Benthic Diatoms in Arctic Seas –
Ecological Functions and Adaptations

by Ulf Karsten[1], Carolin Schlie[1], Jana Woelfel[1] and Burkhard Becker[2]

Abstract: Arctic coasts exhibit an enormous area of shallow water regions, which are dominated by unicellular benthic diatoms. These microalgae form a community known as microphytobenthos. Microphytobenthic biofilms cover extensive sediment areas and are responsible for high rates of primary production. They stabilize sediment surfaces against erodibility under flow conditions by the excretion of extracellular polymeric substances, thereby affecting the exchange of oxygen and nutrients across the sediment-water interface. Consequently, this community represents a key component in the functioning of Arctic trophic webs, particularly as a major food source for benthic suspension- or deposit-feeders.
Arctic benthic diatoms are confronted with pronounced seasonal variations of solar radiation, low temperatures, hyposaline (meltwater) conditions in summer, as well as long periods of ice and snow cover. From the few data available, it seems that these organisms can easily cope with such environmental extremes. Diatoms show a rather unusual photosynthetic flexibility providing optimum photoprotection and rapid photoacclimation under fluctuating and highly variable radiation conditions. In addition, some benthic diatoms are capable to vertically migrate into the sediment-microphytobenthos matrix, an efficient and energy-saving mechanism to avoid, for example, photodamage. These microalgae can survive the polar night, but the underlying processes are unknown. Although comprehensive data are still lacking, some studies indicate that Antarctic benthic diatoms are rather polar stenothermal and psychrophilic, while their Arctic pendants are more eurythermal and psychrotolerant. If these conspicuous differences in temperature requirements of both benthic diatom floras are underlined by more ecophysiological investigations, the data could be related to the different cold-water histories of the Arctic and Antarctica. If environmental changes such as the observed Arctic warming are negatively affecting the dark survival potential of benthic diatoms, their ecological function as important primary producers in polar regions may be strongly reduced. Climate change in the Arctic predicts other multifactorial stressors, such as increase in precipitation and permafrost thawing with consequences for the shallow water regions. However, complex factor interactions, as well as the full genetic diversity and physiological plasticity of Arctic benthic diatoms are still not deeply studied.

Zusammenfassung: Arktische Küsten weisen große Flachwassergebiete auf, welche von einzelligen benthischen Diatomeen dominiert werden, die eine als Mikrophytobenthos benannte Lebensgemeinschaft ausbilden. Mikrophytobenthische Biofilme bedecken riesige Sedimentflächen und tragen dort zu hohen Primärproduktionsraten bei. Sie stabilisieren die Sedimentoberflächen gegenüber strömungsbedingten Erosionsprozessen durch die Fähigkeit extrazelluläre polymere Substanzen zu exkretieren, wodurch der Austausch von Sauerstoff und Nährstoffen an der Sediment-Wasser-Grenzschicht beeinflusst wird. Aufgrund dieser besonderen Fähigkeiten übt diese Lebensgemeinschaft eine Schlüsselrolle in den trophischen Nahrungsbeziehungen der Arktis aus, insbesondere als wichtige Nahrungsquelle für benthische Suspensions- und Sedimentfresser.
Benthische Diatomeen der Arktis sind mit ausgeprägten saisonalen Variabilitäten der Sonnenstrahlung, niedrigen Temperaturen, hyposalinen Bedingungen aufgrund von Schmelzwasser im Sommer sowie langen Perioden einer Eis- und Schneebedeckung konfrontiert. Die wenigen verfügbaren Daten zeigen jedoch, dass diese Organismen mit solchen extremen Umweltbedingungen gut klar kommen. Diatomeen zeigen eine ungewöhnliche Flexibilität der Photosynthese, welche sowohl einen optimalen Schutz als auch eine schnelle Anpassung an fluktuierende und hoch variable Strahlungsbedingungen ermöglicht. Zusätzlich sind einige benthische Diatomeen befähigt

eine Vertikalwanderung in das Sediment durchzuführen, was beispielsweise einen effizienten und energiesparenden Mechanismus zur Vermeidung von Fotoschäden darstellt. Diese Mikroalgen überleben die Polarnacht, aber die zugrunde liegenden Prozesse sind unbekannt. Auch wenn nur wenige Studien vorliegen, so weisen benthische Diatomeen der Antarktis scheinbar stenotherme und psychrophile Verhaltensweisen auf, im Gegensatz zu den eher eurythermen und psychrotoleranten arktischen Vertretern. Diese offensichtlichen Unterschiede in den Temperaturansprüchen beider Diatomeen-Floren müssen durch weitere ökophysiologische Untersuchungen untermauert werden, lassen sich aber trotzdem mit den unterschiedlich langen Kaltwassergeschichten der Antarktis und Arktis erklären. Falls Umweltveränderungen wie die beobachtete Erwärmung der Arktis das Dunkel-Überlebenspotential benthischer Diatomeen negativ beeinflusst, dann wird deren ökologische Funktion als wichtige Primärproduzenten der Polargebiete stark beeinträchtigt. Klimaänderungen in der Arktis prognostizieren weitere multifaktorielle Belastungen wie erhöhte Niederschläge und ein Auftauen des Permafrost was eine starke Beeinträchtigung der Flachwassergebiete nach sich zieht. Jedoch sind solche komplexen Einflussgrößen, als auch die genetische Diversität und physiologische Plastizität der benthischen Diatomeen der Arktis bisher kaum untersucht.

INTRODUCTION

The Arctic Ocean includes all water bodies above the Arctic Circle (66° 33' N) and, thus, the area behind the approximate limit of the midnight sun and the polar night. It covers a total area >20 x 106 km^2 and about 25 % of the global coastal region (JAKOBSSON et al. 2008). The shelf area (depths of <200 m) of the Arctic is large and accounts for approximately 22 % of the global shelf area (MENARD & SMITH 1966). As a consequence, Arctic coastal regions are estimated to cover approximately 6 x 106 km^2 with an average water depth of 80 m (GATTUSO et al. 2006, JAKOBSSON et al. 2008). This enormous shallow water area is biologically very active as it is characterised by high biomasses and abundance of infaunal and epifaunal organisms (PIEPENBURG et al. 1995, SEJR et al. 2000), as well as by high benthic mineralisation processes (RYSGAARD et al. 1998). All of these heterotrophic organisms strongly depend on the activity of primary producers. Although pelagic and ice-related primary production can be high, it is of more seasonal and local significance, respectively (HSIAO 1988). In addition, efficient microbial turnover rates for carbon and nutrients have been documented in the Arctic water column (RYSGAARD et al. 1999), resulting in reduced sedimentation events of particulate organic material. Consequently, at many locations heterotrophic benthic organisms do not benefit from the primary production of phytoplankton and ice-algae, and hence have to rely on benthic primary producers as main food source (GLUD et al. 2002). The most abundant benthic primary producers in terms of biomass in the Arctic shallow water regions are represented by seaweeds such as kelps (WIENCKE 2004) and sediment-dwelling diatoms (GLUD et al. 2009). While kelps usually form high standing-stock biomass on hard substrata, benthic diatoms preferentially

_____

[1] Institute of Biological Sciences, Applied Ecology, University of Rostock, Albert-Einstein-Straße 3, D-18059, Rostock, Germany.
[2] University of Cologne, Cologne Biocenter, Botany, Otto-Fischer-Straße 6, D-50674 Cologne, Germany.

occupy sandy and muddy sediments.

