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Polar Biol (1996) 16: 573–579

ORIGINAL PAPER

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Competitive trade-off strategies in Arctic *Daphnia* linked to melanism and UV-B stress

Received: 29 September 1995 / Accepted: 29 January 1996

Abstract Different high-Arctic, freshwater localities at Ny-Ålesund, Svalbard (79°N) were examined for their UV-absorbing properties, depth and presence of melanic or non-melanic morphs of the planktonic crustacean *Daphnia pulex*. Light regimes in two localities with each of these morphs were measured by using underwater spectroradiometer. Most localities have low absorbance of short-waved light, but no clearcut relationship between UV transparency and occurrence of melanic morphs was detected. Yet, in the laboratory, the melanic morph showed far lower growth rates, thus being competitively inferior to the non-melanic. Conversely, the melanic morph was more resistant to UV light, suggesting a trade-off between the metabolic tax paid for the melanin synthesis and its UV-protecting abilities, or a staggered growth capacity possibly owing to polyploidy. Frequency of melanic or non-melanic clones could thus be directly linked to ambient UV-B stress and serve as an indicator thereof, but the apparently extensive need for UV protection under the Arctic light regimes is still puzzling, and the role of melanism and polyploidy in these organisms cannot be considered finally settled.

Introduction

The Arctic environment is harsh to life in most regards, notably due to short growing seasons and low temperatures. Freshwater life in particular suffers from a short productive season and low levels of nutrients. The Arctic freshwater systems comprise simple ecosystems, and yet the species are highly adapted, they are few and thus susceptible to food web manipulations and environmental stress. While the Antarctic "ozone-hole" has been well recognized for the last decade, there has been recent concern that the Arctic and sub-Arctic stratospheric ozone layer has also decreased (Kerr and McElroy 1993; Madronich et al. 1995), posing additional constraints on Arctic life and productivity. Over the northern hemisphere a significant 10% loss of the stratospheric ozone layer has been observed over the past decade, and this trend is continuing. So far this decrease has been most observable in late winter (February/March), hence extending well into the marine spring bloom, but with no apparent effects on the freshwater biota. There have, however, also been recorded ozone anomalies during the ice-free season, and such anomalies with concomitant peaks in UV-B could induce significant biological effects. Hence temporary episodes may be of equal importance to average concentrations.

There has been particular concern about such effects in the marine environment, owing to the large commercial pelagic fish stocks and the biological CO_2 consumption in Arctic oceans. To some extent, early effects in marine areas may be difficult to assess, due to the complexity, interannual variability and presence of depth refugia. However, the simple communities in shallow ponds without depth refugia could, in particular, be susceptible to UV, and serve as appropriate units for monitoring levels and effects of UV stress. In the numerous shallow ponds and small lakes distributed over the Arctic and sub-Arctic areas, the crustacean zooplankter *Daphnia pulex* constitutes a key species. This species has a circumpolar distribution, and may be described as a species complex with an astonishing clonal complexity and genetic variability (Hebert 1983 and McWalter; Weider et al. 1987; Hobæk and Wolf 1991). A remarkable feature is the presence of distinctly different melanized and non-melanized clones within the same area. These properties are assumed to be linked to the ambient UV stress.

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While carotenoids play an important role in protecting copepods from short wave light (Hairston 1978, 1979; Ringelberg et al. 1984), they apparently play a less important role for cladocera (Hessen and Sorensen 1990; Hessen 1994). Highly light-exposed *Daphnia* populations of various species do, however, possess a carapace melanization (Brooks 1957; Löffler 1969; Luecke and O'Brien 1983; Wolf and Hobæk 1986), a property apparently linked to light exposure (Siebeck 1978; Hebert and McWalter 1983; Hebert and Emery 1990). The melanized clones are genetically distinctly different from non-melanic clones (Hebert and McWalter 1983; Weider et al. 1987; Hobæk and Wolf 1991) and almost uniquely occur in alpine localities or Arctic ponds. Within a region these clones often occur in the clearest ponds and are replaced by non-melanic clones when vegetation cover increases or water transparency decreases (Hebert and Emery 1990; Hessen and Sørensen 1990; Hobæk and Wolf 1991). It has been suggested that the non-melanic clones are competitively inferior to these in the absence of UV stress owing to the metabolic tax paid for melanin synthesis (Hebert and Emery 1990). They would also suffer a competitive drawback in the presence of vertebrate visual predators like fish. There is a close association between melanism, polyploidy and obligate parthenogenesis in Arctic *Daphnia* (Weider et al. 1987; Beaton and Hebert 1988), and while the latter two attributes seem selected for in extreme environments (Beaton and Hebert 1988), the causalities for these pheno- and genotypic associations are not finally settled.

