copepod family Sapphirinidae are distributed throughout the epipelagic zone (the upper 200 m layer of water in the ocean).[16,17] Their striking iridescent colors are thought to be important in intra species communication and mate recognition.[13,15] It was

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previously postulated that the iridescent colors of the males are related to their distribution in the epipelagic zone.[16] We have recently demonstrated that differences in the cytoplasm layer thickness account for the different colors observed in different males.[18] We also showed that the reflected light color strongly depends on the angular orientation of the copepod relative to the incident light, which can account for its appearance and disappearance during spiral swimming in the natural habitat.[18]

Here, we set out to determine if the variety of colors observed in males is due to fundamental differences between individuals of the same species or alternatively different colors originate from dynamic changes of the photonic structures. Sapphirinid copepods are known to migrate vertically in the water column,[16] and the spectrum of incident light significantly changes with water depth. We therefore also investigated the possibility that the trigger for the change in color might be light itself.

## 2. Results

We studied two species of the Sapphirinidae: *Sapphirina metallina*, which exhibits a variety of brilliant colors, and the blue *Copilia mirabilis*. Both species were collected off the coast of Eilat in the Red Sea where the intensity of solar insolation dramatically differs between shallow and deep water. To check the influence of light on the structural colors 50 sapphirinid males (40 *S. metallina* and 10 *C. mirabilis*) were collected and divided into two groups: one was exposed to light, and the second group was kept in the dark. Remarkably, *S. metallina* males were all magenta in their dark-adapted state, whereas those that were exposed to light all changed to yellow (**Figure 1**A,B). *C. mirabilis*, which is blue in its dark-adapted state, becomes completely transparent in its light-adapted state (Figure 1C,D). In both cases the color change is completely reversible, and all specimens changed their color consistently through at least two full cycles of changing light conditions (see the Supporting Information for more details).

Time lapse optical microscopy was used to dynamically follow the color change. Copepods were kept in the dark overnight. They were then exposed to light under a microscope, and their optical response was recorded (**Figure 2**). These studies were conducted using incident light from different sources which had different intensities (**Table 1**). Interestingly, the rate of the observed color change is directly proportional to the incident light intensity (Table 1). At low light intensities the color change is slow and can take up to 9 h, whereas at high light intensities, comparable to that of sunlight illumination, the color change is much faster and can take as little as 3 min (Table 1 and Movies S1 and S2 in the Supporting Information).

In order to elucidate the physical mechanism responsible for the color change we designed a correlative experiment where the reflectance of individual copepods in the dark-adapted state or light-adapted state was measured using a tailor made microscope. The thicknesses of the crystals and cytoplasm layers were measured using cryo-SEM on the same individuals. Based on the cryo-SEM measurements the reflectance was simulated using the Monte Carlo transfer matrix calculation (see the Experimental Section) and was compared to the

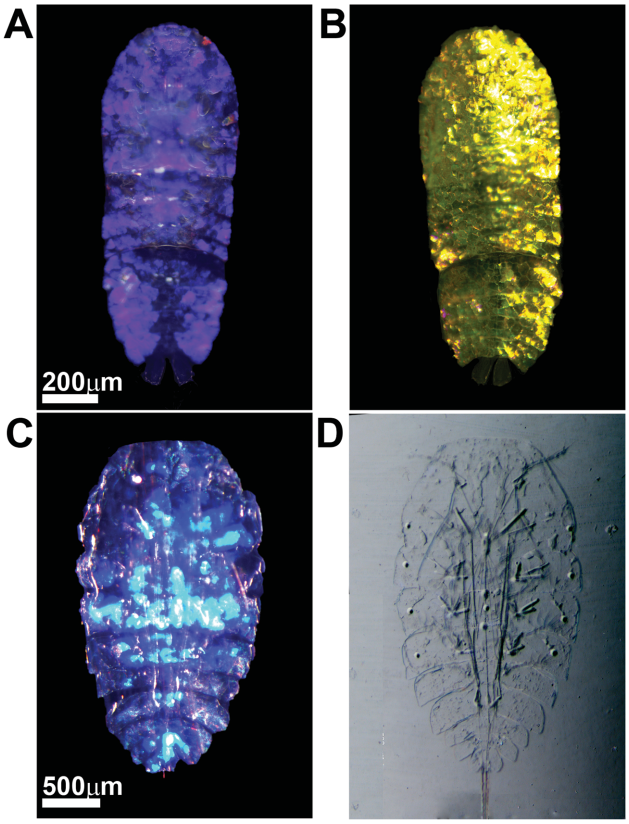


**Figure 1.** Optical response of sapphirinid males to either dark or light conditions. A) Dark-adapted *S. metallina*, B) light-adapted *S. metallina*, C) dark-adapted *C. mirabilis*, and D) light-adapted *C. mirabilis*. A–C) Reflection mode, D) transmission mode.

