

Benthic primary production in Young Sound, Northeast Greenland

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Abstract

The extreme and variable light climate of polar marine environments imposes a substantial limitation on benthic primary production and demands efficient adaptive capacities of the primary producers. This chapter reviews the composition, abundance, primary production and adaptive strategies of benthic primary producers in Young Sound. Benthic primary producers occurred in the 0-50 m depth range and the relative importance of microalgae, crustose coralline macroalgae and foliose macroalgae varied systematically with depth. On a summer day with optimal light conditions benthic primary production showed a maximum of c. 70 mmol O₂ m⁻² d⁻¹ in shallow water. Production rates declined gradually to c. 20 mmol O₂ m⁻² d⁻¹ at 10–20 m depth and to 2.5 mmol O₂ m⁻² d⁻¹ at 30 m depth. Foliose macroalgae contributed markedly to primary production in shallow water but became insignificant at water depths >15 m, while benthic diatoms contributed most to primary production at intermediate water depths (5-30 m). At water depths greater than 30 m only coralline algae occurred, but their production was low because of their low abundance, low P_{max} and the low ambient irradiance at those depths. All algal groups were well adapted to the ambient irradiance and could, within minutes, acclimate their photosynthetic performance to changing light conditions. The benthic primary production in Young Sound markedly surpassed the pelagic primary production down to water depths of 20 m and the results thereby underline the potential importance of benthic primary production in shallow-water Arctic ecosystems.

9.1 Introduction

Benthic primary producers can contribute significantly to the production of shallow-water ecosystems in temperate and tropical regions (e.g. Mann, 1973; Borum & Sand-Jensen, 1996; Cahoon, 1999), but their importance for ecosystem primary production in the Arctic is only sparsely explored.

Annual primary production of Arctic phytoplankton can be surprisingly high despite the harsh conditions (Sambrotto et al., 1984; Subbarao & Platt, 1984), but the extent to which benthic production matches planktonic production is unknown. The few previous studies on benthic microalgal produc-

tion show contrasting results; microalgae range from playing an insignificant role in primary production (Horner & Schrader, 1982) to being the most important contributors (Matheke & Horner, 1974). Existing information on area production of polar macroalgae is also sparse, although several studies have evaluated photosynthesis and growth of macroalgae on an individual basis (e.g. Chapman & Lindley, 1980; Dunton, 1985; Dunton, 1990). The work in Young Sound provides the first estimates of the area production of coralline macroalgae (Roberts et al., 2002) and hence, in combination with area production estimates of foliose macroalgae (Borum et al., 2002), contributes to the very limited database on area production of Arctic kelp (e.g. Chapman & Lindley, 1981; Dunton et al., 1982). The studies of benthic primary production in Young Sound also provide the first estimate of total benthic production in the Arctic.

The extreme and variable light climate of Arctic marine environments, ranging from winter months of permanent darkness to periods of continuous light during summer, and the simultaneous exposure to low temperatures demand a high capacity for physiological adaptation of the plants. Due to their shorter life cycle, benthic and planktonic microalgae can occur in highest abundance during the summer period when light conditions are optimal. The perennial algae, however, need to cope with the seasonal changes in growth conditions and must rely on extreme plasticity of their photosynthetic apparatus and metabolism. They need a low respiration rate to minimise carbon losses during winter darkness, an efficient light capture in the periods of low irradiance under the ice cover in early and late summer, and an ability to profit maximally from the 24-h light period in mid-summer. On the other hand, the perennial life form with its slow, but continuous, production of new biomass ensures that the algae are ready to start photosynthesis as soon as light becomes available. For some species (e.g. Laminarians) this advantage is enhanced by the ability to extend their surface area before the break-up of the surface ice cover (Dunton, 1985) and thereby increase the capacity for light capture. These algae produce a new thin blade during the period of ice cover through allocation of resources stored in the old thallus (Chapman & Lindley, 1980).