Experiments with UV-B demonstrate a higher light tolerance in alpine, coloured *Daphnia* compared with lowland species (Siebeck 1978; Siebeck and Böhm 1994), pointing towards inherent differences in UV-B tolerance related to ambient exposure. These experiments also demonstrate the potential, detrimental role of UV-B to zooplankton. There is no direct evidence for the effects of melanism on UV-B damage, but in situ experiments and experiments with UV-A suggest that carapace melanin, in general, offers protection from short-waved light (Luecke and O'Brien 1983; Hebert and Emery 1990). These experiments also indicate that present day light levels are close to the tolerance limits for both coloured and hyaline morphs. It thus appears that present levels of UV or near-UV light may act as an ecological determinant, influencing survival, geographical and horizontal distribution, vertical migration and competitive abilities of freshwater organisms, and as such deserve increased attention irrespective of any changes in the ozone layer.

This paper address some of these aspects and pays special attention to the competitive trade-offs between these two different pigmentation strategies in the high-Arctic *Daphnia pulex* species complex. It further reviews the question of the apparent susceptibility to UV of these high Arctic-organisms, in spite of low UV intensities at high latitudes.

Materials and methods

During late July and early August 1994, a number of localities in the vicinity of Ny-Ålesund (79° N) at the Svalbard Archipelago were examined for the presence of melanic or non-melanic (hyaline) morphs of the crustacean zooplankter *Daphnia pulex*. This is an area with high clonal diversity (Weider and Hobæk 1994). All localities are shallow (maximum depths ranging from approximately 5 to 0.3 m), oligotrophic and surrounded by very sparse tundra vegetation, but may to some extent be influenced by bird colonies. Taken from seven ponds with *Daphnia* populations, water samples – for analysis of UV absorbance (257 nm) – were stored in the dark in the refrigerator until analysis (2 weeks). Zooplankton samples from the same localities were collected with a 250 µm-mesh plankton net, and frozen immediately for later confirmation of morphotype. From two of the localities, one with melanized and one with mixed populations, live animals were brought to the laboratory (Oslo), and cultured for further experiments. Underwater light regimes were assessed at different depths in these two localities using a LI-COR 1800 spectroradiometer with a 2-nm resolution over the range from 300 to 850 nm.

Incubation experiments with melanic and hyaline *Daphnia pulex* were performed in Tvillingvatn at depths of 0.5, 1 and 2 m in 250-ml glass (transparent to UV-A and PAR light) and quartz bottles (transparent to UV-B, UV-A and PAR light). For each depth and for each morph, duplicates were run with ten adults for 5 days.

A simple assessment of population growth for a hyaline morph and a melanic morph was performed in semi-batch cultures in the laboratory. Duplicates with 25 juveniles of each morph were incubated in 4-l polycarbonate flasks with algal medium. Twice a week, animals were randomly distributed by gentle shaking, and a 250-ml subsample was taken for counting individual numbers and sizes. This water volume was replaced by a culture of the green algae *Selenastrum capricornutum* (0.8–1.2 mg Cl^{-1}) from a chemostate. The population growth was followed for 4 weeks, until population density peaked and growth ceased. The life span was determined under excess food conditions in ten separate beakers (50 ml), where newborn neonates were added, and transferred to fresh medium every 3rd day.

