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ORIGINAL PAPER

The adaptive significance of chromatophores in the Arctic under-ice amphipod *Apherusa glacialis*

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Abstract Solar radiation is a crucial factor governing biological processes in polar habitats. Containing harmful ultraviolet radiation (UVR), it can pose a threat for organisms inhabiting surface waters of polar oceans. The present study investigated the physiological color change in the obligate sympagic amphipod *Apherusa glacialis* mediated by red-brown chromatophores, which cover the body and internal organs of the species. Short-term experimental exposure to photosynthetic active radiation (PAR) led to pigment dispersal in the chromatophores, resulting in darkening of the animal. Irradiation in the PAR range (400–700 nm) was identified as the main trigger with high light intensities evoking marked responses within 15 min. After exposure to high PAR, darkness led to a slow aggregation of pigments in the cell center after 24 h. Experiments revealed no statistically significant change in coloration of the animal when exposed to different background colors nor UV radiation. Our results point to a dose- and time-dependent photoprotective role of chromatophores in the amphipod, presuming a shielding effect from harmful radiation in a dispersed state. The reversible nature

of the physiological color change enables the species to adapt dynamically to prevailing light conditions and thereby minimize the cost of increased conspicuousness toward visually hunting predators.

Keywords Photoprotection · Ultraviolet radiation · Color change · Sympagic · *Apherusa glacialis* · Chromatophores · Sea ice fauna · Svalbard · Arctic

Introduction

Chromatophores are pigment cells, through which a relatively fast physiological color change of the organism can take place. Crustacean chromatophores are generally regarded to serve one or more of the following functions: photoprotection, crypsis, or thermoregulation. In photoprotection, the chromatophores are used as shields protecting the animal or sensitive organs against harmful radiation (Miner et al. 2000; Auerswald et al. 2008), such as ultraviolet radiation (UVR), that can damage biological macromolecules like DNA (Malloy et al. 1997). Crypsis is a type of camouflage, where blending into the background reduces the risk of being detected by predators. This is achieved by matching the body color to the background color or using disruptive coloration patterns that break up the body outline and create false boundaries (Stevens and Merilaita 2009). Thermoregulation is mainly occurring among semiterrestrial species inhabiting the tidal zone where diurnal and seasonal changes in the temperature regime are significant (Willmer et al. 1989; Noël and Chassard-Bouchaud 2004). As darker color absorbs more light, and thus heat, the dispersion or contraction of pigments in the chromatophores can help animals control their body temperature. The role of chromatophores as

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thermoregulator is not considered as probable for purely aquatic species (Nöel and Chassard-Bouchaud 2004).

The Arctic amphipod *Apherusa glacialis* is autochthonous to the sympagic habitat fulfilling the life cycle there (Lønne and Gulliksen 1991; Poltermann et al. 2000). The ability of the species to cope with the seasonality and the extreme environmental conditions on the underside of the ice enables it to thrive there during all seasons (Werner 2006; Kiko et al. 2009). It prefers smooth, flat ice and is aggregated at places with high algal biomass such as ice edges and thin ice (Lønne and Gulliksen 1991; Hop et al. 2000). During a cruise to the pack ice north of Svalbard, Norway in 2007, we noted a high variation in the color appearance of sampled *A. glacialis*, and that their color changed after some time. The color change was found to be caused by a dispersion (resulting in darker appearance) or aggregation (resulting in lighter appearance) of pigments in the chromatophores arranged along the body of the amphipod. Based on in situ observations by divers (Berge 2007), the amphipods had a dark appearance on the edges of ice floes, whereas most had a lighter appearance further in under the ice floe (Fig. 1).

In the sea ice environment, conditions are highly variable on both temporal and spatial scales, which make the ability to adapt thereafter advantageous. Chromatophores offer a possibility to adapt to environmental variation with a short response-time. Functions that seem plausible as triggers of the color change in *A. glacialis* are photoprotection and crypsis, since the stable temperature regime in the ice–water interface is unlikely to evoke any compensation for physiological thermoregulation mediated through the chromatophores. Solar radiation is highly seasonal in polar environments, and during the polar summer, the animals are exposed to continuous light (of varying intensity) for a period of up to 6 months. Due to depletion of ozone in polar areas (Kerr and McElroy 1993; Müller et al. 1997), the incoming UVR reaches biologically harmful levels (Madronich et al. 1998) that can penetrate

down to 20–30 water depth (Karentz and Lutze 1990). Harmful effects of UVR have been documented for various organisms, including polar crustaceans (Malloy et al. 1997; Obermüller et al. 2005; Ban et al. 2007; Krapp et al. 2009). Even though factors like low sun angle, clouds, snow and ice cover and thickness, and particles incorporated in the ice reduce the light intensity penetrating to the underside of the ice, harmful levels of UVR have been recorded under the ice. For example, Lesser et al. (2004) linked mortality and DNA damage in sea urchin larvae in the water below 2- to 3-m-thick first-year ice (FYI) to UVB transmittance through the ice. Thus, it seems realistic to propose photoprotection as a reason for the physiological color change in *A. glacialis*, which thrives under FYI and close to ice floe edges.