ENVIRONMENTAL CONDITIONS

Arctic waters are characterised by pronounced seasonal variations of solar radiation and, as a consequence, of sea-ice cover and low temperatures. In coastal areas with high wave energy benthic communities are often strongly impacted by icebergs and accumulated sea ice. Multi-year sea ice can reach depths of about 40 m thereby scratch the sea floor, which may result in strong mechanical damage to benthic organisms (GUTT 2001). Benthic primary producers experience only short periods with sufficient photosynthetically active radiation (PAR, 400-700 nm) because of extended periods of darkness (polar night). The polar night lasts for about four months, and the annual solar radiation at 80° N is 30-50 % less compared to temperate and tropical regions, respectively. 80° N is the pole ward distribution limit of phototrophic organisms (LÜNING 1990). The extreme fluctuating radiation conditions in Arctic waters have strong implications for primary production and seasonal growth of benthic phototrophs. In addition, the long periods of darkness are further extended due to the formation of sea ice. If the ice is also covered by snow, irradiance can be diminished to less than 2 % of the surface value. Consequently, phototrophic benthic communities may be exposed up to about 10 months of darkness or very low radiation conditions (CHAPMAN & LINDLEY 1980, DUNTON 1990). After sea-ice break-up in spring, solar radiation penetrates deeply into the water column. UV-radiation (UVR, 280-400 nm) and blue light are, however, strongly attenuated in coastal waters because of the prevailing optical properties, which are influenced by particles and yellow substances. The 1 % depth for UVB (280-315 nm) radiation, which represents the approximate threshold irradiance of UVB with the potential to negatively affect primary plant productivity, is located between 4 and 8 m on Spitsbergen (HANELT et al. 2001). Deeper penetration depths for UVB can be measured, for example, in oligotrophic tropical waters (DUNNE & BROWN 1996). During summer, coastal water transparency in most Arctic regions strongly decreases due to the development of phytoplankton blooms and the inflow of melt water that typically carries fine sediment particles. With increasing turbidity, radiation quality shifts from blue to green wavebands in deeper waters (Jerlov 1976). Consequently, benthic primary producers are generally exposed to mainly low irradiances.

In contrast to such qualitatively and quantitatively variable radiation conditions, temperatures in shallow Arctic waters typically change only slightly between -1.8 °C in winter and about 5.0 °C in summer as reported for Kongsfjorden (Spitsbergen) (HANELT et al. 2001). However, any increase in water temperature, as predicted by global change scenarios, would affect marine organisms in the Arctic Ocean. The increase in near surface air temperature in the Arctic, which has been observed during the past 25 years (RIGOR et al. 2000), is accompanied by a decrease in annual average extent of sea ice (LUKOVICH & BARBER 2007). In addition, the influence of warmer Atlantic-derived water masses has also become stronger in the Arctic. Independent of the underlying mechanisms, the signals of a currently ongoing warming of the Arctic ocean are numerous (POLYAKOV et al. 2005).

During summer the inflow of melt water has strong effects on the salinity and temperature regime in inshore waters. During times of calm weather, stratified water bodies often occur with a layer of fresh water above a layer of denser sea-water. However, due to wave- and wind-induced vertical mixing also deeper water layers may become affected, and reductions in salinity down to about 20 m depth can be recorded as documented for Kongsfjorden, Spitsbergen (HANELT et al. 2001).

Macronutrients such as nitrogen and phosphorus show strong seasonality in Arctic waters. The European Arctic belongs to the most productive seas in the world (ORHEIM et al. 1995), because it obtains nutrient-rich water from the south during parts of the year via the so-called Spitsbergen Current. While nitrogen and phosphorus levels are relatively high in the water column during the winter months both macronutrients are almost fully depleted in summer after the phytoplankton blooms. In pore water of the sediments nutrient concentrations are generally much higher (approximately factor 5 to 10) than in the surrounding water column (WOELFEL et al. 2009), and these high amounts are available all around the year for benthic organisms. Consequently, benthic diatoms are generally expected not to experience strong nutrient-limitation, except during periods of highest primary production.

ECOLOGY OF BENTHIC DIATOMS

Benthic diatoms form an assemblage on top of sediments and other hard substrata known as microphytobenthos. Pelagic and benthic diatoms together represent one of the ecologically most important microalgal groups in the oceans. They strongly participate in the biogeochemical cycles of carbon, nitrogen, phosphorus and silicon, with a significant impact on global climate (WILHELM et al. 2006). Although evolutionarily with 250 million years relatively young, they dominate today phytoplankton and microphytobenthic communities. Diatoms contribute with about 20 % (FALKOWSKI & RAVEN 2007) to total global primary production, they exhibit an enormous biodiversity with at least 100,000 extant species (ROUND & CRAWFORD 1990) and their valves represent important geological proxies for paleoclimatic reconstructions.

Microphytobenthic communities are generally known from temperate to tropical marine shallow water regions as being highly productive and providing a major food source for benthic suspension- or deposit-feeders (CAHOON 1999). Further important ecological functions include those as biological filter for oxygen and other elemental fluxes at the sediment/water interface (RISGAARD-PETERSEN et al. 1994), and as stabiliser of sediment surfaces by the excretion of extracellular polymeric substances (DE BROUWER et al. 2005). Consequently, microphytobenthic diatom assemblages represent a key component in the functioning of trophic webs in many coastal regions. Some marine ecosystems, such as the German Wadden Sea, are mainly dependent on the production of benthic diatoms. However, structure and function of microphytobenthic communities are still not understood in Arctic waters (GLUD et al. 2009). In their review on Arctic microphytobenthos GLUD et al. (2009) came up with only ten peer-reviewed and three unpublished studies. Although based on a very small data set the authors nevertheless concluded that benthic diatoms contribute with up to 1.6 x 10^7 t C year^{-1} signi-

ficantly to coastal ecosystem production (down to 30 m depth) in the Arctic. GLUD et al. (2002) were one of the first to document by direct measurements high biomass and high primary production of microphytobenthic assemblages in the Young Sound, a high Arctic fjord at the northeastern coast of Greenland. In their study microphytobenthos accounted about 40 % of total benthic primary production (60 % derived from seaweeds) under polar conditions, indicating an ecologically important role for trophic relationships at these high latitudes. In addition, at most shallow water stations studied the benthic microphytic production exceeded the pelagic production rates by a factor of 1.5 for water depths between 0 and 30 m (GLUD et al. 2009).

Measured primary production rates of benthic diatoms in Arctic waters are similar to those in temperate waters despite lower water temperatures (GLUD et al. 2002, 2009, WOELFEL et al. 2010). Most interesting is the observation that the relatively high microphytobenthic primary production rates are not negatively affected by increasing water depth and hence decreasing radiation availability down to 30 m. Benthic and other diatoms are capable to quickly and flexibly optimise their photosynthetic apparatus to the prevailing irradiance conditions (GLUD et al. 2002, KARSTEN et al. 2006, WILHELM et al. 2006). Although the summer primary production rates of Arctic benthic microalgae may be high, the annual rates are low because of the long periods of radiation limitation. The ice-free summer of 90 to 120 days reflects undoubtedly the main period for benthic production. GATTUSO et al. (2006) estimated that 25 % of the Arctic coastal seabed on average received >1 % of the surface irradiance during the five summer month and that a much larger fraction can be expected to occasionally receive irradiance of this magnitude. So far, not much is known to what extent Arctic benthic diatoms are able to cope with prolonged periods of low or even lacking radiation.

Assuming 90 days of an open water period, the yearly benthic gross primary production extrapolated to the whole Arctic region amounts to 1.1-1.6 x 10^7 t C year^{-1} (GLUD et al. 2009). This number seems low when compared to the existing estimates on the pelagic production of the Arctic Ocean ranging from 21 to 42 x 10^7 t C year^{-1} (SUBBA RAO & PLATT 1984, GOSSELIN et al. 1997). However, most of the benthic primary production is confined to regions with water depths shallower than 30-40 m which accounts for only ~10-14 % of the Arctic Ocean, and in those coastal areas the relative benthic contribution is correspondingly higher.