UV-B tolerance in both morphs was assessed in the laboratory by adding ten juveniles in 500 ml beakers (15 cm deep), and applying a 6-h irradiation regime using a 15-W Wilber-Lourmat lamp with peak intensity at 312 nm (range 280–380 nm). The experiments were performed in triplicate for each of three light intensities: level 1, 0.067 mW cm^{-2} or 0.004 J cm^{-2} min^{-1}; level 2, 0.020 mW cm^{-2} or 0.0013 J cm^{-2} min^{-1}, and level 3, 0.004 mW cm^{-2} or 0.00025 J cm^{-2} min^{-1}. The doses were assessed using a Vilber-Lourmat VLX-3 W radiometer with peak sensitivity at 312 nm. In addition, an incubation with level 1 intensity but with a Mylar sheet cover was performed for a selective screening of the UV-B. The Mylar sheet had a cut-off at 320 nm, and was replaced every 3rd day. Standard blue-white light (100 µE m^{-2}) was applied for photorepair at all UV intensities. Spectral distribution and intensity for all three levels in the presence or absence of the Mylar coverage are given in Fig. 1. For comparison, the UV-B spectrum for all three levels is compared with outdoor solar radiation (bright sun, noon, mid-July at 62° N). The number of animals was visually inspected every 3rd day over a 12-day period, and the total number of living individuals was counted after the experimental termination. Food levels were kept low (100–200 µg algal C l^{-1}) under the exposition to minimize chlorophyll absorbance of UV-B.

Simple competition experiments were run by adding ten juveniles of each morph to corresponding beakers at corresponding light intensities. Experiments were performed in triplicate for each light intensity, and all experiments were run in beakers covered with Mylar film. Melanized morphs tend to reduce their melanin production in the laboratory, but low levels of blue-white light, extending into UV-A (> 360 nm) were sufficient to maintain a constant carapace melanization even in culture.

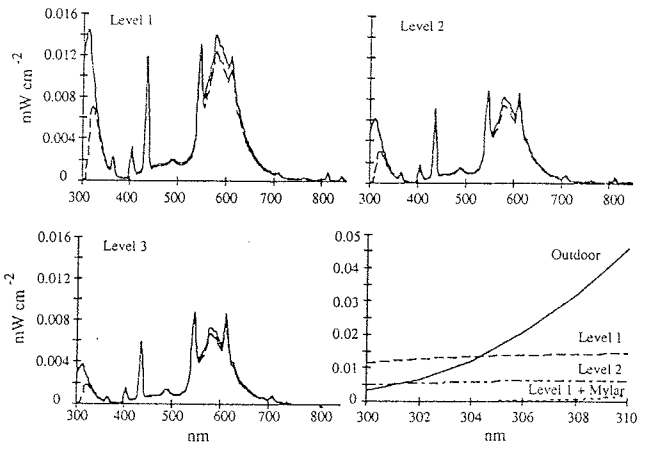

Fig. 1 Light intensity and spectral distribution for the three levels of experimental UV-B exposure. For all levels, light intensity in unshaded beakers is given as *solid lines*, while the corresponding doses under Mylar cover (selectively removing wavelenghts < 320 nm) are given as *broken lines*. *Lower left panel* gives experimental doses over the range 300–310 nm for levels 1 (with and without Mylar cover) and 2 relative to outdoor irradiance (bright sun, mid-summer noon)

Results

Field data

All water bodies have low levels of dissolved organic carbon DOC, with typical spectrophotometrical UV absorbance (253 nm) ranging from 0.114 to 0.010 (Table 1). The highest UV-B absorbance was recorded in the Solvatn locality at Ny-Ålesund. This lakelet is surrounded by bogs and is slightly eutrophied from bird colonies; it still possessed a population of melanized daphnids only. The lowest UV absorbance was recorded in the ultraoligotrophic Lake Tvillingvatn, as well as in small ponds (maximum depth < 50 cm) at the moraine from the Lowén glacier, both types of localities possessing melanized individuals. There was no distinct relation between clonal distribution and UV absorbance or depth of the localities. Spectral distributions for the one locality with a mixed population (Brandallaguna) and a locality with only melanized Daphnia (Tvillingvatn) are given in Fig. 2. The recordings were made on consecutive days with highly different cloud cover, reflecting the day-to-day variability. Nevertheless, they both confirm the low DOC contents as reflected in low absorbance of short-waved light. Light attenuation at 310 nm in the clear lake Tvillingvatn at noon and late evening gave a close fit (Fig. 3), yielding 10% of surface irradiation (0.1 m) at 1.0 m. For comparison, results from an alpine lake from the mainland with melanized *Daphnia longispina* are given, indicating a nearly twice as high transparency.

