Ecophysiological Strategies of Arctic Seaweeds in a Changing Environment

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ABSTRACT

Littoral and sublittoral hardbottom zones of the Arctic are mainly dominated by dense macroalgal communities producing high amounts of biomass, which represent a major trophic contribution to these systems. Research on the ecophysiology of polar macroalgae originally focussed on depth zonation pattern as well as basic photosynthetic, nutritional and growth characteristics at near freezing temperatures. More recently a number of studies have dealt with functional and structural strategies that allow polar species to cope with the long periods of darkness during winter and excess light and nutrient limitation during summer. Lately, research efforts have also devoted to gain knowledge on the effects of excess ultraviolet radiation on these organisms caused by stratospheric ozone depletion. Other threats linked to global change in polar ecosystems are increasing load of nutrients dissolved in seawater, increasing levels of atmospheric CO_2 and occasional episodes of drastic decrease in salinity caused by thawing of large masses of ice. This mini-review aims to update the knowledge on the survival strategies of macroalgae that evolved genetically to inhabit the Arctic, and their mechanisms to overcome predicted environmental changes. From the presence of an internal clock synchronising nutrient assimilation and light harvest operating at species and community levels to mechanisms of defence against high light stress, polar macroalgae appear to be not as fragile as originally thought. However, some predictions on the disturbance of the community species composition are also discussed.

CONTENTS

INTRODUCTION

It has become widely accepted that the Arctic is the region where changes in climate, hydrography and ecology, related to global warming, are expected to be strongly expressed and, hence, the Arctic can serve as a primary site for research on global change and its consequences. However, there is still a debate on the relative importance of the disturbance caused by global warming with respect to the natural variability of the Arctic climate (MacDonald 1996; MacDonald *et al*. 1999; Venegas and Mysak 2000). The pan-Arctic shelves have experienced completely different states in the geologically recent past, separated by abrupt shifts. The immense changes in climatic forcing of the Arctic over relatively short evolutionary time scales suggests that its ecosystems are capable of coping with further climatic changes, even abrupt ones, but the range and survival of individual species is less certain (Carmack and Wassmann 2006). It seems evident that Artic shelves are likely to be particularly sensitive due to their shallowness, their seasonally variant sea-ice cover, which dominates major processes, and the influence of waters coming from oceans to the south. On the other hand, due to natural environmental disturbances in the past, they are also expected to be well adapted to extreme climatic variations in terms of resilience (Dayton 1990). But even given the increasingly evident resilience (Gordillo *et al*. 2006), a climate change so drastic to provoke a shift from abundant cold ice to limited warm ice will most likely have profound ecological consequences propagating through all trophic levels, as sea-ice dynamics is the prime physical factor driving marine Arctic biology from cellular physiology and biochemistry to food web and habitat structure (Piepenburg 2005). Adaptation and relocation of one species relative to another within the system may lead to fundamental changes in trophodynamic phasing, with major consequences on biogeochemical fluxes (Carmack and Wassmann 2006).

It is now known that deep Arctic temperatures have increased over the past 30 years (Dickson 1999). Reduced sea-ice cover will possibly lead to higher primary production, resulting in higher removal of atmospheric CO_2 and increased sequestration of carbon on the Arctic shelves. In addition, a possible decrease in stratification would also bring warmer water to the surface.

The aim of this review is to elucidate to what extent is the current macroalgal community ready to face these changes in the light of our actual knowledge on their ecophysiological plasticity, and predict the directions of presumed changes in species composition.