Growing directly at the sediment surface microphytobenthic assemblages can exploit nutrients released by the underlying biogeochemical mineralization processes and can thus deprive the pelagic community of nutrients. In contrast, pelagic phototrophs can better exploit the down welling irradiance as compared to communities constrained to a narrow zone on the sediment surface. Consequently, nutrient availability often regulates the relative importance of pelagic versus the benthic microalgal productivity (GLUD et al. 2009). Eutrophic conditions favour pelagic production rates, while oligotrophic settings favour benthic production (CHARPY-ROUBAUD & SOURINA 1990, MACINTYRE et al 1996). Even though numerous rivers discharge nutrient-enriched water into the Arctic Ocean and thus stimulate pelagic production that locally reduces radiation availability for microphytobenthos (PARSONS & LALLI 1988, SPRINGER & MCROY 1993), Arctic coastal waters are generally pristine with low nutrient concentrations during summer.

ADAPTATIONS OF BENTHIC DIATOMS

Radiation acclimation

As described before, Arctic benthic diatoms generally live most of the time under low radiation conditions. However, these microalgae have been documented to adjust very efficiently their photosynthetic activity to current radiation conditions (KÜHL et al. 2001, WULFF et al. 2008, 2009). Photosynthesis in diatoms occurs in chloroplasts, which are endosymbiotic organelles derived during evolution from cyanobacteria. Since these eukaryotes acquired photosynthesis via endosymbiosis of another eukaryotic alga that already had plastids, the resulting organisms are chimaeras with major genomic contributions from two or even more sources (DELWICHE 2007). As a consequence of this genomic mixing the diatom lineage with specific and often unique physiological and biochemical properties evolved. Four diatom genomes have been sequenced so far (ARMBRUST 2009). The emerging picture is that the different species of diatoms are characterized by a complex combination of genes and metabolic pathways acquired from a variety of sources such as red algae, green algae, a chlamydial parasite and bacteria (ARMBRUST 2009). The consequences of this genetic mixture are reflected in specific biochemical capabilities. Diatoms, for example, combine an animal-like ability to generate chemical energy from the breakdown of fat with a plant-like ability to generate metabolic intermediates from this catabolic reaction (ARMBRUST 2009). Such a unique combination of a metabolic pathways probably allows diatoms to survive long periods of darkness in the polar regions or when temporarily buried in sediments. Numerous other examples of this mix-and-match compilation of characteristics reiterate the simple fact that diatoms are neither plant nor animals (ARMBRUST 2009).

The shade acclimation of benthic diatoms in Arctic shallow waters was exemplarily and experimentally documented by the low radiation requirements for growth in *Nitzschia* cf. *aurariae,* an abundant taxon, isolated from sediment cores of Kongsfjorden, Spitsbergen (Fig. 1). Under continuous irradiation this species exhibited already under 0.5 μmol photons m^{-2} s^{-1} a relatively high growth rate of 0.18 d-1 (Fig. 1). 4.6 μmol photons m^{-2} s^{-1} are equivalent to approximately 1 W m^{-2}, i.e. these values represent extremely low radiation conditions. A small rise to 3 μmol photons m^{-2} s^{-1} was accompanied by an almost 3-fold increase in growth (0.52 d^{-1}). Treatment with 10 μmol photons m^{-2} s^{-1} led only to a small additional stimulation of the growth rate up to the maximum value of 0.61 d^{-1}. Further increases of the photon fluence rate to 20, 40 and 60 μmol photons m^{-2} s^{-1} resulted in a linear decline of the growth response in *N. aurariae* (Fig. 1).

At 60 μmol photons m^{-2} s^{-1} growth was even inhibited. *Nitzschia* cf. *aurariae* exposed to the same photon fluence rates under a photoperiod of 16 h light and 8 h darkness showed a different picture. Under all photon fluence rates tested the growth rates were always higher compared to the continuously
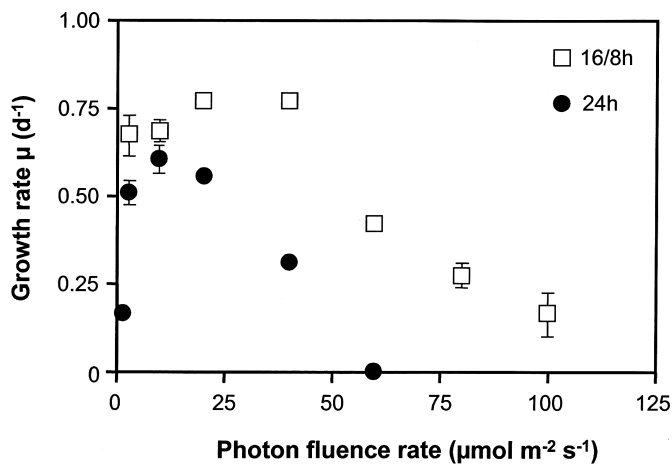
Fig. 1: The effect of increasing photon fluence rates on the growth rate of the benthic diatom *Nitzschia* cf. *aurariae* isolated from a sediment core of Kongs-fjorden, Spitsbergen. This species was kept at 15 °C under continuous radiation or a 16h:8h light dark cycle. Growth rates were measured as increase in chloro-phyll fluorescence according to GUSTAVS et al. (2009). Cells were grown in ste-rilized Baltic seawater enriched with sea salt (Sel marin hw professional, Wie-gandt GmbH, Krefeld, Germany), vitamins and silicate resulting in a salinity of 33 PSU. Data shown represent mean values ± SD (n = 3).

Abb. 1: Einfluss steigender Photonenfluenzraten auf das Wachstum der benthi-schen Diatomee *Nitzschia* cf. *aurariae,* die aus einem Sedimentkern aus dem Kongsfjord, Spitzbergen isoliert wurde. Diese Art wurde bei 15 °C im Dauer-licht oder einem 16h:8h Licht-Dunkel-Rhythmus gehältert. Die Wachstumsrate wurde über die Zunahme der Chlorophyll Fluoreszenz bestimmt nach GUSTAVS et al. (2009). Die Zellen wuchsen in sterilisierten Ostseewasser, welches mit Meersalz (Sel marin hw professional, Wiegandt GmbH, Krefeld, Deutschland), Vitaminen und Silikat auf eine Salinität von 33 PSU eingestellt wurde. Die dar-gestellten Daten entsprechen Mittelwerten ±SD (n = 3).

irradiated samples, i.e. the highest rate amounted for 0.77 d^{-1} (Fig. 1). In addition, the optimum shifted from 10 to 20-40 μmol photons m^{-2} s^{-1} (Fig. 1). Further increases in photon fluence rate were also accompanied by a continuous decline of the growth in *N. aurariae,* but the rates under all conditions were higher compared to continuous irradiation, and the cells still grew at 100 μmol photons m^{-2} s^{-1} with a rate of about 0.19 d^{-1} (Fig. 1). The dark phase is generally important for all repair processes of radiation-induced damages.