Background adaptation has been found in several crustacean species (Fingerman 1965, 1970; Johnson 1974; Willmer et al. 1989) and represents one of the most common methods of crypsis (Endler 2006; Stevens 2007). During the bloom of ice algae and at locations where detritus has aggregated or sediments are incorporated in the ice, the underside of the ice is patchy in color (Werner and Lindemann 1997). An ability to adapt to the different background shades could prevent detection by visual predators such as polar cod (*Boreogadus saida*), making crypsis an advantageous reason for color change in *A. glacialis*.

The aim of this study was to investigate the role and use of chromatophores in *A. glacialis*. Hence, we designed an experimental setup to examine the above-described predictions. Based upon our field observations, we hypothesize that physiological color change is an adaptive trait in this species. In the experiments, the following questions were addressed: (1) Are the animals responding differently to light exposures with different intensities or wavelengths? A stronger response to higher intensity or UVR could indicate photoprotection. (2) Are the animals responding to different background shades? An adjustment of the body coloration depending on the background shade

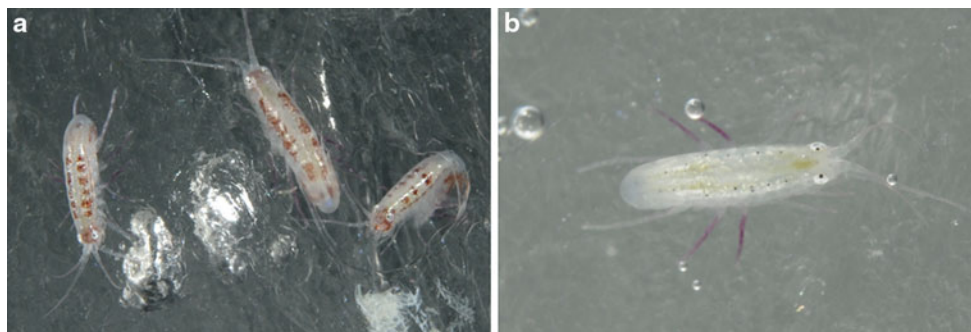


Fig. 1 Under-ice photographs taken in September 2009 at the edge of an ice floe (a) and at 15-m distance from the edge underneath the ice (b). Note the different color shade of the animals due to a difference

dispersion of pigments within the chromatophores. Size of animals approximately 7 mm. Photographed by Erling Svensen

could indicate crypsis. (3) Can thermoregulation be excluded as a reason for the color change? The temperature variations are rather small in the ice–water interface, and therefore a thermoregulatory function of the chromatophores is regarded unlikely, but if present, thermoregulation should result in aggregation of pigments at elevated temperature.

Materials and methods

Experimental animals

The experimental animals were sampled September 1–2, 2008, and September 3, 2009, during cruises with RV *Jan Mayen* to the pack ice north of Svalbard, Arctic Ocean (station coordinates: 81.05°N, 14.54°E; 81.15°N, 13.12°E). The animals were collected by SCUBA divers using both hand-held nets (0.5-mm mesh) and an electric suction pump (Lønne 1988). *Apherusa glacialis* were immediately separated from other amphipods and maintained in a climate chamber on-board the ship where they were reared in aquaria until arrival in Longyearbyen, Svalbard 7 days later. In Longyearbyen, the animals were transferred to The University Centre in Svalbard (UNIS), where they were reared in a cold cabinet at a temperature of $0 \pm 1^\circ\text{C}$. Water was exchanged once a week during the rearing. Food was provided 2–3 times per week and consisted of cultivated ice algae (monoculture of *Thalassiosira gravida* or field extractions of ice algae) frozen into small ice blocks. Molting was observed occasionally, evidenced by exuviae found in the tanks. Animals for the experiments were picked out randomly. The mean size of the experimental animals was 6.5 mm (range 4.0–13.2 mm) and consisted of two cohorts. No sex determination was done. All experiments took place at UNIS during daytime, and all animals used in the study ($n = 64$) were adapted to darkness for a minimum of 24 h prior to the experiments.