Invited Mini-Review

LESSONS FROM THE ANTARCTIC

The two polar coastal regions share some major characteristics. Temperature and light regimes are quite similar, as well as seasonal melting events of large ice masses that decrease the salinity of the waters where macroalgae develop. These characteristics are unique for Polar Regions, so that studies performed in one Polar Region are a useful reference to studies carried out in the other. But these similarities have a limit. There are also key factors differentiating both systems. In the Arctic, nutrients drop below detection limits during spring due mainly to phytoplanktonic blooms, and remain low until autumn (Aguilera *et al.* 2002). The Antarctic, however, is considered as virtually not limited by nutrients all year-round. This affects internal regulation and strategies of light harvesting and nutrient assimilation. The kelp-like *Himantothallus grandifolius* (Desmarestiales), endemic to the Antarctic, is largely restricted to the ice-free summer months (Drew and Hastings 1992), while the kelp *Laminaria solidungula*, endemic to the Arctic, stops its growth during N-depleted summer and accumulates carbon skeletons to grow later in winter once N becomes available (Henley and Dunton 1995). According to Korb and Gerard (2000a), *L. solidungula* can be considered a 'storage specialist' for nitrogen assimilation. Its high *Vmax* for nitrate, coupled with low growth rates allows Arctic plants to take advantage of seasonally elevated concentrations to accumulate large internal pools of nitrate and organic N-reserves. Antarctic *H. grandifolius*, in contrast, does not accumulate nitrate, so that N-uptake characteristics may be adapted to optimise energy consumption rather than N-assimilation. Preferential use of NH_4^+ over nitrate displayed by *H. grandifolius* (but not by *L. solidungula*) would add evidence of a energy-saving strategy (Korb and Gerard 2000a). It is then expected that these two different strategies will ultimately condition the ability to face a given environmental change.

LIGHT

The coastal areas of the Polar Regions suffer extreme changes in light conditions at different time scales (Hanelt *et al.* 2001). Seasonally, complete darkness for months in winter alternates with constant solar irradiance during the summer months. But also in the short term, episodes such as occasional ice presence and increased turbidity from inland ice melting reaching the coast condition the light environment for photosynthesis. In general, in the poles, when light is present, it is usually in excess of that needed by photosynthetic organisms. In Kongsfjorden (79º N), as in many other polar coastal sites, the break up of the ice cover coincides with the time of the year of highest solar radiation (Aguilera *et al.* 1999; Hanelt *et al.* 2001; Aguilera *et al.* 2002), provoking a drastic change in the environmental light condition below the water surface. Following this event, macroalgae show a general decrease in the content of chlorophyll *a* and other pigments of up to 50% (Aguilera *et al.* 2002), as well as a decrease in optimum quantum yield of photosynthesis (Bischof *et al.* 2002). Evolution of polar algae to cope with excess light involves at least two different strategies. On one hand, some species show a remarkably low light requirement to grow and complete their life cycle. The endemic Arctic *Laminaria solidungula* needs only 49 mol photons m^{-2} in a full year for completion of its life-cycle (Chapman and Lindley 1980). This adaptation is even more pronounced in the endemic Antarctic *Himantothallus grandifolius* and *Desmarestia anceps*, with a light requirement for completion of its life-cycle of only 31 mol photons m^{-2} (Wiencke 1990a, 1990b). This is about the same light dose that an upper intertidal species gets within 12-15 hours in the Arctic or within 1.3 days in the Mediterranean in summer. In this way, these species are able to inhabit deep waters, far from the excess light of clear summer days. In *H. grandifolius* and *D. anceps* growth can proceed at very low irradiance and is saturated

at 4 to 20 µmol m^{-2} s^{-1} (Wiencke and Fischer 1990). It has been shown that some species are able to tolerate complete darkness for periods of up to 1 year without suffering irreversible damage (Wiencke 1988, 1990a). In the Arctic location of Kongsfjord the 1% water depth for photosynthetically active radiation is about 18 m in spring and 7 m in summer (Hanelt *et al.* 2001) and *L. solidungula* is found below 30 m deep (Wiencke et al. 2004a). In the Antarctic, Gómez (1997) calculated from the photosynthetic performance of a number of macrolagae that some may well survive below 40 m deep, and samples were collected from 30 m with a measured *in situ* irradiance of 21 µmol m^{-2} s^{-1}.

