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Can bottom ice algae tolerate irradiance and temperature changes?

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ABSTRACT

Sea ice algae are significant primary producers of the ice-covered marine environment, growing under typically cold, dim conditions. During ice break-up they are released to the water column, where temperatures can be several degrees higher and irradiance can increase by orders of magnitude. To determine how sea ice algae respond to such rapid changes, we carried out incubations to examine their tolerance to environmentally realistic levels of change in temperature and PAR, as expressed by photosynthetic response and production of mycosporine-like amino acids (MAAs). The algae were also exposed to a broader range of temperatures, to evaluate their potential to function in warmer seas in the event, for instance, of anthropogenic transfer to locations further north. When subjected to PAR (0–100 μmol m^{-2} s^{-1}) at ecologically relevant temperatures (−1 °C, 2 °C, 5 °C), the algae showed tolerance, indicated by a lack of decline in the quantum efficiency of photosystem II (PSII). The data show that bottom ice algae can tolerate increasing temperature and PAR comparable to the changes experienced during and after sea ice melt. MAA production increased at higher PAR and temperature. At ambient PAR levels, increased temperatures resulted in lower ϕ_{PSII}. However, as PAR levels were increased, higher temperature reduced the level of stress as indicated by higher ϕ_{PSII} values. This result suggests, for the first time in sea ice algal studies, that higher temperatures can ameliorate the negative effects of increased PAR. Exposure to much higher temperatures suggested that the algae were capable of retaining some photosynthetic function at water temperatures well above those currently experienced in some of their Antarctic habitats. However, when temperature was gradually increased past 14 °C, the photosystems started to become inactivated as indicated by a decrease in quantum yield, suggesting that the algae would not be viable if transferred to lower latitude cold temperate areas.

1. Introduction

The seasonal formation and melting of sea ice are two of the most striking features of the Antarctic marine environment (Convey et al., 2014). As sea ice algae play an important role in primary production in the Southern Ocean and are the only source of fixed carbon for all other life in ice-covered habitats of this region (Arrigo et al., 1997), it is important to understand their responses to environmental variability and change. During sea ice melt algae are exposed to higher temperatures and levels of UV-B and PAR than they experience in the ice matrix (Arrigo and Sullivan, 1992; Ralph et al., 2007; Ryan et al., 2011). Indeed, temperatures above zero and even up to 5 °C can be experienced by algae derived from sea ice in shallow waters as well as in the open sea during summer in the Antarctic Peninsula region and northern zones of the Southern Ocean close to the Polar Front (Morley et al., 2010). Likewise, PAR levels exceeding 100 μmol m^{-2} s^{-1} can be experienced during thinning and melting of sea ice (Ryan et al., 2011). Therefore, quantifying the ability of algae to withstand these conditions is ecologically relevant.

Productivity in Antarctic sea ice and Southern Ocean algae is mainly restricted to a three to four month period in summer (Arrigo, 2014; Peck et al., 2006; Smetacek and Nicol, 2005). Antarctic bottom ice algal communities are thought to be extremely shade-adapted, with low E_k values (saturation irradiance, a measure of the intensity of PAR required to permit maximum photosynthesis), and are able to adjust photosynthetic rates to suit changing diurnal irradiance levels (Arrigo et al., 1997; Ryan et al., 2009). Low PAR conditions are typical of the under-ice environment (Lizotte, 2001). Measurements of daily average PAR under 2.5 m thick spring pack ice in the Ross Sea region have shown a range of 5.6 to 10.6 μmol m^{-2} s^{-1} in the under-ice habitat (Lazzara

Abbreviations: PAR, photosynthetically-active radiation; UV-B, ultraviolet B; MAAs, mycosporine-like amino acids; PSII, photosystem II; E_k, saturation irradiance; HPLC, high performance liquid chromatography; PAM, pulse amplitude modulation; RLC, rapid light curve; F'_m, maximum fluorescence in the light; F^o_m, maximum fluorescence level; F_v/F_m, maximum quantum yield of PSII; $F'_m - F_t$, ratio of variable fluorescence; ETR, electron transport rate; F′, fluorescence yield; T_c, critical temperature where permanent damage occurs; T_p, temperature of peak fluorescence; ϕ_{PSII}, effective quantum yield of PSII.