Chromatophore index (CI)

In order to document the color change, digital images were taken before and after the treatments, and, depending on

treatment, also during the exposures. For the photographing, animals were placed in a drop of sea water on a pre-cooled petri dish under a Leica MZ 9.5 stereomicroscope equipped with a Sony HDR-HC7R video camera with still photo recording mode, or a Nikon D300 equipped with a Tamron 90 mm/f2.8 macro lens was used. The whole procedure was limited to a few seconds, after which the animals were placed back in the experimental jar. No change in CI was detected during this procedure.

To quantify the chromatophoric response from the pictures, a chromatophore index (CI) was established based on Hogben and Slome (1931), on a scale from 1 (pigment maximally concentrated) to 5 (pigment maximally dispersed; Fig. 2). For the picture analyses, three chromatophores, located on the first, second, and third segment of the pleon, were chosen. The reasons for choosing these were as follows: (1) they were almost always present, (2) the contrast between the chromatophore and the body tissue was good, and (3) adjacent chromatophores did not merge when expanded and therefore could be analyzed individually. If different stages were observed in the three chromatophores, the mean value was given as the CI of the individual.

Experiments

PAR exposure

Experimental irradiation in the PAR range was provided by a 14-W fluorescent tube (Philips Master TL5 HE). Light intensity was measured using a cosine-corrected flathead sensor (LICOR Quantum Li190SA), measuring the photosynthetic photon flux density (PPFD) in the range of PAR (400–700 nm). Measures were recorded in air, and the light intensity was regulated by adjusting the height of the lamp to the experimental jars. Two exposure treatments were established, being low PPFD ($33\text{--}34 \mu\text{mol m}^{-2} \text{s}^{-1}$; 35-cm distance) and high PPFD ($300\text{--}400 \mu\text{mol m}^{-2} \text{s}^{-1}$; 15-cm distance), respectively. In the experimental setup, specimens of *A. glacialis* were put in small glass jars (5 cm in diameter, 60 ml seawater) placed on an ice bath to keep the temperature low. Two individuals, which could be distinguished by different size, were put in each jar. Exposure

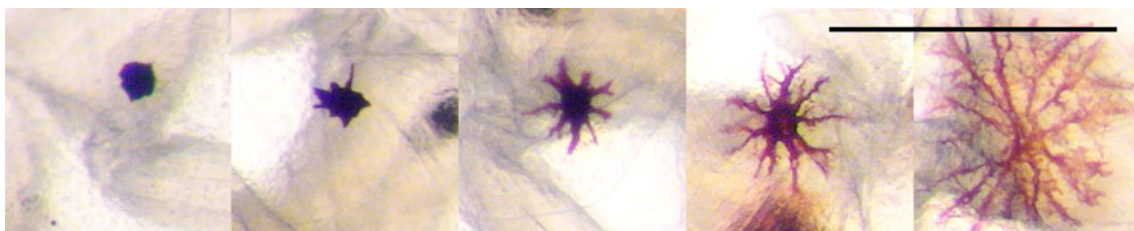


Fig. 2 Chromatophore index (CI) from 1 to 5 of representatively selected pigment cells from the pleon of *Apherusa glacialis*. Scale bar = 1 mm

time was set to 60 min (low PPFD treatment) and 45 min (high PPFD treatment), respectively. Chromatophore response was recorded before the start of exposure and at intervals of 15 min thereafter.

To test the reversibility of the response, amphipods were exposed to $350\text{--}500\ \mu\text{mol m}^{-2}\ \text{s}^{-1}$ for 180 min and then put into darkness for 24 h. The chromatophoric response was recorded before and after exposure and in intervals during the darkness treatment.

UVR exposure

Irradiation in the UVR range was provided by a 400-W high-pressure lamp (Osram, HQI-BT), with an emission spectrum close to sun light, containing wavelengths in the UV spectrum (280–380 nm) as well as in the PAR range (with a peak at 540 nm). At a distance of 70 cm, the lamp emitted $114 \pm 2\ \mu\text{mol m}^{-2}\ \text{s}^{-1}$ in the PAR range and $2\text{--}3\ \text{W m}^{-2}$ in the UV range. This intensity can be expected under thin ice where *A. glacialis* is most commonly found (Hop et al. 2000), as Hanelt et al. (2001) measured atmospheric intensities of UVR up to $16.8\ \text{W m}^{-2}$ in Kongsfjorden, Svalbard, and Belzile et al. (2000) report a transmittance of 5–19% UVA and 2–13% UVB through 0.5- to 1.3-m-thick FYI. Additionally, in situ measurements of UVR under multi-year sea ice in September 2005, at a similar latitude as where the experimental animals were sampled, show intensities up to $0.18\ \text{W m}^{-2}$ (Fig. 3). UVR was measured using a UV-meter (UV-IR-Technology, 250–410 nm). Two amphipods, distinguished by size, were put in plastic aquaria (6 l volume) filled with seawater up to 10 cm. A control