measured reflectance (**Figure 3**). In both the dark-adapted and the light-adapted states of *S. metallina* the crystal thickness was ≈70 nm (72 ± 4 nm, $n = 112$ and 69 ± 5 nm, $n = 105$ correspondingly), whereas the thickness of the cytoplasm changed from 190 ± 8 nm ($n = 140$) in the dark-adapted state, to 135 ± 5 nm ($n = 135$) in the light-adapted state. Similarly, in *C. mirabilis* the thickness of the crystals was similar in both the dark- and light-adapted states (63 ± 6 nm ($n = 146$) and 60 ± 8 nm ($n = 85$), respectively), whereas the thickness of the cytoplasm changed from 58 ± 8 nm ($n = 114$) in the dark-adapted state, to as little as 31 ± 9 nm ($n = 80$) in the light-adapted state.

For both species there is a good agreement between the simulated and measured reflectance spectra for both dark- and light-adapted states, confirming that indeed variations in the cytoplasm spacings modulate the reflected colors. We also confirmed that in both species the crystals in the dark- and light-adapted states are aligned with the surface of the animal, without a substantial change in the crystal orientation. We thus demonstrate that the color change is a result of shrinking and expanding of the cytoplasm spacings in an "accordion"-like manner. Exposure to light promotes shrinking of the intercrystal spacings, leading to a blue shift in the reflected light spectrum. In the case of dark-adapted *C. mirabilis* where the reflectance peak is at ≈460 nm, exposure to light and the subsequent shrinking of the cytoplasm spacings cause

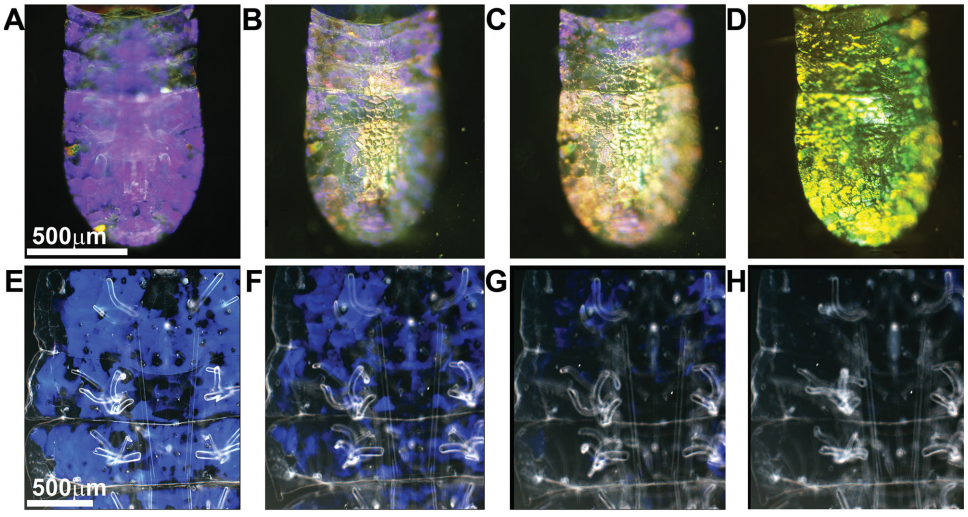


**Figure 2.** Color change time lapse study of male copepods: A–D) Reflectance mode images of *S. metallina*. A) The *S. metallina* male is magenta in its dark-adapted state. It gradually changes its color to yellow in response to light B) 3.5 h, C) 5.5 h, D) 9 h. E–H) Inverted transmission mode images of *C. mirabilis* (see the Supporting Information). E) The *C. mirabilis* male is blue in its dark-adapted state. It gradually becomes transparent in response to light F) 1 h, G) 2 h, H) 3 h.