Physical disturbance in the shallow depth range constitutes another limitation on benthic primary producers. Ice scouring along the coast may detach

the algae from their substrata or destroy the thallus and thus induce a significant loss of biomass (Gutt, 2001). Moreover, intense walrus feeding in some depth intervals (Born et al., 2003; Chapter 10) may seriously affect the abundance of benthic micro- and macroalgae in Young Sound.

In spite of these limitations, the benthic algal community likely contributes significantly to the primary production of Young Sound, as the annual primary production of phytoplankton and sea-ice algae cannot account for the annual C input required by the benthic secondary producers (See Chapter 4, 5, 7 & 8).

Here we review the importance of benthic micro- and macroalgae for the primary production in Young Sound. We analyse their composition, distribution, abundance and productivity as well as their adaptive strategies. The results are discussed together with the relatively sparse knowledge available of benthic primary production in polar regions. Parts of the results are also included in a comparison of benthic versus pelagic production on an annual basis (Chapter 11).

9.2 Methods

Most of the information compiled in this chapter is based on methods described in the study of Arctic benthic microalgae by Glud et al. (2002), the study of Arctic coralline macroalgae by Roberts et al. (2002), the study on Arctic foliose macroalgae by Borum et al. (2002) and the study of photosynthetic performance of all three algal groups by Kühl et al. (2001). The following paragraphs provide a brief summary of the methodology used, but for details, please refer to the studies above.

All types of benthic primary producers were collected by divers and identified to genus/species in the laboratory. Distribution and cover of diatoms, foliose macroalgae and encrusted algae were estimated from numerous digital photographs and video recordings of the seafloor. Biomass of foliose macroalgae along the depth gradient was assessed through harvest.

Net benthic microalgal photosynthesis was assessed as i) the sum of the upward and downward diffusive O₂ fluxes calculated from oxygen micro-profiles measured in darkness and at increasing irradiance (Fig. 9.1a), and ii) the total oxygen or DIC exchange rate of intact sediment cores incubated in darkness and at increasing irradiance under *in situ*

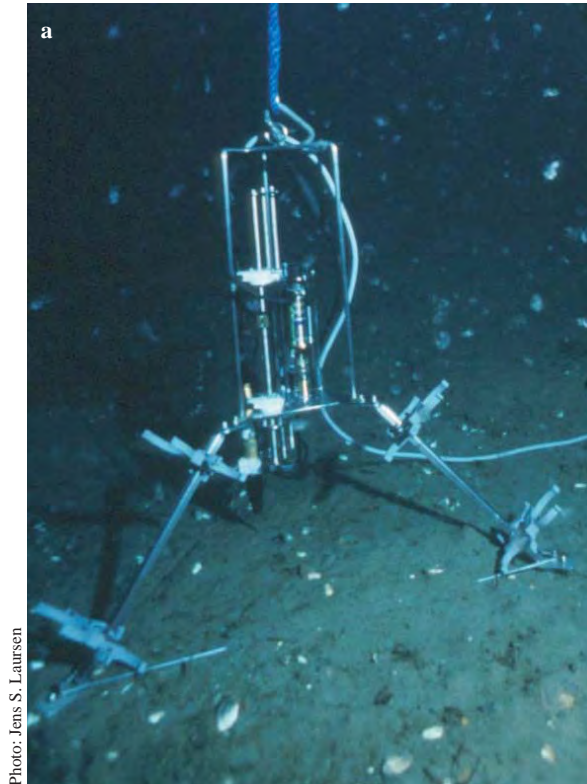


Photo: Jens S. Laursen



Photo: Søren Rysgaard

Figure 9.1 Illustration of (a) the oxygen microsensor technique used to measure production of benthic microalgae and crustose coralline algae and (b) of the pulse-amplitude-modulated (PAM) fluorometer.