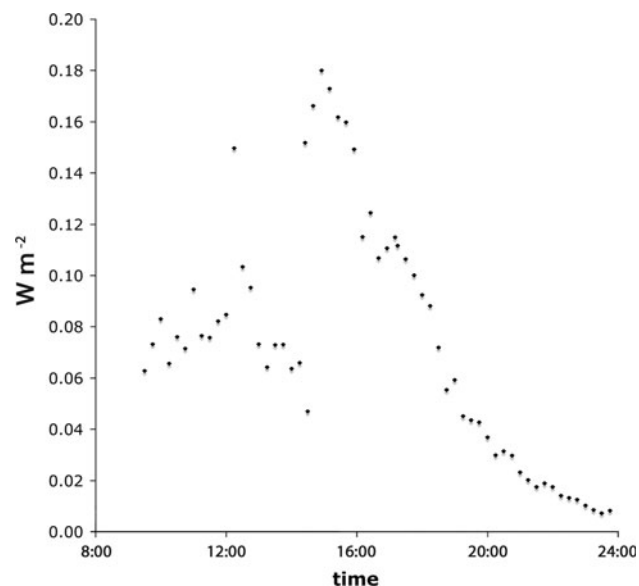


Fig. 3 Diurnal variation in UVR measured under multi-year sea ice in September 2005

was performed by placing a polycarbonate sheet (Lexan) over the aquaria to cut off the UV wavelengths. The aquaria were placed 70 cm under the UV-lamp and exposed for 30 min. The polycarbonate sheet slightly altered the intensity in the PAR range from 114 ± 2 to $107 \pm 2\ \mu\text{mol m}^{-2}\ \text{s}^{-1}$ PPFD.

Background experiments

In order to study the influence of different backgrounds on the chromatophores, a setup with light and dark backgrounds was established. Specimens of *A. glacialis* were kept in 200-ml plastic jars containing seawater in a cooling cabinet (0°C). The jars were covered with white or black plastic from the outside leaving the top open. Control specimens were collected by covering the jars with aluminum foil shielding them from any light. Illumination in the cooling cabinet was provided from the inbuilt fluorescent tube, with an intensity varying between 30 and $35\ \mu\text{mol m}^{-2}\ \text{s}^{-1}$ PPFD. Chromatophore response was recorded at start, after 24, and 48 h.

Temperature experiments

The influence of temperature on chromatophores was investigated by exposing experimental animals to increasing temperatures from 0 to 8°C for various intervals in glass jars (200 ml) containing seawater. This was achieved by leaving the experimental jars at room temperature and allowing the water to heat up slowly. Pictures of the animals were taken at 0, 2, 4, 6, and 8°C (accuracy $\pm 0.5^\circ\text{C}$) under the stereomicroscope. All experiments were carried out in darkness (apart from short interruptions in order to take photographs) by covering the jars with aluminum foil. Water temperature was monitored using a core thermometer (Ebro TFX 410).

Statistical analyses

Statistical analyses were carried out using the software package Statistica 7. Nonparametric tests (Mann–Whitney U test and Kruskal–Wallis test for independent samples; Wilcoxon Signed-Rank tests and Friedman’s tests for dependent samples) were applied, since the sample size was low and requirements for a normal distribution were not met in most cases. Statistical significance was accepted at $P < 0.05$. Multiple comparisons following a Friedman’s test were corrected using the Bonferroni–Holm adjustment for multiple P -levels. Results are expressed as means with the standard deviation or medians with standard errors. Change in the CI was calculated by subtracting the initial stage from the observed stage after each interval of exposure.

Results

Arrangement of chromatophores

Chromatophores were present in various body regions of *A. glacialis*. The chromatophores on the pleon used in the analyses were arranged superficially, one on each side on all three segments. On the pereon, profound chromatophores were arranged in lateral rows on each side (usually one cell per segment), covering internal organs laterally, but leaving a gap on the dorsal side (Fig. 1). Assemblages of chromatophores around the brain were present in most specimens and mouthparts seemed to carry chromatophores too. Occasionally, chromatophores were also found on the appendages or other body parts.