the reflectance peak to shift into the UV. The result is that the *C. mirabilis* specimens become almost completely transparent (Figures 1C,D and 3C,D). In the magenta dark-adapted *S. metallina*, the main peak is at ≈800 nm and the second order peak is at ≈420 nm. Light promotes a blue shift of both peaks. The first order peak shifts to yellow and the second order peak shifts into the UV, resulting in yellow reflectance (Figures 1A,B and 3A,B). Considering that the spacing between the crystals shrinks from ≈190 nm (in the dark-adapted state) to ≈135 nm (in the light-adapted state), a gap of ≈700 nm should form between the membrane bound crystal stacks, the nuclei, and the other cell organelles in the more condensed light-adapted state. No such gaps were observed in iridophore cells in the light-adapted state (**Figure 4**). When *S. metallina* is exposed to high light intensity, i.e., in the light-adapted state, they are yellow, implying that all the visible and UV wavelengths, yellow excluded, are transmitted through the crystal arrays, with subsequent potential tissue damage.

**Table 1.** Light intensity dependence of color change. Table showing the different light intensities used and the corresponding time required for complete color change. The light intensities range from low intensities equivalent to room lighting (0.15 mW $cm^{-2}$) to an intensity comparable to that of sunlight at the water surface (50 mW $cm^{-2}$). The end point for the color change was determined using processing of the time lapse images (see the Experimental Section). Consecutive numbers are individual repeats using the same conditions.

| Intensity [mW $cm^{-2}$] | Time [min] |
|---|---|
| 0.15 | 500, 560 |
| 0.4 | 300, 250, 220 |
| 2 | 110, 128 |
| 3 | 50 |
| 6 | 15 |
| 50 | 3 |

In *S. metallina* light promotes the spreading of pigments that expand to cover the whole surface of the animal (**Figure 5** and Movie S3 in the Supporting Information). This is presumably a defense mechanism against UV radiation. While in the dark-adapted state the pigments are concentrated in small areas.

We studied the spectral dependence of the induced color change behavior by exposing dark-adapted *S. metallina* males to spectrally filtered light. Each specimen was exposed to blue, yellow, or red light together with a specimen that was exposed to white light as a control. Specimens exposed to both blue or yellow light changed their color within 2–3 h in a similar manner to the control sample, whereas exposure to red light did not induce any color change (**Figure 6** and Movie S3 in the Supporting Information).

## 3. Discussion

The *C. mirabilis* male modulates the structure of its crystal stack so that it is adapted to reflect light in the lower part of the photic zone (the surface layer of the ocean that receives sunlight), where the spectrum of the filtered solar light is primarily in the blue green range. Its reflection peak at 460 nm fits very well with the sea water absorption minimum.[19] This means that it has optimized its ability to communicate with females in deep waters. In fact, depth distribution studies have shown that the depth of maximum abundance for both males and females lies between 40 and 80 m, corresponding to the lower photic zone for the different stations that were surveyed.[16,20] When the male rises near the surface its spectral reflectance shifts to the UV in response to the higher light intensity. The *C. mirabilis* males consequently lose the ability to use visible light for signaling, but gain superb camouflage, as they become virtually invisible against any background and are therefore hidden from most potential predators (that do not possess photosensitivity in the UV region).