The field exposure experiments yielded no acute mortality. A 100% survival was found at all depths both in glass and quartz bottles during the 5 days incubation. During all days there was foggy and rainy weather, with light intensities of less than 25% of that recorded under the brief periods of clear sky.

Table 1 UV absorbance (at 253 nm), approximate maximum and mean depths (m), conductivity (mS/m) and presence of melanized (*m*) or hyaline (*h*) clones in seven localities

Location no	Name	UV absorbance	Conductivity	Max depth	Mean depth	Clone
1	Solvann	0.114	39.2	1.5	1	m
2	Knuth.vann	0.082	18.8	2	1	m
3	Blomstr.nedre	0.059	20.7	1	0.5	m
4	Brandallaguna	0.026	37.5	1.5	0.7	h,m
5	Blomstr.ovre	0.023	11.4	2	0.7	m
6	Tvillingvann	0.011	10.5	5	2.5	h
7	Lovénbre	0.01	13.5	0.5	0.3	m

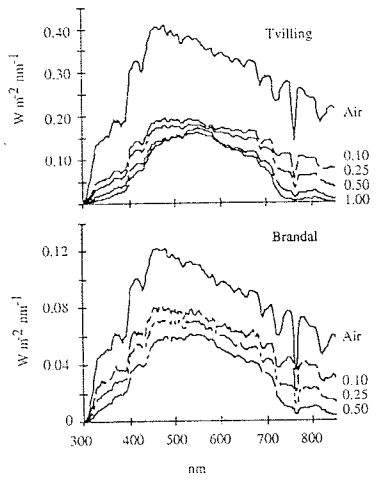

Fig. 2 Underwater light intensity at various depths (meters) over the spectral range 300–850 nm for localities Tvillingvatn (melanized *Daphnia pulex*) and Brandal-laguna (mixed population of melanized and hyaline *Daphnia pulex*). The relative differences in intensity between the localities are due to variable cloud cover

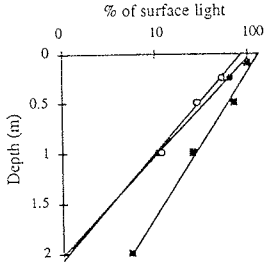

Fig. 3 Light absorbance as log UV_{310} versus depth in Lake Tvillingvatn on a clear (*unfilled circles*) and cloudy day (*filled circles*). Corresponding absorbance for an alpine pond at Finse with melanized *D. longispina* is given for comparison (*filled squares*)

Laboratory experiments

Growth rates in the two morphs were markedly different. The hyaline morph reached a maximum of near 700 individuals per bucket (4 l), and the population peaked within 20–25 days (Fig. 4). In contrast, the melanized morph had a slower and more steady increase, reaching a maximum of 200–300 individuals after 25–30 days. The actual intrinsic rate of increase could not be computed from these crude experiments,