Experiments

PAR exposure

A. glacialis responded to visible light in the PAR range by dispersing pigments within the chromatophores, depending on light intensity and exposure time. Figure 4 shows the dispersion of pleon chromatophores of an experimental

animal exposed to the high-light treatment from CI 1 to stage 4 after 45 min. Chromatophores on the rest of the body generally responded in the same way to the light treatment.

High-intensity light treatments evoked a significant increase in the CI of experimental animals after only 15 min of exposure (Paired Wilcoxon Signed-Rank test, $P < 0.01$). After 30 min, all animals had a CI higher than 2, and after 45 min, the mean increase in CI was 1.7. The low-intensity light treatment did not result in significant change of the CI (Fig. 5) even after an exposure time of 60 min. Multiple Mann–Whitney U tests using the Bonferroni–Holm adjustment showed significant differences in the change of CI between low- and high-light treatment for each time interval (15, 30, 45 min; $P < 0.01$).

In the experiment, to study the reversibility of the response, a significant increase in CI (Wilcoxon Signed-Rank test, $P = 0.01$), from 1.6 initially to 3.6 after 180-min exposure to PAR, was observed. The subsequent dark adaptation caused aggregation of the pigments (Fig. 6), but at 240 and 360 min (60 and 180 min after put into darkness), the CI still differed significantly from the starting value. After 24 h in darkness, the CI had decreased to 2.8, which was insignificant to the initially recorded CI of 1.6

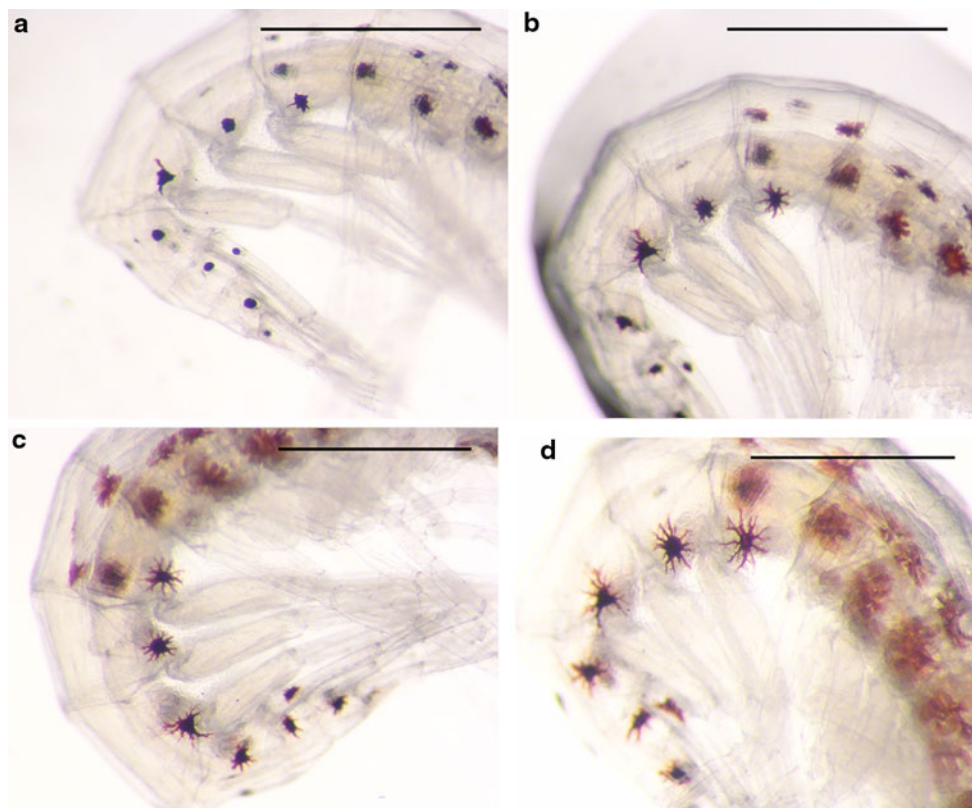


Fig. 4 Pigment dispersion in chromatophores of *Apherusa glacialis* before (a) and after exposure to PAR ($300\text{--}400\ \mu\text{mol m}^{-2}\ \text{s}^{-1}$) for 15 min (b), 30 min (c), and 45 min (d). Scale bars = 1 mm