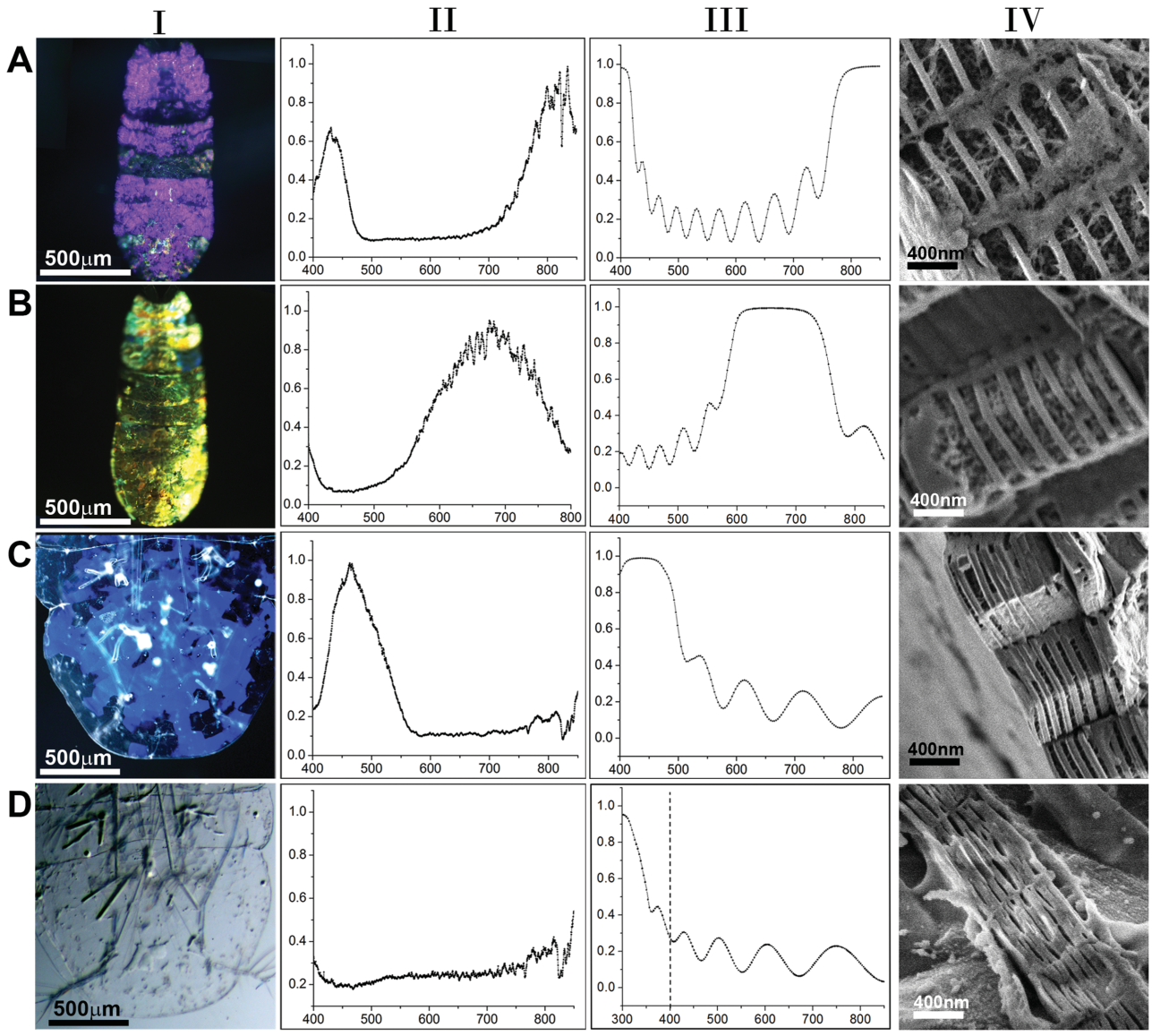


**Figure 3.** The reflectance and structural properties that accompany the male sapphirinid color change. A) Dark-adapted *S. metallina*. B) Light-adapted *S. metallina*. C) Dark-adapted *C. mirabilis*. D) Light-adapted *C. mirabilis*. Column I: light microscope images of the specimens [(A + B): reflectance; (C + D): inverted transmission]. Column II: measured reflectance. Column III: simulated reflectance spectrum. The simulated reflectance was calculated based on the cytoplasm (Cy) and the crystal (Cr) thicknesses measured in cryo-SEM images: Dark-adapted *S. metallina*—Cy: 190 ± 8 nm ($n$ = 140), Cr: 72 ± 4 nm ($n$ = 112). Light-adapted *S. metallina*—Cy: 135 ± 5 nm ($n$ = 135), Cr: 69 ± 5 nm ($n$ = 105). Dark-adapted *C. mirabilis*—Cy: 58 ± 8 nm ($n$ = 114), Cr: 63 ± 6 nm ($n$ = 146). Light-adapted *C. mirabilis*—Cy: 31 ± 9 nm ($n$ = 80), Cr: 60 nm ± 8 nm ($n$ = 85). The dashed line in D-III (simulated) marks the UV regime, into which the reflection of the light-adapted *C. mirabilis* shifts. Column IV: representative cryo-SEM images of the crystal–cytoplasm layer arrays.