temperature conditions (Glud et al., 2002). Photosynthesis of crustose coralline algae was assessed based on diffusive O_2 fluxes calculated from oxygen microprofiles measured in the diffusive boundary layer over the coralline surface in darkness and at

increasing irradiance (Roberts et al., 2002). Respiration and photosynthesis of thallus discs of *L. saccharina* were measured in a small glass chamber as O_2 consumption in darkness and O_2 production at increasing levels of irradiance (Borum et al., 2002). Data on maximum photosynthetic rate (P_{max}), light utilisation efficiency (α), respiration rate (R), compensation irradiance (E_c) and the irradiance at onset of saturation (E_k) for each algal group were derived from the measured P-E curves. Subsequently, daily rates of area photosynthesis along the depth gradient were assessed for a summer day with optimal light conditions, using the formula of Platt et al. (1980):

$$P = P_{max} [1 - \exp(-\alpha E / P_{max})] + R \quad (1)$$

The irradiance (E) at specific depths was calculated based on data on surface irradiance and light attenuation in the water column (Glud et al., 2002). Photosynthetic rates were corrected to represent the actual cover/biomass of the algal groups at each depth. The productivity of *L. saccharina* was also assessed from annual growth rates of the blade at specific water depths.

Relative measures of the photosynthetic activity of all algal groups were obtained both in the laboratory and *in situ* by active fluorescence measurements using an *in situ* measuring device (Diving-PAM, Walz GmbH, Effeltrich Germany) (Kühl et al., 2001; Fig. 9.1b). We used the so-called 'saturation pulse method' (Schreiber et al., 1995) to measure quantum yields of PSII under various actinic light conditions in order to characterise the *in situ* acclimation of the photosynthetic apparatus to irradiance. We measured so-called rapid light curves, (RLC) within 1-2 min or 'light curves (LC)' within longer time periods (30-40 min). In both cases, the light curves, express relative rates of PSII-related electron transport as a function of irradiance (Schreiber et al., 1995). During RLC measurements, the brief (10-20 s) incubation periods at each irradiance level do not allow the phototrophs to acclimate, and these measurements thus provide a snapshot of the photosynthetic capacity at the current ambient irradiance. During LC measurements, the relatively slow increase in irradiance over a 30-40 min period allows the photosynthetic apparatus to acclimate as the experiment is conducted. Consequently, these measurements show the potential short-term photosynthetic capacity of the organisms.

9.3 Results & discussion

9.3.1 Composition and distribution of benthic primary producers

Diatoms were the dominant benthic microalgae in Young Sound and formed a brownish biofilm on the sediment (Fig. 9.2a), while benthic macroalgae included a variety of algal groups. Crustose, coralline species dominated by the red algal genus *Phymatolithon* formed pink crusts on the scattered stones (Fig. 9.2b) while large leathery brown algae of the genera *Fucus* and *Laminaria* dominated the foliose macroalgal community (Fig. 9.2c). Other upright foliose species of brown and red algae, including filamentous brown algae of the genus *Desmarestia* and leathery red algae of the genus *Coccotylus*, were also common (Table 9.1).

Benthic microalgae occurred in the upper sediment layers from shallow depths down to water depths >30 m, while crustose coralline macroalgae covered much of the available rock surface in the depth range 15–50 m. The depth limit at 50 m corresponds to about 0.004% of surface irradiance in the open-water season (Roberts et al., 2002) and the crustose corallines were the deepest-growing macroalgae in Young Sound. The

Table 9.1 Overview of the dominant algal classes and genera/species within the 3 types of benthic primary producers: 1) Microalgae (based on Glud et al., 2002), 2) crustose coralline macroalgae (based on Roberts et al., 2002) and 3) foliose upright macroalgae (based on Borum et al., 2002) and unpublished data).

Algal class	Dominant genera/species
Microalgae	
– Diatoms	<i>Pinnularia</i> <i>Nitzschia</i> <i>Navicula</i>
Macroalgae – crustose coralline	
– Red algae	<i>Phymatolithon foecundum</i> <i>Phymatolithon tenue</i>
Macroalgae – foliose	
– Brown algae	<i>Fucus evanescence</i> <i>Fucus serratus</i> <i>Laminaria saccharina</i> <i>Laminaria solidungula</i> <i>Desmarestia aculeata</i> <i>Desmarestia viridis</i>
– Red algae	<i>Coccotylus truncatus</i>
– Green algae	No dominant species



Photo: Peter B. Christensen

Figure 9.2 Photo of (a) benthic microalgae, (b) crustose, coralline macroalgae of the genus *Phymatolithon* and (c) the foliose, upright macroalga *Laminaria saccharina*.

foliose macroalgae occurred on rocks as well as on scattered stones and gravel. In protected, sandy sites of Young Sound, the brown macroalga, *L. saccharina*, grew with its widely branched haptera attached to small-sized gravel. Foliose macroalgae occurred in the depth range 2–25 m. The depth limit of *L. saccharina* was located at about 20 m depth and corresponds to c. 0.7% of surface irradiance (Borum et al., 2002).