The data are in agreement with those on two *Fragilaria* species isolated as epiphytes from Arctic macroalgae. Both diatom taxa grew also optimally already at very low photon fluence rates of 10-20 μmol photons m^{-2} s^{-1}. Even at the lowest photon fluence rate tested (2 μmol photons m^{-2} s^{-1}), half of the maximum growth rate could be measured (KARSTEN et al. 2006). Support for the shade acclimation of the few benthic diatoms studied so far in polar areas comes also from the low radiation requirements for photosynthesis. The benthic diatom *Trachyneis aspera* was growing at ambient radiation of less than 0.6 μmol photons m^{-2} s^{-1} (the limit of detection for the radiometer used) with saturated photosynthetic rates (E$_k$ values) between 7 and 16 μmol photons m^{-2} s^{-1} (PALMISANO et al. 1985). This species can also be strongly photo-inhibited already at 6-10 μmol photons m^{-2} s^{-1} (RIVKIN & PUTT 1987). Hence benthic diatoms in virtue of their low radiation require-ments for photosynthesis, are capable to colonize deep bottoms at least down to 40 m (CAHOON 1999). In a more recent study by MCGEE et al. (2008), living benthic diatoms were found even down to 191 m water depth where the mid-day insolation averaged 0.1 μmol photons m^{-2} s^{-1}, representing <0.03 % of surface incident radiation.

The ability of Arctic benthic diatoms to acclimate not only to such extreme low-radiation conditions but also to high-radia-tion conditions has been shown in a number of studies mainly from Antarctica emphasising that polar benthic diatoms are very well adapted to fluctuating radiation conditions (WULFF et al. 2008). To cope with such highly variable radiation regime, diatoms have evolved various physiological mecha-nisms to guarantee photoprotection of their photosynthetic apparatus. Two processes for the regulation of a rapid switch from a light harvesting to a photoprotecting state have been reported in diatoms. One is the so-called non-photochemical fluorescence quenching. This mechanism involves the quench-ing of singlet excited state chlorophylls via enhanced internal conversion to the ground state of these pigments. As a consequence, excessively absorbed radiation energy is harm-lessly dissipated as heat through molecular vibrations (WILHELM et al. 2006). Non-photochemical fluorescence quenching in diatoms is tightly coupled to the diadinoxanthin cycle, a xanthophyll cycle that consists in the conversion, under an excess of radiation, of diadinoxanthin into its de-epoxidised form diatoxanthin, and vice versa under low radia-tion conditions or darkness (WILHELM et al. 2006). The second process is the cycling of electrons around photosystem II and/or photosystem I (WILHELM et al. 2006). This is attributed to an electron transfer pathway from the plastoquinone pool or the acceptor side of photosystem II to the donor side of photo-system II. This process is accelerated at excess irradiance (WILHELM et al. 2006). Both mechanisms guarantee the safe dissipation of excessively absorbed radiation energy during a sudden rise in the incident light field. Structure, biochemistry and regulation of the photosynthetic apparatus in diatoms show various specific peculiarities which may be related to the chimaeran character of these organisms as described before. The consequences seem to be reflected in a rather unusual photosynthetic flexibility providing optimum photoprotection and rapid photoacclimation under fluctuating and highly variable radiation conditions, all of which well explaining the ecological success of diatoms in the oceans.

Besides photoregulatory and photoprotective mechanisms many, but not all benthic diatoms exhibit also a behavioural capability in response to changes of the light field, i.e. they are able to vertically migrate in the sediment-microphytobenthos matrix. Migration into deeper sediment layer may be an effi-cient and energy-saving mechanism to avoid photoinhibition or even photodamage.
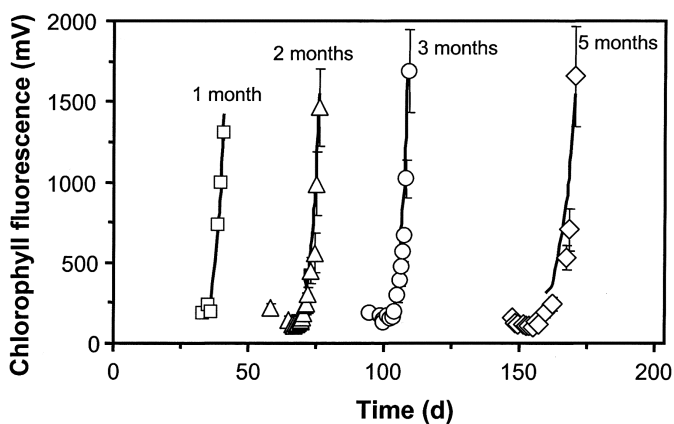
Dark survival potential

In addition to their low radiation requirements for growth and photosynthesis polar benthic diatoms exhibit also a pronounc-ed dark survival potential as they can live at least up to two months in complete darkness (WULFF et al. 2008), which may be beneficial when considering the polar night. In addition, benthic diatoms experience shifts to dark and partly anoxic conditions due to vertical migration into the sediment, and because of burial by bioturbating animals.

The photosynthetic apparatus of dark-incubated temperate pelagic diatoms seems to be impaired already after few weeks as is evident by a very long recovery phase after re-irradiation. In contrast, light harvesting for photosynthesis and growth can
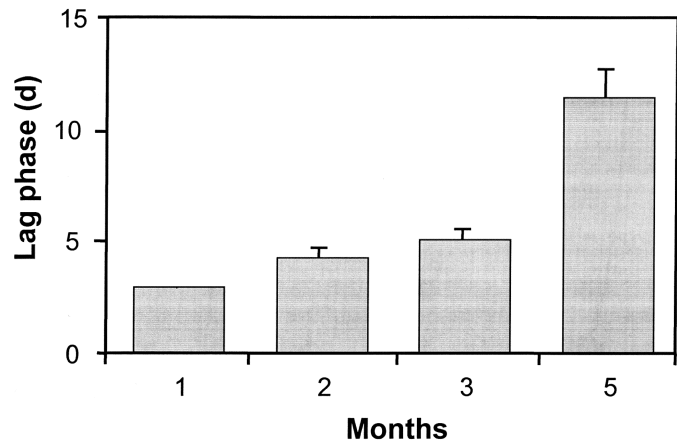
quickly resume in their Antarctic pendants after the polar night (PETERS & THOMAS 1996). There are also reports that the survival of temperate diatoms can be enhanced by lowering the dark incubation temperature (ANTIA 1976). However, a systematic investigation of temperature effects on dark survival periods in benthic diatoms from the Arctic and Antarctica is lacking.

Experiments on the dark survival potential were performed with the Arctic benthic diatom *Nitzschia* cf. *aurariae.* This species was kept for more than 5 months in darkness and sub-samples were re-irradiated each month under continuous low photon fluence rates (10-15 μmol photons m^{-2} s^{-1}). After 1, 2, 3 and 5 months dark incubation, *N. aurariae* exhibited within few days growth rates of μ = 0.2-0.4 d^{-1} in the light pointing to a high capability to withstand the polar night (Fig. 2). However, the longer the dark incubation time the longer the lag-phase before optimum growth could be established again (Fig. 3). After 1, 2 and 3 months darkness the lag-phase only slightly increased to 3, 4 and 5 days, respectively. However, after 5 months treatment, it took 11 days under re-irradiation before *N. aurariae* grew (Fig. 3). Other benthic diatom species from Arctic waters such as *Fragilaria striatula* showed a 30-40 % reduction in chloroplast lengths after 3 months of dark incubation at 5 °C, indicating the recruitment of energy for a maintenance metabolism through decomposition of organelle components (data not shown). Since the dark survival strategies of Arctic benthic diatoms are badly understood, a comprehensive and precise evaluation of the underlying mechanisms is currently carried out by the authors in the frame of a project funded by the Deutsche Forschungsgemeinschaft (DFG). The mechanisms to be studied include the determination of the maximum survival period using various cell biological

Fig. 3: Lag-phase for regain of growth in *Nitzschia* cf. *aurariae* isolated from a sediment core of Kongsfjorden, Spitsbergen. Cells were kept at 5 °C for 1, 2, 3 and 5 months in darkness followed by re-irradiation with low photon fluence rates (10-15 μmol photons m^{-2} s^{-1}). Growth rates were measured as increase in chlorophyll fluorescence according to GUSTAVS et al. (2009). Cells were grown in sterilized Baltic seawater enriched with sea salt (Sel marin hw professional, Wiegandt GmbH, Krefeld, Germany), vitamins and silicate resulting in a salinity of 33 PSU. Data represent mean values ±SD (n = 3).