The *S. metallina* male has the ability to reflect light in both the higher and lower parts of the photic zone. Indeed, depth distribution studies have shown that *S. metallina* males and females are located in both the shallow and deeper regions of the photic zone.[16,20] In its dark-adapted state, where the secondary reflectance peak is at ≈430 nm, the male *S. metallina* has the ability to reflect light when in deep waters. Near the water surface where longer wavelengths are not filtered by water absorption and the radiation intensity is at a maximum, the *S. metallina* males reflect light in the yellow range, peaking at ≈680 nm. In parallel, spreading of pigments under high intensity radiation probably provides protection from radiation, as was documented for other species.[6]

By comparing the ultrastructure of the dark-adapted state and the light-adapted state it is clear that shrinking and expansion of the cytoplasm spacings are responsible for the color changes. This observation can provide a partial explanation for the variety of colors observed in *S. metallina* in our earlier study, in which variations of the cytoplasm layer thickness were found to regulate the different colors observed for different males.[18] This explanation is not sufficient, however, to explain all the colors observed in copepods of the same

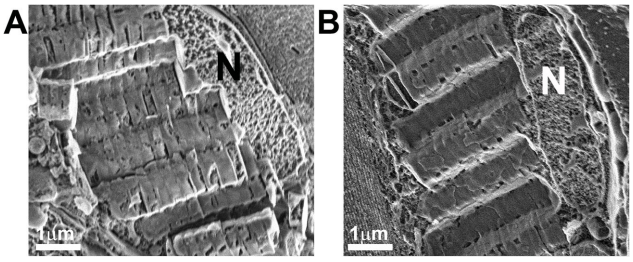


**Figure 4.** Iridophore cells in different light-adapted states. High pressure frozen, freeze fractured cryo-SEM images, showing A) a dark-adapted iridophore, and B) a light-adapted iridophore. In both cases there is no gap between the membrane bound crystal stacks, the nuclei and the rest of the cell organelles. (N) The cell nucleus.

species, which may be due to genetic variability between individuals.

The cellular machinery responsible for the dynamic ultrastructural change in crystal spacing is not known. Two possibilities are that the change might be mediated by a mechanical trigger, such as tension applied by the cytoskeleton of the cells, or by a change in osmotic pressure. A cytoskeletal change will likely affect the cell morphology. Since the iridophore cells are tightly packed, it is unlikely that such a change occurs. It is more likely that the change is driven by osmotic pressure that affects the whole cell.

Red light does not promote a color change in the copepods. This is consistent with the fact that even in clear waters red light is already absorbed at a depth of several meters, and therefore will not be available to the copepod.

In many visual and other light sensitive systems, rhodopsin or rhodopsin-like molecules are the primary light receptors.[21] Rhodopsin, associated with copepods, has its maximum

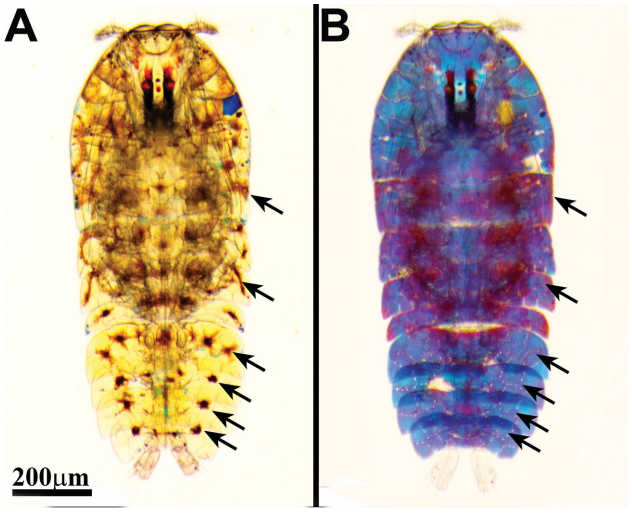


**Figure 5.** Pigments spreading in response to light. Transmission images of the same specimen, in A) dark-adapted state: the pigments are concentrated in specific areas as dark brown spots (black arrows); B) light-adapted state: the pigments have spread to uniformly cover the whole body. The concentrated pigments spots (position indicated by black arrows) disappeared. Note that in transmission mode the reflectance color is inverted (see Figure S1, Supporting Information).