The depth penetration of macroalgae seems to be determined largely by light availability, which in turn depends on solar radiation and light attenuation in the water column. Depth limits tend to occur at a smaller percentage of the surface irradiance near the equator where annual solar radiation is high as compared with temperate and polar regions (see Lüning, 1990). Crustose coralline macroalgae are the world's deepest-growing macroalgae and their depth penetration has been reported to range from 15 m, corresponding to 0.05% of surface irradiance in the turbid waters of Helgoland, to 268 m, corresponding to 0.001% of surface irradiance in the clear waters around Bahamas (Lüning & Dring, 1979). Laminarians also generally penetrate to relatively deep waters and the lower depth limit of *L. saccharina* recorded at Young Sound agrees well with the range of minimum light requirements reported for cold-water Laminarians in general (e.g. Lüning & Dring, 1979; Chapman & Lindley, 1980; Dunton, 1990).

The relatively large depth penetration of these species of benthic macroalgae indicates capacity for shade adaptation, which is considered a general feature of polar macroalgae enabling them to cope with the dark winter months (Kirst & Wiencke, 1995). Shade

adaptation generally involves slow growth rates that reduce respiration, storage of carbon reserves during periods of favorable growth conditions, long life span and resistance to grazing (Lüning, 1990).

It is remarkable that many of the dominant benthic algae of Young Sound also occur in temperate regions and hence possess a substantial capacity for climatic adaptation, not only to the seasonal variations within the Arctic but also across a wide geographical range. *L. saccharina* thus occurs from Spain in the south to Peary Land at 82°N in North Greenland (Lüning, 1990), and coralline algae also occur from polar regions to the tropics (Johansen, 1981; Steneck, 1986).

9.3.2 Abundance of benthic primary producers in Young Sound

The *in situ* area cover of diatoms and coralline algae was measured by visual analysis of digital images facilitated by the characteristic brownish colour of diatom films and the pink colour of the corallines (Glud et al., 2002; Roberts et al., 2002).

Benthic microalgae covered 23–70% of the sea floor down to water depths of 30 m. Their abundance showed a maximum at 20 m depth before declining towards the deeper, shaded parts (Fig. 9.3; Glud et al., 2002). The horizontal distribution of the microalgae was examined at water depths of 10 m and was found to be very patchy, with marked differences between sites 5–8 m apart, most probably influenced by the intensive feeding activity of walrus in this depth range (Glud et al., 2002).

As the abundance of rocks is very patchy in Young Sound, coralline algae covered only 1–2% and occa-