A second strategy consists of an optimised ability to photoprotect the photosynthetic apparatus from excess light. Exposure to high light affects the convexity of the photosynthesis vs. irradiance (P-I) curves. These alterations are referred to as photoinhibition. It consists of at least two components: i) The regulated decrease in excitation energy transfer to Photosystem II (PS II) reaction centres; this affects the initial slope (α), the so-called photosynthetic efficiency. And ii) the inactivation and degradation of the reaction center D1 protein, which if beyond certain capacity of repair could ultimately be reflected in a lower maximum photosynthetic rate (P_{max}) (Gordillo *et al.* 2001a). The first process involves non-photochemical quenching regulated by the cell, and it depends on the dissipative mechanisms able to operate under excess light circumstances. The occurrence of this ability correlates with depth zonation of macroalgal species from both Polar Regions (Hanelt *et al.* 1997). In this sense, algae growing near the water surface are not expected to be severely stressed by an irradiance of 500 µmol photons m^{-2} s^{-1}, and are well adapted, maintaining their α, and their P_{max}. These species show a good ability to adapt to higher, excess irradiance (700-800 µmol photons m^{-2} s^{-1}), with rapid photosynthetic acclimation and high rates of recovery (Hanelt *et al.* 1997). Algae inhabiting middle and upper subtidal zones show slower recovery rates than their neighbours above and their P_{max} are not so resilient to excess light (Hanelt *et al.* 1997). In the lower intertidal zone, where excess light does not occur, algae show both decreased α and P_{max} and very low recovery rates, if any (Hanelt *et al.* 1997), so that in an event of excess light they would become easily photodamaged.

Since the referred study was performed using algae in culture and acclimated for a long time (more than 1 month) to laboratory conditions, it is presumed that the differential ability that species showed to cope with excess irradiance is a genetic adaptation.

One of the major components of global change is the increase in CO_2 concentration both in the atmosphere and the surface of the ocean. Recently, it has been found that CO_2 might also contribute to photoprotection under excess light conditions. Gordillo *et al.* (unpublished) found that midday photoinhibition can be alleviated by about 56 % in the presence of a CO_2-enriched environment in the upper intertidal *Ulva rigida* from the Mediterranean incubated under natural solar irradiance. We hypothesise that increased CO_2 might force Rubisco to carboxylate at a higher rate, increasing the demand of excitons from the light harvesting system, and so alleviating the excess of negative charges in the photosynthetic electron transport system. If this is also the case with Arctic macroalgae, the presence of a strong adaptation to overcome photoinhibition might not be so necessary in a CO_2-enriched world, and an invasion of species from temperate waters might become a threat to intertidal and upper subtidal species. In contrast, macroalgae inhabiting deep waters relying on low light requirements would not be threatened by invasive temperate species to the same extent as their neighbours above.

Further photoprotective mechanisms involve the level of interaction with other organisms. Thalli of some species such as the brown *Ascoseira mirabilis* are commonly found covered with epibiota which shade the photosynthetic cells. It is still to be determined whether this kind of interaction is an adaptation mechanism to overcome events of excess ir-

radiance in the Arctic.