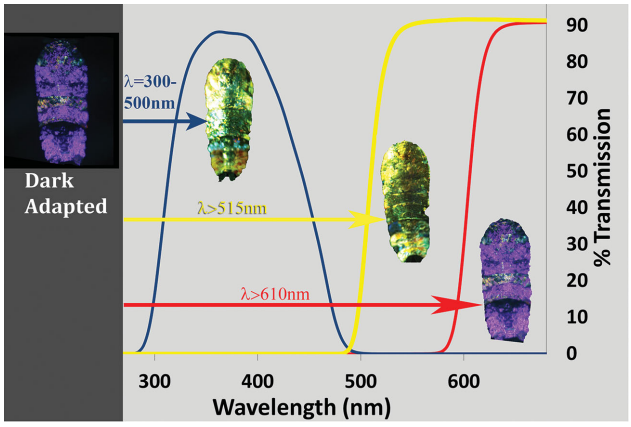


**Figure 6.** Spectral dependence of induced color change. Dark-adapted *S. metallina* males (magenta) were subjected to irradiation with either blue, yellow, or red light within the indicated spectral region. Specimens exposed to blue ($\lambda = 300–500$ nm) or yellow light ($\lambda > 515$ nm) changed their color to yellow, whereas exposure to red light ($\lambda > 610$ nm) did not induce color change.

absorption at ≈500 nm, and absorption at wavelengths higher than 650 nm is very poor.[22] It is therefore conceivable that male sapphirinids are also using a rhodopsin-like primary light receptor. In certain color changing fish, the photosensitive site appears to be located within the iridophores.[23] The fact that in the copepod we studied the color change does not occur simultaneously throughout the animal, but in segments, may indicate that indeed the light response mechanism is located within the segments (Movies S1 and S2 in the Supporting Information).

The self-assembled organic based color producing system of the copepod not only presents an efficient solution to the challenge of producing a tunable photonic crystal, but also possesses light-induced intensity dependent tunable color capabilities, that are currently by and large beyond the state-of-art in artificial systems. The sophisticated approach used by these copepods may thus serve as an inspiration for the development of artificial light-induced tunable photonic crystals.

## 4. Experimental Section

*Animals*: Sapphirinid copepods were collected from epipelagic waters (0–20 m) in the Gulf of Eilat either by plankton-net tow or by using a light trap equipped with a 200 μm mesh net. Sapphirinid males were identified to species level, *S. metallina* and *C. mirabilis*, using the identification keys of Björnberg[24] and Boxshall and Halsey.[25]

*Influence of Light on the Male Coloration*: Fifty sapphirinid males (40 *S. metallina* and 10 *C. mirabilis*) were collected, placed separately in Petri dishes with fresh filtered sea water, and maintained at ambient sea surface temperature (22 °C). Specimens were divided into four groups. Each group was subjected to three consecutive changes of light regime, each lasting 20–24 h. Two groups were first exposed to light, and subsequently switched to darkness, whereas the two other groups were kept first in darkness and then switched to light.

*Photometry and Time Lapse Study*: High-quality color images and time lapse studies were performed using an inverted microscope (Eclipse Ti-U, Nikon) equipped with Nikon High-Definition Color Camera Head (DS-Fi2, Nikon) or using a stereomicroscope (SMZ800, Nikon) equipped with Nikon High-Definition Color Camera Head (DS-Fi1 Nikon). Images

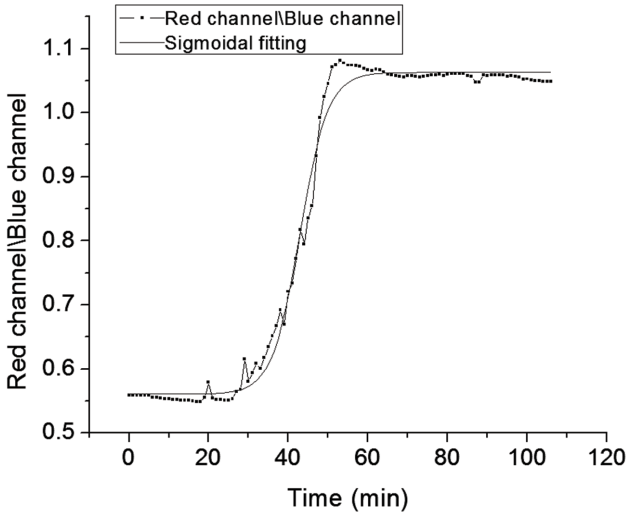


**Figure 7.** Color change dynamics. A graph showing the ratio between the red and blue signals across time for one time lapse series. A sigmoidal curve was fitted to the data to define the end point of the color change.

were recorded in a time lapse mode at either 1 min or 30 s intervals. The image stacks were converted into a movie using the open source software Fiji. The end point for the color change in the time lapse study was determined by integrating the different RGB channels separately for each image, while excluding the background using a threshold. The ratio between the red and blue channels for each image was then plotted vs time (**Figure 7**). The end point was extracted by fitting the curve to a sigmoidal shape.