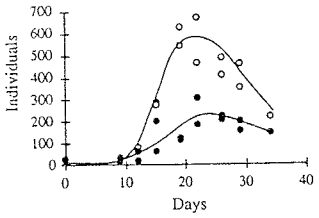

Fig. 4 Smoothed curves for population growth (batch culture, stable food supply) of a hyaline clone (*unfilled circles*) and a black clone (*filled circles*) from Svalbard. Each clone was run in duplicates represented as *single dots*

but from maximum exponential population increase, doubling times of approximately 0.5 d^{-1} and 0.25 $^{-1}$ were estimated for the hyaline and black morph respectively. The laboratory experiment clearly confirmed the expected higher tolerance in the melanized morph. At level 1 (cf. Fig. 1), corresponding to a UV-B dose of 0.004 J cm^{-2} min^{-1}, both morphs were extinct within the 12-day period, yet with a distinctly prolonged survival in the melanized morph, relative to the hyaline. At level 2 (0.004 J cm^{-2} min^{-1}), the hyaline morph persisted for a longer period, but still became extinct within 12 days, while the melanized morph gained a positive population growth at this level. At the lowest UV-B intensity (0.00025 J cm^{-2} min^{-1}), population growth in both morphs closely resembled that of the Mylar-shielded, level 1 treatments (Fig. 5). These results also confirm the markedly slower growth rate among the melanized *Daphnia*. Both morphs had a similar life span (range 47–51 days), under the given conditions (18°C, surplus food). The slower growth rates point to a competitive inferiority of the melanized individuals in the absence of UV-B stress. This was clearly confirmed by the simple competition experiments performed in batch cultures, where the melanized clone was strongly suppressed to extinction over a 4-week experimental period (Fig. 6).

Discussion

The a priori assumption that presence or absence of melanized clones is strictly linked to water transparency or extremely shallow water bodies was not confirmed by these data. The two clearest localities both possessed melanic clones, but so also did the two localities with the highest UV absorbance. This is, however, based on a very limited number of localities, and previous studies have unambiguously demonstrated a good correlation between UV transparency and presence of melanic vs non-melanic clones (Hebert and Emery 1990). There is little information on clonal stability and replacement in these Svalbard localities. It is

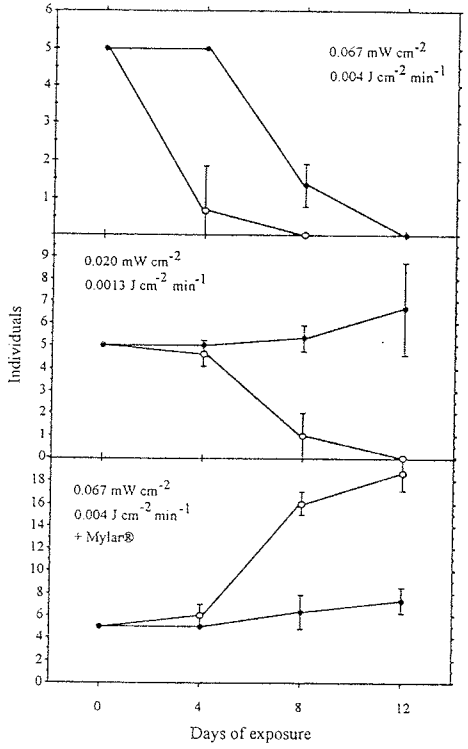

Fig. 5 Survival of hyaline (*unfilled circles*) and melanized (*filled circles*) morphs of *Daphnia pulex* at different experimental light regimes. *Upper panel*, level 1; *mid panel*, level 2; *lower panel*, level 1, but with Mylar cover. Applied doses represent integrated total UV dose from the UV-B lamp with peak intensity at 312 nm. SDs of three replicate experiments represented as *bars*

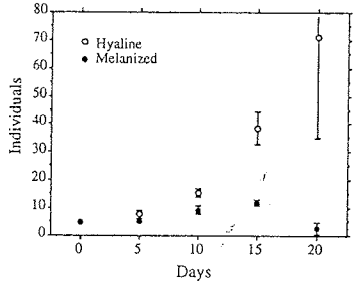

Fig. 6 Outcome of competition experiments where hyaline (*open circles*) and melanized (*filled*) *Daphnia pulex* that are incubated together in batch cultures with constant food supply. SD's of three replicates given as vertical bars

noteworthy, however, that locality 4, which in 1992 was populated solely by a hyaline clone (Hobæk et al. 1993), now had a mixed population. The melanic morph in this locality showed up after the unusually sunny summer of 1994, but any causality here remains speculative.