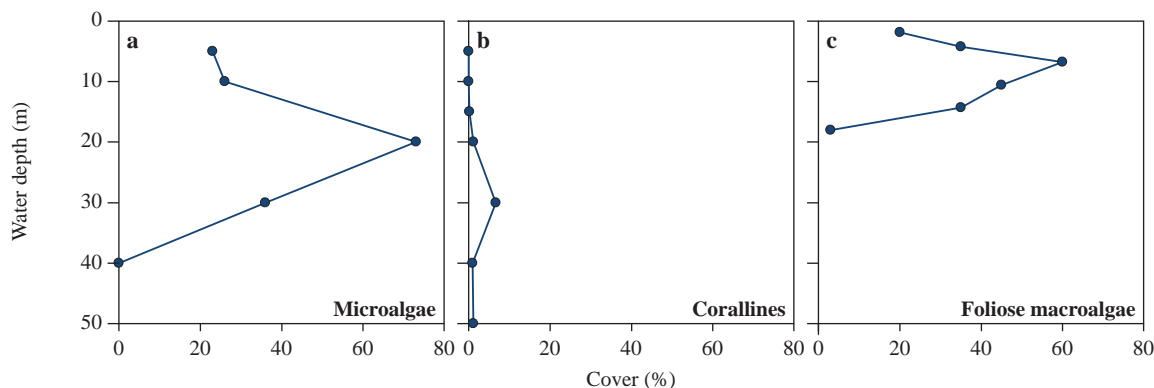


Figure 9.3 Depth distribution of the cover of (a) benthic microalgae (from Glud et al., 2002), (b) crustose coralline algae (redrawn from Roberts et al., 2002) and (c) *Laminaria saccharina* (P.B. Christensen unpublished data, estimated from video recordings).

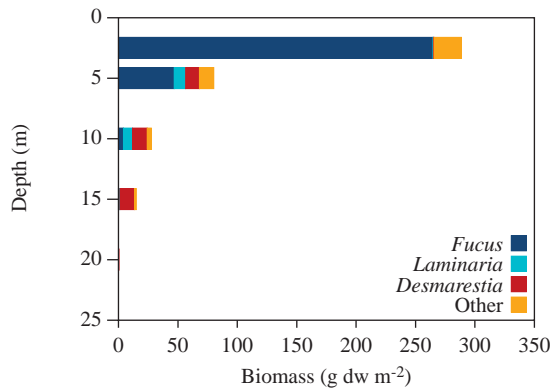


Figure 9.4 Biomass of foliose macroalgae along a depth gradient at Daneborg, Young Sound.

sionally 7% of the sea floor (Fig. 9.3; Roberts et al., 2002). The peak abundance of 7% at 30 m depth was not a consistent feature at this depth in Young Sound but rather resulted from a higher local abundance of rocks at this specific sampling site. The minimum depth range of 15 m was probably due to a combination of ice scouring, walrus feeding disturbance and overgrowth by foliose macroalgae in shallow water, while the maximum depth range of the coralline algae was light regulated.

The cover of foliose macroalgae almost matched that of benthic microalgae, but the macroalgae reached maximum levels at shallower depths (Fig. 9.3). Biomass measurements provided a more precise estimate of the abundance of foliose macroalgae and

also showed how different algal species contributed to the total biomass (Fig. 9.4). The total biomass of foliose macroalgae showed a maximum of almost 290 g dw m⁻² in shallow water and declined towards greater water depths. In shallow water *F. evanescence* dominated the community of foliose macroalgae while *L. saccharina* and the two species of *Desmarestia* were more important at 10–15 m depth. The abundance of foliose macroalgae was probably limited by a combination of lack of suitable substrata, light limitation at greater water depths and intensive feeding activity of walruses from 5–20 m depth. Ice scouring in shallow waters was clearly observed as scouring tracks on the sea floor but apparently did not prevent *F. evanescence* from occurring at a relatively high biomass. At the mouth of Young Sound, where stronger currents created a longer ice-free period, the abundance of kelps was markedly higher (pers. obs.).

9.3.3 Production of benthic primary producers in Young Sound

On a summer day with optimal light conditions, the daily net photosynthetic rate of the total benthic algal community showed a maximum of about 70 mmol O₂ m⁻² d⁻¹ in shallow water (2.5 m), declined gradually down to about 20 mmol O₂ m⁻² d⁻¹ at 10–20 m depth and then declined markedly to 2.5 mmol O₂ m⁻² d⁻¹ at 30 m depth (Fig. 9.5). Foliose macroalgae contributed most to primary production at the shallowest depths with a maximum of about 70 mmol O₂ m⁻² d⁻¹ at 2.5