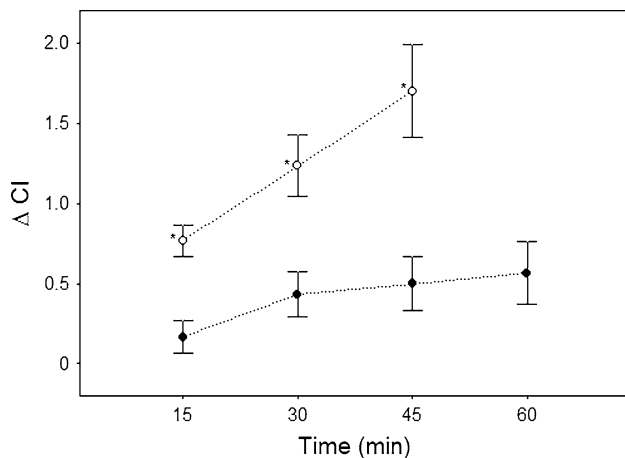


Fig. 5 Time course of the change in the chromatophore index (CI) after exposure to a high and low light intensity: *open circles*, 300–400 $\mu\text{mol m}^{-2} \text{s}^{-1}$; *filled circles*, 33–34 $\mu\text{mol m}^{-2} \text{s}^{-1}$. Data expressed as means \pm SE ($n = 10$). *Significantly different from the low-light treatment ($P < 0.01$, Multiple Mann–Whitney U tests using Bonferroni–Holm adjustment)

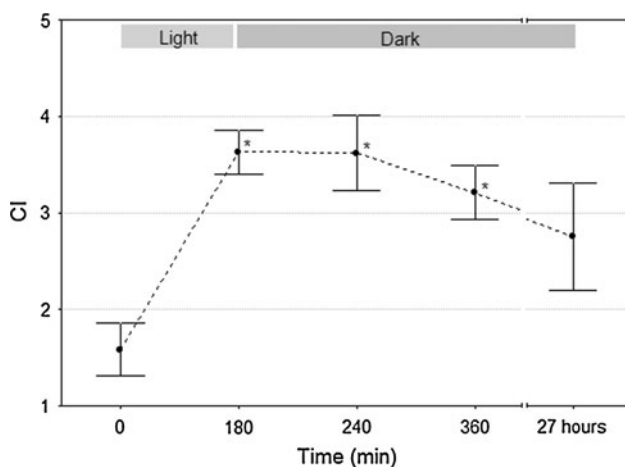


Fig. 6 Development of the chromatophore index (CI) after experimental animals were exposed to high light intensities (350–500 $\mu\text{mol m}^{-2} \text{s}^{-1}$) for 180 min and then put back in darkness. Values are means, *error bars* denote the SE ($n = 8$). *Statistically different compared to initial CI (0 min) ($P < 0.05$, Wilcoxon Signed-Rank tests)

(Wilcoxon Signed-Rank test, $P = 0.13$). Thus, pigment aggregation in the chromatophores occurred clearly more slowly than had dispersion at high light intensities.

UVR exposure

The exposure to UV wavelengths in addition to PAR also caused pigment dispersion in chromatophores in *A. glacialis*. The change in CI after 30 min was greater in the UVR treatment (0.9) than in the control (0.5), but no

statistical difference was observed (Mann–Whitney U test, $P = 0.08$; see Table 1). Note that the sample size in the control group was smaller ($n = 10$) than in the UVR treatment group ($n = 16$).

Background and temperature experiments

A. glacialis did not show any background matching behavior mediated by chromatophores. Both on white and black backgrounds, the CI increased slightly (0.4 and 0.3, respectively, after 24 h), but no difference was found between the treatments (Mann–Whitney U tests, $P = 0.46$). Only in the treatment with white background, a significant change in CI, compared to the control, was observed after 24 h (Wilcoxon Signed-Rank test, $P = 0.04$; see Table 1).

Higher temperatures led to a slight dispersal of pigments in chromatophores in *A. glacialis*. An increase in the mean CI of 0.6 ± 0.3 was recorded when temperature increased from 0 to 8°C (data not shown). A Friedman’s test showed this to be a significant increase, but multiple comparisons (Wilcoxon Signed-Rank tests using Bonferroni–Holm adjustment) were unable to detect differences between the initial CI and the individual temperature intervals. Elevation of the temperature to 10°C was tolerated by the amphipods.

Discussion

The present study describes for the first time the physiological color change of the Arctic under-ice amphipod *A. glacialis*, a process that is mediated by chromatophores. Based on our findings, the chromatophores appear to have a photoprotective function and provide an adaptation to short-term changes in solar irradiation.