Abb. 3: Lag-Phase (Verzögerungsphase) für das Wiedererlangen des Wachstums von *Nitzschia* cf. *aurariae,* die aus einem Sedimentkern aus dem Kongsfjord, Spitsbergen isoliert wurde. Die Zellen wurden bei 5 °C für 1, 2, 3 und 5 Monate in Dunkelheit gehältert, und anschließend mit niedrigen Photonenfluenzraten wiederbestrahlt (10-15 μmol Photonen m^{-2} s^{-1}). Die Wachstumsrate wurde über die Zunahme der Chlorophyll Fluoreszenz bestimmt nach GUSTAVS et al. (2009). Die Zellen wuchsen in sterilisierten Ostseewasser, welches mit Meersalz (Sel marin hw professional, Wiegandt GmbH, Krefeld, Deutschland), Vitaminen und Silikat auf eine Salinität von 33 PSU eingestellt wurde. Die dargestellten Daten entsprechen Mittelwerten ±SD (n = 3).

markers as well as genetic markers using a transcripttomic approach such as the expression of functional genes involved in the degradation of storage compounds. The main question is to evaluate whether environmental changes such as the observed Arctic warming are indeed negatively affecting the dark survival potential of benthic diatoms, which would strongly reduce their ecological function as important primary producers with consequences for all higher trophic levels.

A new bacterial-like mechanism explaining how benthic diatoms may survive long periods of darkness was recently suggested by KAMP et al. (2011). These authors revealed a strong correlation between the dark survival potential and the ability to intracellularly accumulate NO_{3-}. The stored NO_{3-} is dissimilatorily reduced to ammonium in darkness, i.e. the diatoms seem to be capable to respire nitrate to keep their maintenance metabolism.

Fig. 2: Dark survival potential of *Nitzschia* cf. *aurariae* isolated from a sediment core of Kongsfjorden, Spitsbergen. Cells were kept at 5 °C for 1, 2, 3 and 5 months in darkness followed by re-irradiation with low photon fluence rates (10-15 μmol photons m^{-2} s^{-1}). Growth rates were measured as increase in chlorophyll fluorescence according to GUSTAVS et al. (2009). Cells were grown in sterilized Baltic seawater enriched with sea salt (Sel marin hw professional, Wiegandt GmbH, Krefeld, Germany), vitamins and silicate resulting in a salinity of 33 PSU. Data represent mean values ±SD (n = 3).

Abb. 2: Das Dunkelüberlebenspotential von *Nitzschia* cf. *aurariae,* die aus einem Sedimentkern aus dem Kongsfjord, Spitsbergen isoliert wurde. Die Zellen wurden bei 5 °C für 1, 2, 3 und 5 Monate in Dunkelheit gehältert, und anschließend mit niedrigen Photonenfluenzraten wiederbestrahlt (10-15 μmol Photonen m^{-2} s^{-1}). Die Wachstumsrate wurde über die Zunahme der Chlorophyll Fluoreszenz bestimmt nach GUSTAVS et al. (2009). Die Zellen wuchsen in sterilisierten Ostseewasser, welches mit Meersalz (Sel marin hw professional, Wiegandt GmbH, Krefeld, Deutschland), Vitaminen und Silikat auf eine Salinität von 33 PSU eingestellt wurde. Die dargestellten Daten entsprechen Mittelwerten ±SD (n= 3).

Temperature acclimation

Benthic diatoms in polar waters are preferentially growing in the subtidal on top of sediments at low, but relatively constant temperatures. As far as we know today, the temperature demand for growth of Arctic benthic diatoms is somewhat higher compared with endemic Antarctic species. Two *Fragilaria* species from the Arctic Kongsfjorden (Spitsbergen) with optimum growth rates at 12-14 °C grew still well but with reduced rates at 0 °C and did not survive 20 °C (KARSTEN et al. 2006). Similarly, *N. aurariae* from the same location grew between 5 and 15 °C, did not grow at 0 °C and died at 23 °C (Fig. 4). The optimum growth temperature of *N. aurariae* was
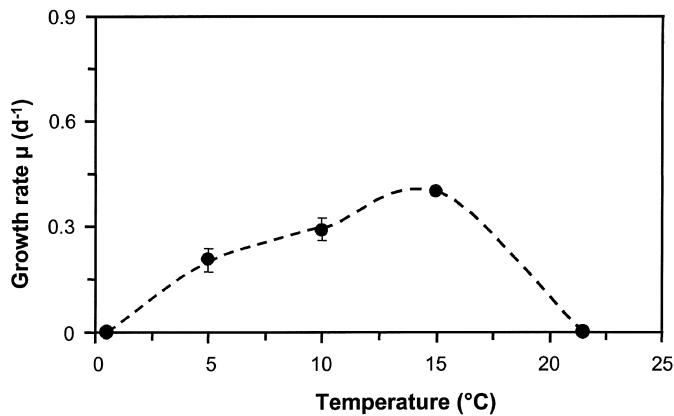
Fig. 4: The effect of increasing temperatures on the growth rate of the benthic diatom *Nitzschia* cf. *aurariae* isolated from a sediment core of Kongsfjorden, Spitsbergen. Growth rates were measured as increase in chlorophyll fluorescence according to Gustavs et al. (2009). Cells were grown in sterilized Baltic seawater enriched with sea salt (Sel marin hw professional, Wiegandt GmbH, Krefeld, Germany), vitamins and silicate resulting in a salinity of 33 PSU, and kept at 50 μmol photons m^{-2} s^{-1} under a 16:8h light:dark cycle. Data represent mean values ±SD (n = 3) and were fitted according to the model of Blanchard (1996).

Abb. 4: Einfluss steigender Temperaturen auf das Wachstum der benthischen Diatomee *Nitzschia* cf. *aurariae,* die aus einem Sedimentkern aus dem Kongsfjord, Spitzbergen isoliert wurde. Die Wachstumsrate wurde über die Zunahme der Chlorophyll Fluoreszenz bestimmt nach Gustavs et al. (2009). Die Zellen wuchsen in sterilisierten Ostseewasser, welches mit Meersalz (Sel marin hw professional, Wiegandt GmbH, Krefeld, Deutschland), Vitaminen und Silikat auf eine Salinität von 33 PSU eingestellt wurde, und bei 50 μmol Photonen m^{-2} s^{-1} unter einem 16h:8h Licht-Dunkel-Rhythmus gehältert. Die dargestellten Daten entsprechen Mittelwerten ±SD (n = 3) und wurden nach dem Model von Blanchard (1996) gefittet.

at 15 °C, which clearly points to moderate temperature requirements.

Based on available data, Arctic benthic diatoms can be characterised as eurythermal and psychrotolerant microalgae (organisms tolerant of low growth temperatures). This seems to be in sharp contrast to a related Antarctic taxon, *Odontella litigiosa,* which typically exhibited maximum growth at 0 °C and full inhibition of cell division already at 7-9 °C (Longhi et al. 2003). Consequently, this studied Antarctic benthic diatom showed polar stenothermal and psychrophilic features (organisms with a requirement for low growth temperatures). Whether other Arctic and Antarctic benthic diatoms follow the respective temperature demand for growth is unknown, but already Wiencke & tom Dieck (1989, 1990) reported extremely low temperature requirements for growth and survival in macroalgae endemic to Antarctica compared to more temperate regions. Although the number of available data is small, it can be speculated that the conspicuous differences in the temperature requirements for growth in Arctic and Antarctic benthic diatoms are related to the much longer isolation and cold water history of the Southern polar region (at least 14 million years) compared to the Northern high latitudes (approximately 3.5 million years) (Longhi et al. 2003), i.e. a longer exposure time and a higher degree of endemism in Antarctica. While the Antarctic benthic diatom taxa investigated are indeed characterised as endemic species, the respective information on strains from the Arctic is still missing. It is even still unclear, whether endemic Arctic benthic diatoms actually exist.