A special case of photodamage is that produced by ultra-violet radiation (UVR). An increasing awareness of the environmental stress caused by increased levels of UVR due to global stratospheric ozone depletion has stimulated research on its impact on marine photosynthetic organisms. Most of the research in this field in Arctic macroalgae has been carried out by Wiencke et al. (e.g. 2004b). UVR represents a significant ecological threat for the survival of species and thereby for the health and diversity of marine coastal ecosystems. During early summer, when sea ice begins to break, biologically significant UV-B radiation has been reported to reach 8 m depth in Kongsfjorden, Svalbard (Hanelt et al. 2001). Enhanced UV-B radiation has been reported to cause severe effects on physiology and productivity of macroalgae, such as photoinhibition and eventual photodamage to the photosynthetic apparatus (Hanelt et al. 1997), photochemical degradation of biomolecules (Franklin and Forster 1997), formation of cyclobutane pyrimidine dimers in the DNA, inhibiting DNA replication (Wiencke et al. 2000), and production of reactive oxygen species responsible for oxidative damage of cell components (Rijstenbil et al. 2000; Aguilera et al. 2002). The sensitivity of the different species to UVR depends on their morphofunctional and physiological characteristics, their life strategies, phenology, and depth distribution (Bischof et al. 2002); the latter being more evident in the effects on photosynthesis (Aguilera et al. 1999). Species inhabiting shallow waters were more resistant than species inhabiting deeper waters (when exposed to the same UVR levels). Sensitivity can also vary with the season in some species. Bischof et al. (2002) reported that inhibition of photosynthesis by UVR in Laminaria saccharina and Saccorhiza dermatodea remained at the same level but in Desmarestia aculeata it decreased as spring progressed towards summer. In Monostroma arcticum photosynthetic sensitivity to UVR decreased during the study period (late winter-summer) reflecting the life strategy of this annual late winter/spring species. Some species are reported to defend against UVR by producing UV-absorbing compounds such as mycosporine-like amino acids (MAAs) and increasing the activity of the antioxidative system (catalase and superoxide dismutase), the latter also preventing damage from excess PAR radiation (Aguilera et al. 2002). In S. dermatodea and Alaria esculenta, the production of zoospores is accompanied with further UV defence mechanisms. At low zoospore density, they accumulate UV-absorbing compounds that can be released to the external medium. UV transmission through the spores is then decreased which is consistent with the observed enlarged phenolic vesicles triggered by UV exposure (Roleda et al. 2006a).

The physiological balance of the defence mechanisms, however, demands energy that in the absence of UVR is invested in growth. As a result, lower growth rates are recorded (Roleda et al. 2006b). But even that being the case, different species have developed different growth strategies that help to overcome, at least in part, the excess UVR occurring in clear middays. These strategies consist in growth compensation at night observed in Laminaria digitata, time-delayed growth during recovery in L. saccharina, and minimal but continuous growth throughout the light cycle in L. solidungula coupled with effective repair or defence mechanisms (Roleda 2006b).

TEMPERATURE

Temperature requirements for growth, reproduction and survival are the major factor responsible for determining geographical distribution boundaries of macroalgae: Northern distribution limits for Arctic cold-temperate species are determined by summer temperatures which are too low for growth and/or reproduction, whereas southern boundaries are set by either lethally high summer temperatures or extreme winter temperature (van den Hoek 1982a, 1982b; Breeman 1988, 1990). Marine algal floras have developed in the cold waters of Northern and Southern hemispheres as a result of the great glaciations that took place since the Tertiary (Lüning and Dieck 1989). In Antarctica, a cold water environment has prevailed for the last 25-30 Ma with a first glacial peak appearing some 14 Ma ago (Shulmeister et al. 2006). In contrast, in the North Polar Sea the cold environment began much later (about 2 Ma ago, Zahn et al. 1985). Temperate species were pushed southwards during the four glaciations periods, and recolonised northern zones in the interglacial periods as waters became warmer (Hempel 1987). As might be expected from the much longer existence of a cold environment in Antarctica with respect to the Arctic, there is a higher degree of endemism of macroalgae in the South Polar than in the North Polar Region (Lüning 1990; Kirst and Wiencke 1995; Bischoff-Bäsmann and Wiencke 1996; Voskoboinikov et al. 1996; Molenaar and Breeman 1997). Hence, a stenothermal flora (and fauna) developed in Antarctica, with high growth efficiency at low temperature and low tolerance to warm temperatures. In contrast, Arctic species remain relatively eurythermal, with their degree of tolerance to warm water temperature defining their biogeographical distribution (Bolton and Lüning 1982; Bolton 1983; Egan et al. 1990; Bischoff and Wiencke 1993). At least apparently, the eurythermal character of Arctic species should play in their favour in view of the forthcoming expected increase in water temperature. There are many species in the Arctic that also grow in cold-temperate regions. Young sporophytes of Desmarestia aculeata from Disko Island (Greenland) were unable to grow beyond 10ºC, while sporophytes from Helgoland grew up to 25ºC. So that Arctic specimens showed some degree of genetic adaptation in relation to growth as well as reproduction (Bischoff and Wiencke 1993). However it seems that temperature tolerance for survival is – in contrast to temperature requirements for growth and reproduction – a very conservative trait (Breeman 1988; Novaczek et al. 1989; Lüning 1990), which probably only changes over long evolutionary periods. If there is a major characteristic of the global change currently happening it is the speed at which it is happening. Hence, the pace of species adaptation to the new scenario may fall well below that needed for survival. Direct evidence of this already exists. Beuchel et al. (2006) have found that at least 45% of the variability of the benthic community in the period 1980-2003 was linked to variations in the North Atlantic Oscillation Index (NAOI) and its local manifestations in Kongsfjorden (Svalbard). The NAOI is the dominant signal of the interannual variability in the atmospheric circulation across the North Atlantic with a cyclical component of about 7.9 years. The NAOI is usually measured as the mean deviation from the average atmospheric sea level pressure between Iceland and the Azores. It influences the temperature and the current regime of the entire North Atlantic. The temperature of the West Spitsbergen Current (WSC) was a link between NAOI and the benthic community. Biodiversity was negatively correlated to NAOI; severe changes in the benthic community were observed between 1994 and 1996 coinciding with a shift in NAOI from positive to negative mode. The change in biodiversity was accompanied by a decline of actinarians and the appearance of dense carpets of brown algae (Beuchel et al. 2006). Some oceanographic models predict a further warming and broadening of the Atlantic layer in the Arctic Ocean, with a consequence being considerable increase in the retreat of sea ice in the near future (Washington and Meehl 1996; Zhang et al. 1998; Serreze et al. 2007).