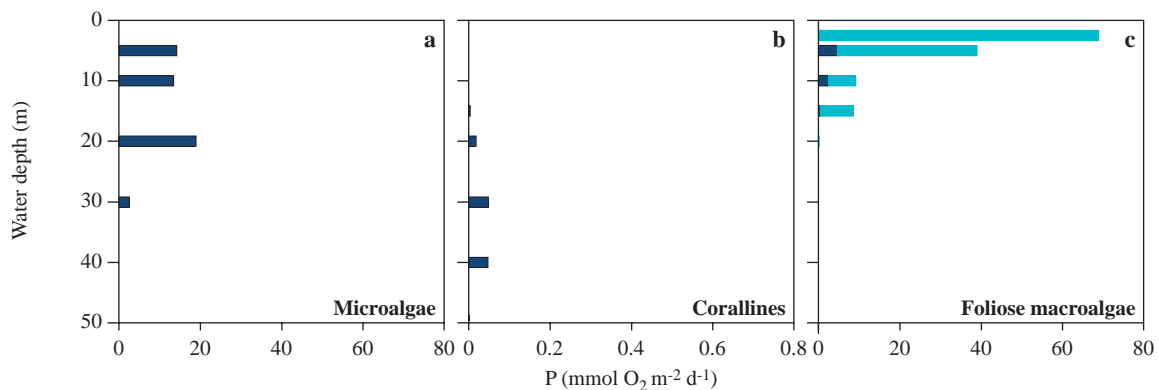


Figure 9.5 Daily rates of area photosynthesis versus depth for (a) benthic microalgae, (b) corallines and (c) foliose macroalgae (dark blue represents *L. saccharina* while light blue bars represent other foliose macroalgae). Based on the equation $P = P_{\max} [1 - \exp(-\alpha E / P_{\max})] + R$ (Platt et al., 1980), using photosynthesis parameters from Table 9.3 and data on surface irradiance and light attenuation during a summer day (1 August 1999). Rates were corrected to represent the actual cover/biomass of the algal groups based on Figs. 9.2 and 9.3. We assumed that the group, other foliose macroalgae, shared the same photosynthetic characteristics as *L. saccharina*. Data include only positive net photosynthetic rates.

m depth. Their production rates declined rapidly with depth and became insignificant at water depths >15 m. Benthic diatoms were the dominant primary producers at intermediate water depths. Their production was high from 5 to 20 m depth (13–19 mmol O₂ m⁻² d⁻¹) and still significant at 30 m depth (2.5 mmol O₂ m⁻² d⁻¹). At water depths >30 m only coralline algae contributed to the benthic production. Their production was very low, showing a maximum of 0.05 mmol O₂ m⁻² d⁻¹ at 30 m depth. Annual production rates of all primary producers, including phytoplankton and ice algae, are presented and compared in Chapter 11.

The daily production rates of microalgae are within the range reported from the Chukchi Sea by Matheke & Horner (1974), one of the few other Arctic studies on benthic microalgal production. Here the primary production of microalgae ranged between 1.9 and 57 mg C m⁻² h⁻¹ corresponding to about 5–137 mmol O₂ m⁻² d⁻¹ (assuming a photosynthetic quotient of 1.2 and 24 h of production per day). Production rates for crustose coralline algae in the Arctic have not previously been published, but these algae are generally known as the least productive algae in any environment (e.g. Littler & Murray, 1974). We have not been able to find any daily area-based production rates of foliose macroalgae from the Arctic for comparison with the studies in Young Sound.

At water depths down to 20 m, the benthic net production in Young Sound by far surpassed the gross production of phytoplankton which was estimated at c. 40 mg C m⁻² d⁻¹ for water depths <30 m (Glud et al., 2002), corresponding to 4 mmol O₂ m⁻² d⁻¹ (assuming a photosynthetic quotient of 1.2). The remaining group of aquatic primary producers, the ice algae, do not contribute significantly to primary production in Young Sound (Rysgaard et al., 2001). The results from Young Sound thus show that benthic primary production may contribute significantly to the primary production of shallow-water Arctic ecosystems.

On a global scale, however, the rates per unit area of benthic production in Young Sound are quite low. A compilation of 319 literature data on maximum integral gross photosynthesis at high midday irradiance showed a maximum of about 60 mmol O₂ m⁻² h⁻¹ in dense communities of phytoplankton and benthic macrophytes (Krause-Jensen & Sand-Jensen, 1998) and mean rates of 17 mmol O₂ m⁻² h⁻¹ for benthic microalgae, 30 for benthic macroalgae and 22 for phytoplankton (Sand-Jensen & Krause-Jensen, 1997).