Diatoms obligatorily or facultatively associated to sea-ice are

able to withstand and partly even to grow at extremely low temperatures of -15 °C (Mock & Gradinger 1999). To successfully colonise low-temperature environments, polar benthic diatoms have developed a range of adaptive strategies. Such cold adaptation is required for the maintenance of all enzymatic activities. The photosynthetic key enzyme ribulose-1,5-bisphosphate carboxylase/oxygenase (RUBISCO), for example, has a poor catalytic efficiency at low temperatures, which, however, can be overcome by an increase in enzyme concentration (Devos et al. 1998), a phenomenon known as quantitative strategy (Lesser & Kruse 2004). Other adaptive mechanisms to low temperatures include the evolution of cold shock and antifreeze proteins, the modulation of the kinetics of key enzymes as well as the development of more fluid biological membranes by the accumulation of polyunsaturated fatty acyl chains (Morgan-Kiss et al. 2006). In association with some sea-ice diatoms, such as *Navicula glaciei,* extracellular, secreted proteins are described to have an affinity for ice crystals (Janech et al. 2006, Raymond & Fritsen 2001). Ice-binding proteins do not lower the freezing point. They rather seem to prevent membrane damages by inhibiting the recrystallisation of ice and, hence, may act as effective structural cryoprotectants (Janech et al. 2006). Various benthic diatoms from polar waters are known to contain high concentrations of low-molecular weight solutes acting as organic anti-freezing substances such as the amino acid proline (Thomas & Diekmann 2002).

Salinity acclimation

In contrast to the relatively constant salinity throughout all open oceans, it may strongly vary in Arctic near-shore waters where river freshwater or melt water particularly during summer mixes with marine water bodies. Here horizontal and vertical gradients between freshwater and fully marine conditions can be measured. In addition, tidal flows, hydrological conditions, wind, precipitation and evaporation strongly influence salt concentration of the respective water body. Consequently, salinity is typically a local and in the Arctic a seasonal parameter that can be highly variable in coastal regions. The effect of salinity on benthic diatoms and other algae from Arctic and Antarctic waters is generally badly studied in strong contrast to temperate regions (Kirst & Wiencke 1995). While temperate algae from the intertidal zone are generally euryhaline, subtidal organisms are more stenohaline.

The Arctic *Nitzschia* cf. *aurariae* grew between 15 and 45 PSU (Fig. 5). While the growth rates were maximal between 20 and 40 PSU with a preference for slightly hyposaline conditions, growth was inhibited at 10 and 50 PSU (Fig. 5). This species exhibited a growth patterns under the different salinities, which can be characterised as moderate euryhaline. The underlying mechanisms, such as osmotic acclimation, have not been studied so far in Arctic benthic diatoms. In contrast, ice-associated diatoms trapped in the brine channels may experience salinities three times that of seawater. These algae synthesise and accumulate high concentrations of the organic osmolytes and compatible solutes proline, mannitol, glycine-betaine and/or dimethyl sulphoniopropionate (DMSP) in response to hypersaline conditions (Thomas & Dieckmann 2002).
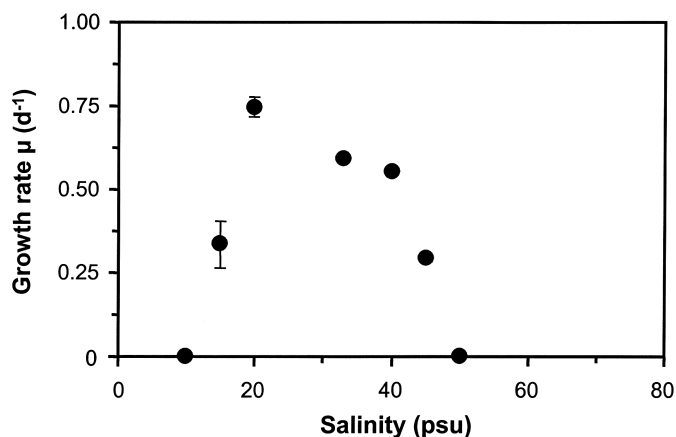
Fig. 5: The effect of increasing salinities on the growth rate of the benthic diatom *Nitzschia* cf. *aurariae* isolated from a sediment core of Kongsfjorden, Spitsbergen. Cultures were incubated at continuous 50 μmol photons m^{-2} s^{-1} and 15 °C. Growth rates were measured as increase in chlorophyll fluorescence according to GUSTAVS et al. (2009). Cells were grown in sterilized Baltic seawater enriched with sea salt (Sel marin hw professional, Wiegandt GmbH, Krefeld, Germany), vitamins and silicate or diluted with distilled water resulting in different saline media. Data shown represent mean values ±SD (n =5).

Abb. 5: Einfluss steigender Salzgehalte auf das Wachstum der benthischen Diatomee *Nitzschia* cf. *aurariae,* die aus einem Sedimentkern aus dem Kongsfjord, Spitzbergen isoliert wurde. Kulturen wurden unter Dauerstrahlung bei 50 μmol Photonen m^{-2} s^{-1} und 15 °C gehältert. Die Wachstumsrate wurde über die Zunahme der Chlorophyll Fluoreszenz bestimmt nach Gustavs et al. (2009). Die Zellen wuchsen in sterilisierten Ostseewasser, welches mit Meersalz (Sel marin hw professional, Wiegandt GmbH, Krefeld, Deutschland), Vitaminen und Silikat auf verschiedene Salinitäten aufgesalzen oder mit destillierten Wasser verdünnt wurde. Die dargestellten Daten entsprechen Mittelwerten ±SD (n = 3).

CONCLUSION AND OUTLOOK

The shallow water region of the Arctic Ocean is dominated by benthic diatoms, which are ecologically very important because of their high primary production during polar day and further functions. However, the entire Arctic region is grossly under-sampled and hence further field studies are urgently needed, particularly in the huge Russian sector.

From the few data available on their physiological performance, it can be concluded that these microalgae can easily cope with very low and high as well as variable radiation conditions. Photosynthesis and growth can quickly be adapted and follow the prevailing photon fluence rates. This pronounced photophysiological flexibility well explains survival and performance under the often radiation-limiting and radiation-fluctuating conditions in the Arctic. On the other hand, sudden exposure to high irradiances can also be compensated by photoprotective and, in some species, behavioural (vertical migration) mechanisms. In addition, Arctic benthic diatoms seem to be capable to survive the polar night. However, the underlying biochemical and molecular mechanisms are not well understood. If environmental changes, such as the observed Arctic warming, are negatively affecting the dark survival potential of benthic diatoms during the polar night, their ecological functions might be strongly reduced.

The few Arctic benthic diatoms studied in detail typically exhibit temperature requirements for growth between 10 and 15 °C and, thus, can be characterised as polar eurythermal organisms. In contrast, their Antarctic pendants can be charac-terised as polar stenothermal species. If these typical differences in the temperature requirements of benthic diatoms from Arctic and Antarctic waters can be confirmed by more comprehensive studies, they could be explained by the much shorter cold water history of the Northern polar region in conjunction with a low degree of endemism compared to the Southern high latitudes.