Most Arctic freshwaters are only modestly influenced by dissolved organic carbon (DOC), and hence are fairly transparent to UV light. The exceptions are glacially fed, turbid lakes and a few guanotrophic localities like that of Solvatn (cf. Table 1), where the higher concentrations of phytoplankton screen off some UV light. A 10% UV-B (310 nm, subsurface) remaining at 1-m depth would be typical for clearwater localities (cf. Kirk 1994), yet less than that recorded in comparable small lakes in alpine areas (cf. comparison in Fig. 3), and considerably less than recordings from ultraoligotrophic clearwater lakes, where the 10% depth may exceed 10 m (Hessen 1993; Kirk 1994). In spite of poorly developed soils, a high water saturation and boggy soils in the catchments yield some DOC even in these Arctic localities, blocking a significant portion of the lower wavelengths.

The laboratory experiments quite convincingly demonstrated the lower susceptibility of melanized *Daphnia* to UV, and the apparent trade-off between growth rate and UV protection. Population doubling time was twice as high in the hyaline clone as compared with the melanized clone. This agrees well with previous observations (Weider 1987) demonstrating delayed age at first reproduction, smaller clutch size but larger offspring size and consequently a lowered intrinsic rate of increase in melanized clones. Previous research has demonstrated that sub-Arctic Canadian melanic clones are polyploid, while hyaline clones are most commonly diploid (Beaton and Hebert 1988). The slower development is a common property of polyploid organisms (Beatty 1957), yet they often acquire larger size than their diploid conspecifics (Lewis 1980). This also holds in general, for melanized versus hyaline *Daphnia* populations (unpublished data). For *Daphnia* spp. it has been assumed that the negative effects of polyploidy on population parameters are counteracted by their somewhat broader tolerance to various environmental parameters (Lynch 1984). The ploidy levels of the tested morphs are not settled however. Data from populations in northern Norway show no clear association between polyploidy and melanization (Ward et al. 1994), and data from this Svalbard area indicated polyploidy also in a hyaline clone (Hobæk et al. 1993). A repeated melanin synthesis may be energetically unfavourable and slow down growth rates, as the melanin has to be resynthesized after each molt (Hebert and Emery 1990). Specific melanin content may show strong clonal and seasonal variability. Hobæk and Wolff (1991) found that melanin constituted no more than approximately 0.03 µg mg DW^{-1} in alpine *Daphnia longispina*, which is tenfold less than that Hebert

and Emery (1990) reported for sub-Arctic *D. pulex*. Even with a maximum estimate of 0.03% melanin of body weight, this would imply a minor cost relative to the total exuvia, which drain off nearly 10% of total body carbon per molt (Lynch et al. 1986). The actual costs of melanin synthesis may be more substantial, however, and constitute a drain of energy. Eumelanin and phaeomelanin are both synthesized by a chain polymerization of phenolic compounds originating from tyrosine, and the initiating enzyme tyrosinase is stimulated by UV light (Blois 1988). When relaxed from exposure to shorter wavelengths, the melanin production ceases off also in *Daphnia* (unpublished data), again indicating that melanin synthesis is counter-selected in absence of UV.

For whatever reason, there seem to be costs associated with the metabolism and life history of the melanized daphnids that apparently make them competitively inferior to their hyaline counterparts. The repeated competition experiments, although only performed at one food concentration, clearly demonstrated the ability of the hyaline clone to suppress the melanized done in the absence of UV stress. These experiments support the assumption that the success of melanized clones hinges on the higher resistance to some environmental stress, of which UV-B radiation seems to be a likely candidate. The applied experimental doses were not unrealistic relative to expected "natural" solar doses in terms of DNA or CIE-weighted Commission Internationale de l'Éclaire biological action spectrum (McKinley and Diffey 1987), though there were clearly spectral anomalies compared with the solar spectrum. For most of the UV-B range, the applied dose-rates were far below that recorded outdoor (cf. Fig. 1); only for wavelengths < 304 nm (which contribute little to the CIE-weighed dose) did the experimental intensity exceed the solar intensity. Although applied total doses in the UV-B range were "realistic" in these experiments, there are at least two factors needing some precaution. First, the visible light applied did neither mimic the spectral quality nor the intensity of solar light, meaning that the light stimulus of photorepair could be subsaturated. Second, the actual action spectrum for cell damage of *Daphnia* is largely unknown, yet the LD_{50} action spectrum resembles that of the DNA action spectrum (cf. Siebeck and Böhm 1994). Hence, while the conclusion of a higher UV tolerance of the melanic clones seem valid, the determination of actual lethal doses and in situ sensitivity in different environments needs further elaboration.