Other aspects of temperature that, in principle, might be relevant to increased CO_2 and algal ecophysiology is the dissolved equilibrium concentration and the diffusion coefficients of CO_2 (Falkowski and Raven 1997). However, a lower concentration of CO_2 at higher temperature compensates for higher diffusion rates (Raven et al. 2002). The question is whether increasing the dissolved CO_2 at the low temperature of Polar Regions will be enough to saturate the carboxylating rate of Rubisco. Maintaining a CO_2-saturated rate of photosynthesis would require a three- to four-fold in-

crease in Rubisco content on a surface area basis when decreasing the temperature from 25ºC to 5ºC (Raven and Geider 1988). In temperate algae, acclimation to low temperature involves the maintenance of high concentrations of Calvin cycle enzymes (Davison 1987; Davison and Davison 1987; Davison *et al*. 1991). In the case that Rubisco is not saturated by environmental CO_2, two other strategies must be taken into account. One is the higher affinity for CO_2 at low temperature exhibited by some Rubiscos (Raven and Geider 1988; Beardall and Roberts 1999) and the other is the role played by an increased activity of external carbonic anhydrase (eCA) in Polar macroalgae as compared to temperate ones reported by Gordillo *et al*. (2006). External carbonic anhydrase catalyses the conversion of HCO_3^- into CO_2 (and *vice versa*). Theoretically, the impact of low temperature on photosynthesis of marine macrophytes is predicted to favour diffusive CO_2 entry rather than a CO_2-concentrating mechanism (Raven *et al*. 2002); however, the average value of eCA was much higher for Arctic species (19 REA g^{-1} FW) than those reported for macroalgae from more temperate waters, such as those from Australia (6.4 REA g^{-1} FW, Graham and Smillie 1976), Scotland (5.5 REA g^{-1} FW, Giordano and Maberly 1989), and Southern Spain (3.6 REA g^{-1} FW, Mercado *et al*. 1998). This is known as 'the Arctic paradox' of the Ci uptake system (Gordillo *et al*. 2006). This higher eCA activity might be part of the adaptation strategy which implies high concentrations of Calvin cycle enzymes referred by Davison (1987), which is also invoked to operate in Arctic macroalgae (Korb and Gerard 2000a, 2000b). As further evidence, increased eCA activity has recently been observed in macroalgae from a temperate environment as an acclimation to a drop in temperature (Gordillo, unpublished).