Photoprotection

The experiments show that the physiological color change mediated through pigment dispersal in chromatophores is most likely triggered by changes in light conditions. In order to evoke a fast response, relatively high intensity of PAR was needed, but intensities likely to occur under sea ice also caused a response (UV-experiment control). Pigment dispersal due to exposure to visible light (PAR) is a common phenomenon and has been shown to occur in various crustacean species, mostly decapods (Perkins 1928; Brown and Sandeen 1948; Pautsch 1953; Rao 1966; Barnwell 1968; Coohill et al. 1970; Johnson 1974; Miner et al. 2000; Auerswald et al. 2008). *Apherusa glacialis* showed an increase in the CI following both higher light intensities and longer exposure times. It is therefore likely

Table 1 Experimental treatments conducted under different light conditions regarding the effect of solar radiation (in the UV and PAR range), background shade and temperature on the chromatophore index (CI)

	Number of experimental animals (<i>n</i>)	Light	Experimental irradiation	Exposure time	Water temperature (°C)	Background	CI	ΔCI
UVR experiments	16	UVR PAR	2–3 mW cm ⁻² 114 ± 2 μmol m ⁻² s ⁻¹	30 min	0 ± 1	–	4.0* ± 0.2	0.9 ± 0.1
	10	Control (PAR only)	107 ± 2 μmol m ⁻² s ⁻¹	30 min	0 ± 1	–	3.5* ± 0.4	0.5 ± 0.2
Background experiments	11	PAR	30–35 μmol m ⁻² s ⁻¹	24 h	0 ± 1	White	4.6* ± 0.2	0.4 ± 0.1
	10	PAR	30–35 μmol m ⁻² s ⁻¹	24 h	0 ± 1	Black	5.0 ± 0.0	0.3 ± 0.1
	9	Dark control	–	24 h	0 ± 1	Non	4.3 ± 0.4	–0.4 ± 0.4
Temperature experiments	7	Darkness	–	39 ± 3 min	0–8	–	3.7 ± 0.5	0.6 ± 0.3

CI and ΔCI values are means ± SE. Temperature experiments performed in intervals of 2°C

* Significantly different to initial CI (Wilcoxon signed-ranks tests, $P < 0.05$)

that *A. glacialis* is able to adapt individually to specific levels of irradiation, rather than responding to a threshold light intensity in an “all-or-nothing” type of response.

The physiological color change in *A. glacialis* is reversible, as pigments aggregated when animals were put back in darkness after exposure to PAR. Adaptation to darkness takes longer (up to 24 h to reach the initial stage of dark-adapted animals) than adaptation to high light intensities, which could ensure a fast protection against harmful radiation in a rapidly changing photic environment. Furthermore, the reversibility of the process demonstrates that pigment dispersion within the chromatophores is not due to damage of cells.

Assuming a photoprotective role of the chromatophores, this is most likely to be a shielding against UVR (e.g. Auerswald et al. 2008), although a direct harmful effect of blue light (450 nm) has been detected for the copepod species *Diaptomus nevadensis* (Hairston 1976). Documented harmful effects of PAR are otherwise rare, although high PAR intensity is known to inhibit photosynthesis in plants (Krause 1988), while UVR commonly known to have harmful effects (Browman et al. 2000; Lesser et al. 2004; Ban et al. 2007; Bancroft et al. 2007). However, the UVR treatment contra the control did not prove any difference in the response of the animals, suggesting that *A. glacialis* is not able to specifically detect UVR. Since UVR probably never occurs without accompanying PAR in nature, there is probably a low selectivity for a specific detection of UVR. The mechanism of light perception, which leads to the cascade of chromatophore response, is unclear and may not involve wavelengths in the UV range. However, since the ratio of UVR to PAR can vary due to different attenuation in sea ice (Belzile et al. 2000) or selective increase in UVR due to ozone depletion

(Kerr and McElroy 1993), it might be of vital importance for organisms to detect these wavelengths (Hessen 2002).

The arrangement of chromatophores in the amphipod points to the purpose of shielding the animal against incident irradiation from above. Whereas chromatophores in Antarctic krill are mainly located dorsally (Auerswald et al. 2008), pigment cells in *A. glacialis* are located at the ventral and lateral body side, a finding that might be related to the upside-down position the organisms take under the ice. Chromatophores are a unique feature of *A. glacialis* among the other sympagic amphipods, enabling the species to thrive at lit flow edges, remain in near-surface waters and even survive in melt ponds (Hop et al. 2000; Kiko et al. 2009). As an exclusive herbivore/detritivore species, the amphipod depends on the high primary production at these localities (Werner and Gradinger 2002).

Crypsis and thermoregulation

No indication of adapting the color appearance to background shade was seen in *A. glacialis*, excluding a cryptic function of chromatophores. Transparency can be regarded as the preferred appearance in the sea ice environment in avoidance of being detected by visual predators, but in patches where ice algae and detritus are aggregated, a dark-colored amphipod could have better camouflage. The arrangement of chromatophores is also not supporting crypsis, since they are basically aligned in a repetitive, rather than a cryptic, pattern on each body segment, as has been suggested for example in the isopod *Idothea baltica* (Merilaita 1998).