9.3.4 Growth measurements of *Laminaria saccharina*

In addition to the photosynthesis measurements described above, production of *L. saccharina* was measured based on leaf growth rates. Every year, *L. saccharina* individuals form a new blade between the stipe and the base of the old blade. The old blade remains attached and a thallus constriction between the old blade and the new one makes it easy to distinguish the two generations of blades (Fig. 9.6). Annual growth of *L. saccharina* can therefore be measured as the total length or biomass of the newest blade when it has reached full length in late summer. As a consequence, annual net growth per m² of sea floor can be assessed by harvesting *L. saccharina* in August and measuring the biomass of new blades (Borum et al., 2002). A leaf-tagging technique also provides a direct measure of annual growth rates (Fig. 9.6) and, in addition, allows assessment of growth rates during various periods of the year. Both techniques showed that large *L. saccharina* individuals produced on average 70–90 cm blade per year, corresponding to relative growth rates of approximately 0.5 per year at water depths from 5 to 15 m (Borum et al.,

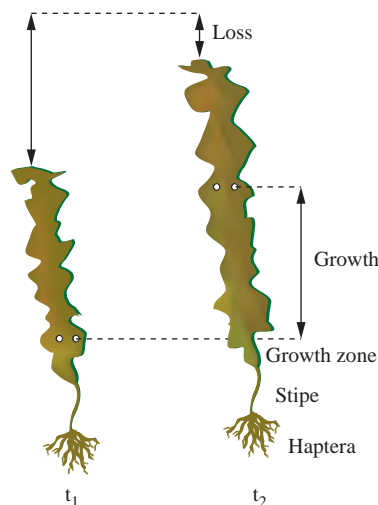


Figure 9.6 Illustration of leaf-tagging technique used to measure growth of *L. saccharina*. The blade is tagged with holes 10 cm above the junction between stipe and blade where the growth zone is located. As the blade grows, the holes are displaced upwards and the distance to the original position of the holes represents new growth. The arrow shows the constriction between the old blade and the new one.

Table 9.2 Mean annual length growth of *L. saccharina* in different sites. All rates were measured by leaf tagging. Most rates have been read and summed from figures showing seasonal changes in growth rate. *Average of 2nd and 3rd growth year. **Located at the lower salinity limit.

Location	Latitude	Depth m	Growth cm yr ⁻¹	No. obs.	Reference
NE Greenland, Young Sound	74 18	5	73	>15	Borum et al. (2002)
NE Greenland, Young Sound	74 18	10	71	>15	Borum et al. (2002)
NE Greenland, Young Sound	74 18	15	89	>15	Borum et al. (2002)
Alaska, Beaufort Sea	70 19	6-7	58	13	Dunton (1985)
Iceland	64 20	5	111	17-32	Sjötun & Gunnarsson (1995)
Norway	60 15	5	230*	<40	Sjötun (1993)
Scotland, Loch Creran	56 34	5	239	?	Johnston et al. (1977)
Scotland, St. Andrews sewer st	56 20		160	20	Conolly & Drew (1985)
Scotland, St. Andrews	56 20		124	50	Conolly & Drew (1985)
Scotland, Kings Barn	56 18		73	50	Conolly & Drew (1985)
Scotland, Fifeness	56 17		82	50	Conolly & Drew (1985)
Scotland, Argyll	56 13	1	311	?	Parke (1948)
Denmark, Århus Bay	56 10	7	136	7-70	Thinggaard (2001)
Denmark, Øresund**	55 35		76	2-9	Weile (1996)
Germany, Kiel Bay	54 24	5	129	20	Schaffelke et al. (1996)
Rhode Island, Narragansett Bay	41 29		332	20	Brady-Campbell et al. (1984)
Rhode Island, Narragansett Bay	41 28.5		293	20	Brady-Campbell et al. (1984)
Rhode Island, Rhode Island Sound	41 21		291	20	Brady-Campbell et al. (1984)

2002; Table 9.2). The leaf-tagging technique was also applied for shorter periods of the year (mid-August to mid-June, mid to late June, late June to mid-August) and revealed that rates of length growth were highest around ice-break, i.e. late June to mid-August, when they averaged 6 mm d⁻¹ (unpublished data).