The sea-ice cover in the Arctic is rapidly declining (SERREZE et al. 2007) and given the tight coupling between sea-ice cover and marine primary production (RYSGAARD et al. 1999) this is expected to stimulate Arctic production. ARRIGO et al. (2008) estimated that the pelagic production of the Arctic Ocean has enhanced by 5-6 % annually in recent years as a consequence of the increased radiation availability. Increased radiation availability is expected to further rise the competition for nutrients and it is reasonable to speculate that benthic primary production may consequently be stimulated significantly more than the pelagic production in the Arctic coastal region (GLUD et al. 2009). However, climate change confronts Arctic shallow water regions with multifactorial stressors, such as predicted increase in precipitation and permafrost thawing. Both will surely increase nutrient-enriched, turbid freshwater runoff and may locally counteract the expected increase in coastal radiation availability. So far complex factor interactions, as well as the full genetic diversity and physiological plasticity of Arctic benthic diatoms are rarely considered.

References

Antia, N.J. (1976): Effects of temperature on the darkness survival of marine microplanktonic algae.- Microb. Ecol. 3: 41-54.
Armbrust, E.V. (2009): The life of diatoms in the world's oceans.- Nature 459: 185-191.
Arrigo, K.R., van Dijken, G. & Pabi, S. (2008): Impact of a shrinking Arctic ice cover on marine primary production.- Geophys. Res. Lett. 35: 1-6.
Cahoon, L.B. (1999): The role of benthic microalgae in neritic ecosystems.- Oceanogr. Mar. Biol. Annu. Rev. 37: 47-86.
Chapman, A.R.O. & Lindley, J.E. (1980): Seasonal growth of Laminaria longicruris in the High Arctic in relation to irradiance and dissolved nutrient concentration.- Mar. Biol. 57: 1-5.
Charpy-Roubaud, C. & Sourina, A. (1990): The comparative estimation of phytoplanktonic, microphytobenthic and macrophytobenthic primary production in the oceans.- Mar. Microb. Food webs 4: 31-57.
DeBrouwer, J.F.C., Wolfstein, K., Ruddy, G.K., Jones, T.E.R. & Stal, L.J. (2005): Biogenic stabilization of intertidal sediments: the importance of extracellular polymeric substances produced by benthic diatoms.- Microb. Ecol. 49: 501-512.
Delwiche, C.F. (2007): Algae in the warp and weave of life: bound by plastids.- In: J. Brodie & J. Lewis (eds), Unravelling the algae – the past, present, and future of algal systematics, CRC Press, 7-20.
Devos, N., Ingouff, M., Loppes, R. & Matagne, R.F. (1998): RUBISCO adaptation to low temperatures: a comparative study in psychrophilic and meso-

philic unicellular algae.- J. Phycol. 34: 655-660.

Dunne, R.P. & Brown, B.E. (1996): Penetration of solar UVB radiation in shallow tropical waters and its potential biological effects on coral reefs; results from the central Indian Ocean and Andaman Sea.- Mar. Ecol. Prog. Ser. 144: 109-118.

Dunton, K.H. (1990): Growth and production in Laminaria solidungula: relation to continuous underwater light levels in the Alaskan high Arctic.- Mar. Biol. 106: 297-304.

Falkowski, P.G. & Raven, J.A. (2007): Aquatic Photosynthesis.- Princeton University Press.

Gattuso, J.P., Gentili, B., Duarte, C.M., Kleypas, J.A., Middelburg, J.J. & Antoinne, D. (2006): Light availability in the coastal Ocean: impact on the distribution of benthic photosynthetic organisms and their contribution to primary production.- Biogeosci. 3: 489-513.

Glud, R.N., Kühl, M., Wenzhöfer, F. & Rysgaard, S. (2002): Benthic diatoms of a high Arctic fjord (Young Sound, NE Greenland): importance for ecosystem primary production.- Mar. Ecol. Prog. Ser. 238: 15-29.

Glud, R.N., Woelfel, J., Karsten, U., Kühl, M. & Rysgaard, S. (2009): Benthic microalgal production in the Arctic: Applied methods and status of the current database.- Bot. Mar. 52: 559-571.

Gosselin, M., Levasseur, M., Wheeler, P.A., Horner, R.A. & Booth, B.C. (1997): New measurements of phytoplankton and ice algal production in the Arctic Ocean.- Deep Sea Res. Part II 44:1623-1644.

Gustavs, L., Schumann, R., Eggert, A. & Karsten, U. (2009): In vivo growth fluorometry: accuracy and limits of microalgal growth rate measurements in ecophysiological investigations.- Aquat. Microb. Ecol. 55: 95-104.

Gutt, J. (2001): On the direct impact of ice on marine benthic communities, a review.- Polar Biol. 24: 553-564.

Hanelt, D., Tüg, H., Bischof, K., Gross, C., Lippert, H., Sawall, T. & Wiencke, C. (2001): Light regime in an Arctic fjord: a study related to Stratospheric Ozone depletion as a basis for determination of UV effects on algal growth.- Mar. Biol. 138: 649-658.

Hsiao, S.I.C. (1988): Spatial and seasonal variations in primary production of sea-ice microalgae and phytoplankton in Frobisher Bay, Arctic Canada.- Mar. Ecol. Prog. Ser. 44: 275-285.

Jakobsson, M.R., Macnab, R., Mayer, L., Andersson, R., Edwards, M., Hatzky, J., Schenke, H.W. & Johnson, P. (2008): An improved bathymetric portrayal of the Arctic Ocean: implications for ocean modeling and geological, geophysical and oceanographic analysis.- Geophys. Res Let: doi: 10.1029/2008/2008g1033520

Janech, M.G., Krell, A., Mock, T., Kang, J.S. & Raymond, J.A. (2006): Ice-binding proteins from sea ice diatoms (Bacillariophyceae).- J. Phycol. 42: 410-416.

Jerlov, N.G. (1976): Marine optics.- Elsevier, Amsterdam.

Kamp, A., de Beer, D., Nitsch, J.L., Lavik, G. & Stief, P. (2011): Diatoms respire nitrate to survive dark and anoxic conditions.- Proc. Nat. Acad. Sci. doi/10.1073/pnas.1015744108

Karsten, U., Schumann, R., Rothe, S., Jung, I. & Medlin, L. (2006): Temperature and light requirements for growth of two diatom species (Bacillariophyceae) isolated from an Arctic macroalga.- Polar Biol. 29: 476-486.

Kirst, G.O. & Wiencke, C. (1995): Ecophysiology of polar algae.- J. Phycol. 31: 181-199.

Kühl, M., Glud, R.N., Borum, R., Roberts, R. & Rysgaard, S. (2001): Photosynthetic performance of surface-associated algae below sea ice as measured with a pulse-amplitude-modulated (PAM) fluorometer and O2 microsensors.- Mar. Ecol. Prog. Ser. 223: 1-14.

Lesser, M.P & Kruse, V.A. (2004): Seasonal temperature compensation in the horse mussel, Modiolus modiolus: metabolic enzymes, oxidative stress and heat shock proteins.- Comp. Biochem. Physiol., A: Mol. Integr. Physiol. 137: 495-504.

Longhi, M.L., Schloss, I.R. & Wiencke, C. (2003): Effect of irradiance and temperature on photosynthesis and growth of two Antarctic benthic diatoms, Gyrosigma subsalinum and Odontella litigiosa.- Bot. Mar. 46: 276-284.

Lüning, K. (1990): Seaweeds. Their environment, biogeography and ecophysiology.- John Wiley, Sons, Inc., New York, 1-527.

Lukovich, J.V. & Barber, D.G. (2007): On the spatiotemporal behaviour of sea ice concentration anomalies in the Northern hemisphere.- J. Geophys. Res. (D Atmos.), 112: no D13.