The apparent vulnerability of Arctic species to UV-B is puzzling, since Arctic light intensities are considerably lower than those of lower latitudes. Using a radiation transfer model (UV dose 2.0; Dahlback et al. 1989; Dahlback and Stamnes 1991), the theoretical, maximum radiation from 290 to 400 nm, weighted with the CIE biological action spectrum (McKinley and Diffey 1987) can be calculated. By assuming zero albedo, no clouds and a stable ozone level of 320 Dobson, it is evident that even during the Arctic summer, the maximum daily CIE-weighed dose would be 35–40% lower at the Ny-Ålesund site (79°N) compared with southernmost Norway (Fig. 7). Further, Arctic lakes are frequently ice covered until late July, where maximum doses are reduced by another 35% relative to mid-summer.

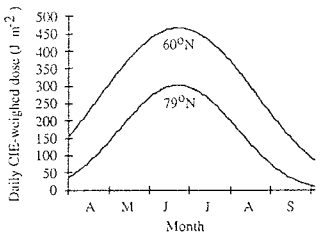

Fig. 7 Calculated daily CIE-weighed UV dose over the summer season for the Ny-Ålesund site (79°N) compared with southern Norway (60°N). For assumptions and reference to model, see text

It is tempting to suggest temperature as one essential parameter to potential UV-B induced cellular damage. The long daylengths could add to this. While most harmful effects of UV-B are not temperature dependent, the repair mechanisms are. DNA-ligase and anti-oxidant expression and activity are kinetic mechanisms that would slow down in cold environments in poikilotherms. Whether this is of importance in cold climates remains speculation, but temperature dependant survival and anti-oxidant expression under UV stress are currently being studied in further experiments. The ability to synthesize melanin in eyes and ephippia (resting eggs) is present in all Cladocera, while the mutation leading to melanin allocation to the carapace seems at least in the *D. pulex* group to be intimately linked to polyploidy (Weider et al 1987; Beaton and Hebert 1988). Melanism is never observed in lowland localities, but has arisen independently in other alpine and Arctic species of *Daphnia*, as well as in epineustonic and highly light-exposed organisms like the cladoceran *Scapholeberis mucronata* where the relationship to polyploidy is not settled. Polyploidy may enhance expression of catalase or other anti-oxidants, and in fact oxidant stress may promote polyploid cell lines (Spitz et al. 1989). Yet preliminary experiments do not confirm higher levels of catalase in melanized *D. longispina* relative to hyaline (unpublished data). The primary function of melanin is probably simple light screening, yet melanin precursors may also serve anti-oxidant purposes, and also, lower temperatures normally induce increased melanin concentration in animals (Blois 1988). A secondary gain from the dark coloration by increased heat absorption as proposed by Byron (1979) is unlikely due to the excessive heat transfer in these tiny aquatic animals (Hairston 1981). The apparently extensive need for UV protection under the Arctic light regimes is still puzzling, and the role of melanism and polyploidy in these organisms cannot be considered finally settled.

Acknowledgements This study was made possible by grants from the Norwegian Council for Sciences and Letters (NFR) and the Norwegian Polar Institute. I am indebted to the staff at the Norwegian Polar Institute and the Kings Bay Company for their hospitality and logistic support of the field work at Ny-Ålesund. Arne Dahlback kindly provided information on latitudinal UV doses. Sincere thanks are given to Hanne Line Daae for cooperation with field work. Three referees provided a valuable criticism of the first draft.

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