NUTRIENTS

Efficient use of low ambient irradiance for C-fixation requires a high concentration of pigments (Falkowski and Raven 1997), and maintenance of metabolic rates at near-freezing temperatures requires a high concentration of enzymatic proteins (Machalek *et al*. 1996), all of which contain nitrogen. Nitrogen has long been recognised to limit macroalgal productivity. Nutrient uptake and assimilation characteristics of macroalgae from temperate waters have been shown to vary among populations and species in ways that optimise survival and growth under local nutrient supply conditions (e.g. Wheeler and Weidner 1983; Hernández *et al*. 1993; Gordillo *et al*. 2001b). Arctic species are also reported to show nutritional strategies that allow them to cope with the long periods of darkness in winter and nutrient depletion in summer (Korb and Gerard 2000a, 2000b). Kelps living in the Arctic rely on stored photosynthates accumulated during the ice-free N-depleted summer period, supporting new growth during ice-covered N-sufficient winter. Traditionally, it was thought that this seasonal growth pattern was a direct consequence of N availability (Chapman and Lindley 1980) as well as light availability (Henley and Dunton 1997). However, it has become apparent that, at least in some species, this pattern is under the control of an endogenous free-running circannual rhythm entrained by a critical minimum daylengh in autumn (Lüning 1991; Schaffelke and Lüning 1994), suggesting that the addition of nitrate-N to summer N-limited kelps would have only a marginal effect on growth and biochemical composition, presumably due to the prevailing internal clock (Henley and Dunton 1997). Gordillo *et al*. (2006) confirmed that the effects of nutrient enrichment on biomass composition play only a marginal role also in a number of species from Kongsfjord (Svalbard). When thalli of 21 species were collected in summer and incubated for 2 days under nitrogen and phosphorus enrichment, the C:N ratio was only affected by a 7% in average. Lack of N accumulation and enhanced photosynthetic ability would be in agreement with the internal clock prevailing over external nutrient conditions, which in summer would promote active

photosynthesis over nutrient use, as mentioned above. The maintenance of a reasonably constant C:N ratio is a quite common priority for algae when acclimating to external nutritional disturbance. Different regulatory mechanisms have been proposed; for instance, organic carbon release has been shown to maintain the metabolic integrity of the cell (Fogg 1983; Ormerod 1983). According to Wood and van Valen (1990), organic carbon release would protect the photosynthetic apparatus from an overload of products that cannot be used for growth or stored. In the green seaweed *U. rigida*, this mechanism seems to be repressed in response to high environmental CO_2 level; thus maintaining the internal C:N balance (Gordillo *et al*. 2001c). It is unknown whether Arctic seaweeds are able to regulate the release of organic carbon, but they seem to maintain their metabolic integrity through a stable C:N ratio rather than accumulation of N-rich compounds during summer.

CONCLUDING REMARKS

The rapid warming affecting the Arctic will result in higher water temperature, increased fluvial run-off and reduced ice cover. All this will give rise to severe ecosystem changes propagating through all trophic levels (Piepenburg 2005). It is hypothesised that despite the number of strategies described in this review, resilience of Arctic macroalgal community will show a limit, threatening primarily the endemic species, which may not be able to adapt to the new conditions. On the other hand, the new scenario will see an invasion of cold-temperate species and a proliferation of the invasive nitrophilic and eurithermic ones already present, outcompeting some of the species inhabiting the upper and mid subtidal areas. If massive proliferation of opportunistic algae is to occur, it may condition the current hypothesis of a shift from benthic algae to phytoplankton dominance of carbon flux in the shelves and towards the pelagic seabed (Carroll and Carroll 2003). Rather than that, highly productive, fast-growing opportunistic species may increase the amount of organic carbon available in the seawater. But, even this latter effect being true for temperate macroalgae, it still needs to be corroborated experimentally in the Arctic.

Although increased knowledge on the ecological consequences of global change are generally regarded to be of high importance, the actual number of studies is currently very scarce. Experience has taught us that bulk processes and rates can only be well understood if there is a sound knowledge on the basic ecophysiology of the key species from an ecological point of view.

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