MacIntyre, H.L., Geider, R.J. & Miller, D.C. (1996): Microphytobenthis: the ecoloical role of the "secret garden" of unvegetated, shallow-water marine habitats. I. Distribution, abundance and primary production.- Estuar. 19: 186-201.

McGee, D., Laws, R.A. & Cahoon, L.B. (2008): Live benthic diatoms from the upper continental slope: extending the limits of marine primary production.- Mar. Ecol. Prog. Ser. 356: 103-112.

Menard, H. & Smith, S.M. (1966): Hypsometry of ocean basin provinces.- J. Geophys. Res. 71: 4305-4325.

Mock, T. & Gradinger, R. (1999): Determination of Arctic ice algae production with a new in situ incubation technique.- Mar. Ecol. Prog. Ser. 177: 15-26.

Mock, T. & Valentin, K. (2004): Photosynthesis and cold acclimation – molecular evidence from a polar diatom.- J. Phycol. 40: 732-741.

Morgan-Kiss, R.M., Priscu, J.C., Pocock, T., Gudynaite-Savitch, L. & Huner, N.P.A. (2006): Adaptation and acclimation of photosynthetic microorganisms to permanently cold environments.- Microbiol. Mol. Biol. Rev. 70: 222-252.

Orheim, O., Allegrini, I., Boissonnas, J., Drewry, D., Gascard, J.C., Hedberg, D., Müller-Wille, L., Prestrud, P., Sors, A. & Tilzer, M. (1995): European research in the Arctic – looking ahead.- Norsk Polarinstitutt, Oslo.

Palmisano, A.C., Soohoo, J.B., White, D.C., Smith, G.A., Stanton, G.A. & Burckle, G.R. (1985): Shade adapted benthic diatoms beneath Antarctic sea ice.- J. Phycol. 21: 664-667.

Parsons, T.R. & Lalli, C.M. (1988): Comparative oceanic ecology of the plankton communities of the Subarctic Atlantic and Pacific Oceans.- Oceanogr. Mar. Biol. Ann. Rev. 26: 317-359.

Peters, E. & Thomas, D.N. (1996): Prolonged darkness and diatom mortality. I: Marine Antarctic species.- J. Exp. Mar. Biol. Ecol. 207: 25-41.

Piepenburg, D., Blackburn, T.H., von Dorrien, C.F., Gutt, J., Hall, P.O.J., Hulth, S., Kendall, M.A., Opalinski, K.W., Rachor, E. & Schmid, M.K. (1995): Partitioning of benthic community respiration in the Arctic (northwestern Barents Sea).- Mar. Ecol. Prog. Ser. 118: 199-213.

Polyakov, I.V., Beszczynska, A., Carmack, E.C., Dmitrenko, I.A., Fahrbach, E., Frolov, I.E., Gerdes, R., Hansen, E., Holfort, J., Ivanov, V.V., Johnson, M.A., Karcher, M., Kauker, F., Morison, J., Orvik, K.A., Schauer, U., Simmons, H.L., Skagseth, Ø., Sokolov, V.T., Steele, M., Timokhov, L.A., Walsh, D. & Wals, J.E. (2005): One more step toward a warmer Arctic.- Geophys. Res. Let. 32: L17605, doi:10.1029/2005GL023740.

Raymond, J.A. & Fritsen, C.H. (2001): Semipurification and ice recrystallization inhibition activity of ice-active substances associated with Antarctic photosynthetic organisms.- Cryobiol. 43: 63-70.

Rigor, I.G., Colony, R.L. & Martin, S. (2000): Variations in surface air temperature observations in the Arctic, 1979-97.- J. Climate 13: 896-914.

Risgaard-Petersen, N., Rysgaard, S., Nielsen, L.P. & Revsbech, N.P. (1994): Diurnal variation of dentrification and nitrification in sediments colonized by benthic microphytes.- Limnol. Oceanogr. 39: 573-579.

Rivkin, R.B. & Putt, M. (1987): Photosynthesis and cell division by Antarctic microalgae: comparision of benthic, planktonic and ice algae.- J. Phycol. 23: 223-229.

Round, F.E. & Crawford, R.M. (1990): The Diatoms. Biology and Morphology of the Genera.- Cambridge University Press, UK, xx-xx.

Rysgaard, S., Thamdrup, B., Risgaard-Petersen, N., Fossing, H., Berg, P., Bondo, P.B. & Dalsgaard, T. (1998) Seasonal carbon and nutrient mineralisation in a high-Arctic coastal marine sediment, Young Sound, NE Greenland.- Mar. Ecol. Prog. Ser. 175: 261-276.

Rysgaard, S., Nielsen, T.G. & Hansen, B.W. (1999): Seasonal variation in nutrients, pelagic primary production and grazing in a high-Arctic coastal marine ecosystem, Young Sound, NE Greenland.- Mar. Ecol. Prog. Ser. 179: 13-25.

Sejr, M.K., Jensen, K.T. & Rysgaard, S. (2000): Macrozoobenthic structure in a high-Arctic east Greenland fjord.- Polar Biol. 23: 792-801.

Serreze, M.C., Holland, M.M. & Stroeve, J. (2007): Perspectives on the Arctic's shrinking sea-ice cover.- Science 315: 1533-1536.

Springer, A.M. & McRoy, C.P. (1993): The paradox of pelagic food webs in the northern Bering Sea. III. Patterns of primary production.- Cont. Shelf Res. 13: 575-579.

Subba-Rao, D.V. & Platt, T. (1984): Primary production of Arctic waters.- Polar Biol. 3: 191-201.

Thomas, D.N. & Dieckmann, G.S. (2002): Antarctic sea ice – a habitat for extremophiles.- Science 295: 641-644.

Wiencke, C. & tom Dieck, I. (1989): Temperature requirements for growth and temperature tolerance of macroalgae endemic to the Antarctic region.- Mar. Ecol. Prog. Ser. 56: 189-197.

Wiencke, C. & tom Dieck, I. (1990): Temperature requirements for growth and survival of macroalgae from Antarctica and southern Chile.- Mar. Ecol. Prog. Ser. 59: 157-170.

Wiencke, C. (2004): The coastal ecosystem of Kongsfjorden, Svalbard. Synopsis of biological research performed at the Koldewey Station in the years 1991-2003.- Rep. Polar Mar. Res. 492: 1-244.

Wilhelm, C., Büchel, C., Fisahn, J., Goss, R., Jakob, T., LaRoche, J., Lavaud, J., Lohr, M., Riebesell, U., Stehfest, K., Valentin, K. & Kroth, P.G. (2006): The regulation of carbon and nutrient assimilation in diatoms is significantly different from green algae.- Protist 157: 91-124.

Woelfel, J., Schumann, R., Leopold, P., Wiencke, C. & Karsten, U. (2009): Microphytobenthic biomass along gradients of physical conditions in Arctic Kongsfjorden, Svalbard.- Bot. Mar. 52: 573–583.

Woelfel, J., Schumann, R., Peine, F., Kruss, A., Tegowski, J., Blondel, P., Flohr, A., Wiencke, C. & Karsten, U. (2010): Microphytobenthos of Arctic Kongsfjorden (Svalbard, Norway) – Quantification of ex situ primary production by use of incubation chambers equipped with planar optode spots and structural analyses of biomass.- Polar Biol. 33: 1239-1253.

Wulff, A., Roleda, M.Y., Zacher, K. & Wiencke, C. (2008): Exposure to sudden light burst after prolonged darkness - A case study on benthic diatoms in Antarctica.- Diatom Res. 23: 519-532.

Wulff, A., Iken, K., Quartino, M.L., Al-Handal, A., Wiencke, C. & Clayton, M.N. (2009): Biodiversity, biogeography and zonation of benthic micro- and macroalgae in the Arctic and Antarctic.- Bot. Mar. 52: 491-507.