*Wavelength Dependence of the Color Change Behavior*: Twelve *S. metallina* males were kept in darkness overnight and their images were recorded (Eclipse Ti-U, Nikon). Next, the males were subjected to either blue ($n = 3$), yellow ($n = 3$), or red ($n = 3$) light together with a specimen that was subjected to white light as a control ($n = 3$). The different illumination wavelength spectra were obtained by filtering a fiber optic white light source using band pass filters (CVI). The optical response was recorded using the microscope after 4 h of exposure to light.

*Cryo-SEM*: Fresh copepods were immersed in fresh filtered sea water, sandwiched between two metal discs (3 mm diameter, 0.1 mm cavities), and cryo-immobilized in a high-pressure freezing device (HPM10; Bal-Tec). The frozen samples were mounted on a holder under liquid nitrogen and transferred to a freeze fracture device (BAF60; Bal-Tec) by using a vacuum cryo-transfer device (VCT 100; Bal-Tec). Samples were observed in a high-resolution SEM (Ultra 55, Zeiss) using a secondary electron in-lens detector, maintaining the frozen-hydrated state by use of a cryo-stage operating at a temperature of −120 °C. Measurements of crystal thickness and cytoplasm spacings were obtained from the cryo-SEM micrographs by choosing the crystals that appeared to be edge-on to the fracture surface. In cases in which adjacent crystals were highly angled one to the other, the specific crystal pairs were not selected for cytoplasm measurements.

*Reflectance Measurements*: Reflectance measurements were carried out as described by Boltovskoy.[24] In brief, the reflectance of fresh copepods placed inside an indented microscope slide while immersed in fresh filtered sea water was measured in vivo. We used a custom built microscope for measuring the reflectance. The reflectance spectrum and the image acquired by the microscope were used to determine the reflectance intensity, which was normalized to the reflectance of a silver mirror. A Halogen lamp light source was coupled to an optical fiber which guided the light into the microscope. It was noted that at wavelengths shorter than 390 nm, the intensity of the light source is significantly reduced. The light was then imaged (through a beam splitter) onto the back aperture of an objective (Olympus, UPLSAPO 60XW, NA 1.2). The objective was used both to illuminate a wide area (≈250 µm width) and to collect the scattered light. The collected light was directed to one of three different paths: (1) CCD camera (Mintron, MTV 13 V5Hc); (2) Fourier transform of the scattered light was captured by imaging the back aperture of the objective onto a similar CCD camera by a set of folding mirrors; and (3) spectrophotometer (Ocean Optics, USB2000).

*Simulations*: Transfer matrix simulations were based on measurements conducted using cryo-SEM. The mathematical formulation for this method was shown in detail.[26] In brief, the percent reflectivity was calculated by averaging 500 runs, assuming normal incident light. Every layer was characterized by $n_j$ (refractive index) and $d_j$ (which is the layer thickness randomly picked from the experimental distribution). Thus, for each layer we defined the following $2 \times 2$ matrix

$$m_j = \begin{pmatrix} \cos\beta_j & -\frac{i}{n_j}\sin\beta_j \\ -in_j\sin\beta_j & \cos\beta_j \end{pmatrix} \quad \text{where} \quad \beta_j = \frac{2\pi}{\lambda} n_j d_j$$

The set of $k$ double layers was characterized by an overall reflectivity $2 \times 2$ matrix

$$M_j = \prod_{j=1}^{j=2k} m_j$$

The reflectivity was extracted from the following expression

$$R = \left| \frac{(m_{11}+m_{12})-(m_{21}+m_{22})}{(m_{11}+m_{12})+(m_{21}+m_{22})} \right|^2$$

The refractive index of the guanine crystal plates was taken as $n = 1.83$, which was the refractive index in the direction of the impinging light. When calculating the simulated reflectance, we neglected the weak dependence of the refractive index on the wavelength and assumed that all the interfaces were parallel (inside a crystal stack and between different crystal stacks). We also assumed that there was no correlation between the crystals spacings within a single crystal stack. In practice the copepod cuticle was curved and thus the measured area contained crystal stacks with slight differences in orientation. Furthermore, there were small variations in the crystal orientation within a stack. These both broadened the reflectance and weakened the higher order reflections which were visible in the calculated reflectance but not in the measured reflectance.

## Supporting Information

Supporting Information is available from the Wiley Online Library or from the author.

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