Acclimatization to a temperature of 8°C resulted in pigment dispersal in the chromatophores in some specimens of *A. glacialis*. The opposite response (contraction of

pigments) would have been expected if the animal was trying to prevent a build-up of heat in the body. A possible explanation for this phenomenon could be that increased metabolic stress leads to dispersion of pigments. Based on our results, we can exclude a thermoregulatory role of the chromatophores in *A. glacialis*.

As an additional note, *A. glacialis* seems to have considerable tolerance for elevated temperatures. Temperatures exceeding the normal variability in the natural habitat were tolerated for exposure times of more than 30 min. These findings correspond to those of Aarset (1991), who reported that short-term exposure to 10°C was not lethal in *A. glacialis*.

Photoprotection versus crypsis—a trade-off

Assuming that chromatophores with dispersed pigments absorb harmful radiation (most likely UVR) and are advantageous at high light intensities, there must be a fitness cost having dispersed chromatophores at low light intensities; otherwise, dispersed chromatophores would be preferred continuously. By dispersing pigments in the chromatophores, the animals appear darker, thus losing transparency. As transparency is regarded to be a successful camouflage in well-illuminated epipelagic layers (McFall Ngai 1990; Johnsen 2001), *A. glacialis* will become easier to detect by predators such as polar cod, which is a visual predator (e.g. Benoit et al. 2010). This is an inevitable risk to gain photoprotection, and *A. glacialis* seems to be able to regulate the pigment dispersion in chromatophores depending on light intensity to minimize the loss of transparency. This kind of compromise between photoprotection by pigments and crypsis has been suggested for various other crustaceans (Morgan and Christy 1996; Auerswald et al. 2008). For instance, Hansson (2000) and Hansson et al. (2007) showed that specimens of Arctic *Daphnia* spp. were more pigmented in lakes without predatory fish and that pigment levels can be adjusted to the prevailing conditions in a matter of days. Antarctic krill, *Euphausia superba*, has lower number of chromatophores and lower pigment concentration in winter than in summer, showing an ability to adapt to seasonal differences in the light conditions (Auerswald et al. 2008).

Color change by chromatophores provides a solution to the conflicting demands of camouflage and photoprotection. However, there are limits to the color change that can be achieved, which will affect the ability of the animal to express an optimal phenotype in a given situation. Such fitness costs are the associated physiological costs, as pigment movement is energy demanding (Miner et al. 2000; Boyle and McNamara 2008). The only indication regarding such costs in *A. glacialis* was that animals tended to aggregate the

pigments in their chromatophores when showing obvious signs of decreased activity or shortly before death, probably due to physiological stress. This could be a simple side effect of a general decrease in metabolism or part of an effort to reduce all energy-requiring processes.

Conclusions

Organisms inhabiting polar marine surface waters may be regarded as particularly exposed to high levels of dissolved oxygen, seasonally intense UV irradiance, and high levels of dissolved organic carbon (Krapp et al. 2009). In order to comply with these and other pro-oxidant challenges, aquatic organisms are known to have developed a number of antioxidant defense mechanisms, including superoxide dismutase (SOD) (McCord and Fridovich 1969), carotenoids (Davenport et al. 2004) as well as other small-molecule antioxidants like dimethyl sulfide (DMS), and mycosporine-like amino acids (MAA's) function as non-enzymatic antioxidants (Lesser 2006). In this study, we have examined the change in coloration of the ice amphipod *Apherusa glacialis* as a response to PAR and UV radiation as well as a potential cryptic effect. Pending further studies into the nature and chemophysical shielding effects of the pigments, we conclude that dispersion of pigments in the chromatophores plays a photoprotective role in *A. glacialis*, the response being triggered by light in the PAR spectrum. A similar response has been described (Auerswald et al. 2008) in the Antarctic krill (*Euphausia superba*), which responds to PAR in order to avoid harmful UV radiation. Specific detection of wavelengths in the UV range was not supported in this study, but it is likely that pigments in *A. glacialis* mainly serve to shield the animals from solar radiation, which is most harmful in the UV range. The dispersion of pigments in the chromatophores is a reversible process, causing aggregation of pigments in darkness. Therefore, the chromatophores enable the sympagic amphipod to react to different levels of solar radiation, balancing photoprotection against conspicuousness for visually hunting predators. Our study shows that *A. glacialis* is equipped to inhabit areas with high solar irradiation such as floe edges and areas of thin ice and can take advantage of the higher primary production there.

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