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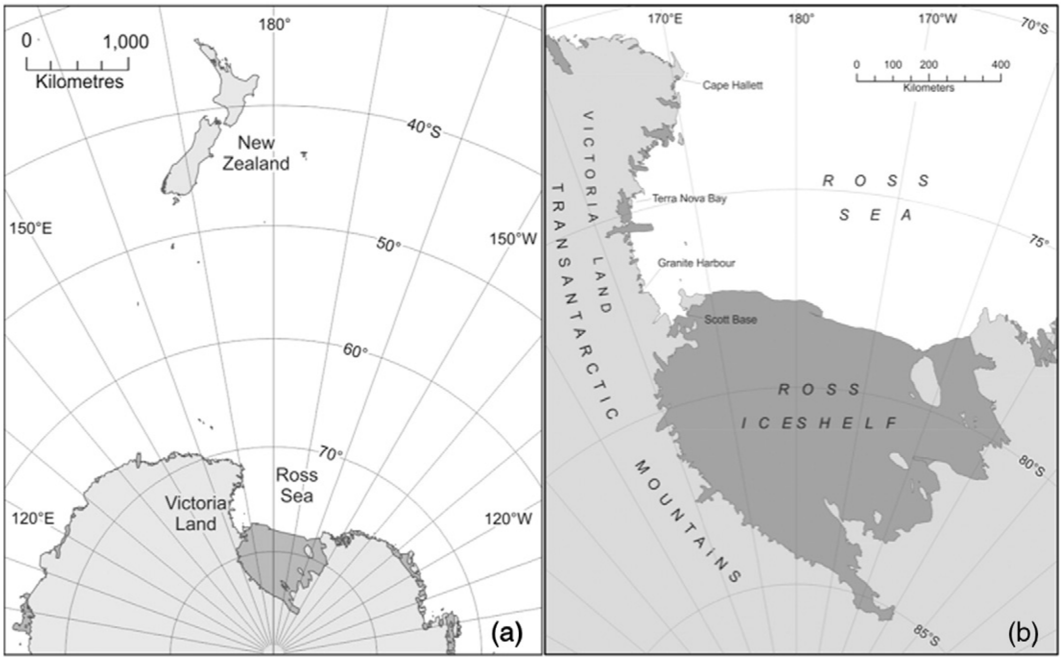

Fig. 1. (a) Map of the Ross Sea region and (b) close up of Ross Sea indicating the three sea ice collection locations of Terra Nova Bay, Granite Harbour and Cape Evans.

et al., 2007). Under 1.8 m thick fast ice in McMurdo Sound, PAR levels can be even lower, with as little as 1 μmol m^{-2} s^{-1} measured at noon on a clear sunny day in spring (Ryan et al., 2011). Low photosynthetic rates, high photosynthetic pigment concentrations and abundance of chloroplasts in algal cells are strong indications of the shade-adapted features of these microalgal communities (Lazzara et al., 2007). In an Arctic study (Manes and Gradinger, 2009), ϕ_{PSII} increased as PAR levels increased from 0 to 32 μmol m^{-2} s^{-1} and temperatures increased from −3.9 °C to −1.6 °C within the sea ice in the transition from winter to summer.

The photosynthetic response of all marine algae to temperature is dependent on the level of PAR (Davison, 1991). However, although the photochemical reactions of photosynthesis are light-dependent, carbon fixation is an enzyme-driven process and therefore highly temperature-dependent (Öquist, 1983). In Arctic sea ice diatoms, photosynthetic efficiency decreases with increasing temperature (Palmisano et al., 1987). Claquin et al. (2008) showed that several temperate marine algae were able to survive a large temperature range, with all the species studied being viable at least between 7 and 24 °C. In contrast, polar diatoms can only tolerate temperature variation over a range of as little as 7 °C (Suzuki et al., 1995). Some species of diatoms found in sea ice have also been observed in areas close to the Polar Front where water temperatures are known to reach up to 5 °C (Atkinson, 1994).

To protect themselves from environmental stresses, many microorganisms produce mycosporine-like amino acids (MAAs) (Vincent, 1988). Other than their production being a response to exposure to biologically damaging short wavelength UV-B radiation (Klisch and Hader, 2008), MAAs may also perform osmoprotective functions (Arrigo and Thomas, 2004; Oren, 1997) and provide antioxidative protection (Dunlap and Yamamoto, 1995; Oren and Gunde-Cimerman, 2007).

Unprecedented global climate change trends have become apparent over the past century. In Antarctica, there are also strong regional trends, and region-specific effects such as the consequences of the annual formation of the anthropogenic Antarctic ozone hole (Convey et al., 2009; Dixon et al., 2012; Turner et al., 2009, 2012). There is currently an overall positive trend in the annual mean ice extent in the Antarctic of 1.2–1.8% per decade (Turner et al., 2013), although this is forecast to reverse over the next century with the latest IPCC AR5 models predicting that there will be a nearly ice-free state around Antarctica in February within the next century (http://www.ipcc.ch/report/ar5/wg1/#.UuhKY2SBoYI, Web 1 May 2014). However, regional sea ice extent and duration have also significantly reduced in the Bellinghausen Sector and west of the Antarctic Peninsula, and maximum ice loss is expected in the central Weddell Sea and the Bellingshausen–Amundsen Seas (Lefebvre and Goosse, 2008), at the same time as increases of about 4.5% in the Ross Sea (Turner et al., 2009). Changes in sea ice extent and duration can have significant impacts on the phytoplankton community, affecting community composition and species abundance (Montes-Hugo et al., 2009; Schloss et al., 2012) and having consequential impacts elsewhere in the food chain

Table 1
Field parameters and dominant taxa present at the three study sites examined. PAR measurements were typical of a clear sunny day at solar noon.

	Terra Nova Bay November 2007	Granite Harbour November 2009	Cape Evans November 2010
Sea ice thickness (m)	1.9	3.2	1.9
PAR level at bottom of sea ice (μmol m^{-2} s^{-1})	~1	~0.5	~1
PAR level at surface (μmol m^{-2} s^{-1})	~1200	~1200	~1300
Dominant taxa	No data available	Haptophyta *Navicula* spp. *Entomoneis* spp. *Fragilariopsis curta*	*Nitzschia stellata Fragilariopsis* spp. *Navicula* spp. *Berkeleya* spp.