Although a mean annual growth of 70–90 cm is impressive considering the 10 months of darkness, much higher growth rates (>3 m per year) of *L. saccharina* have been observed at lower latitudes (Table 9.2). *L. saccharina* is thus able to cope with Arctic conditions but apparently at the cost of reduced growth rates as compared with lower latitudes. We also used the mean biomass of new blades formed per m² of sea floor to estimate the annual primary production of *Laminaria saccharina*. The production increased from 0.1 g C m⁻² yr⁻¹ at 2.5 m depth to a maximum of 1.6 g C m⁻² yr⁻¹ at 10 m depth. Probably because of the relatively low biomass of *Laminaria* in Young Sound, these rates are low compared with the few other published production rates of *Laminaria* from Arctic. *L. solidungula* produced 7 C m⁻² yr⁻¹ in

the Alaskan Beaufort Sea (Dunton et al., 1982) and 20 g C m⁻² yr⁻¹ in the Canadian high Arctic (Chapman & Lindley 1981) and was the dominant macroalgal species in both locations. There are examples of much higher production rates of *Laminaria* in temperate areas, e.g. 1750 g C m⁻² yr⁻¹ in dense kelp forests in Nova Scotia, Canada (Mann, 1972) and 120 g C m⁻² yr⁻¹ in *L. saccharina* communities in Scotland (Johnston et al., 1977).

9.3.5 Photosynthetic strategy under Arctic conditions

Marine benthic primary production in the Arctic takes place at permanently low temperatures (c. –1.5 to –1.8°C) except in some shallow-water areas where temperatures may reach slightly above zero in the summer open-water period. Long periods of ice cover in combination with winter months of total darkness result in low irradiance or total darkness for the benthic primary producers during most of the year. In contrast, irradiance levels in shallow water can be high during the open-water period in summer

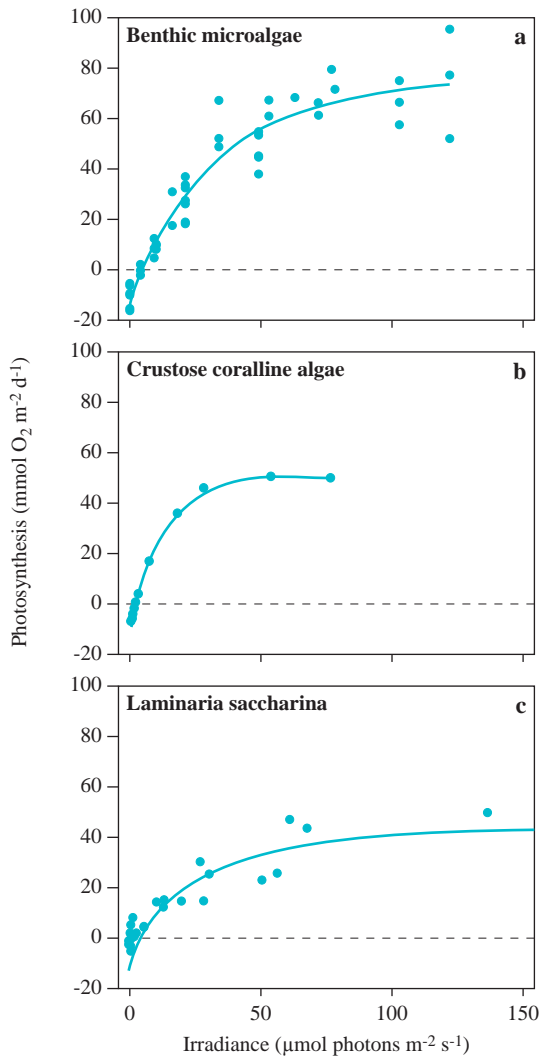


Figure 9.7 P-E curves for (a) benthic microalgae (Glud et al., 2002), (b) crustose coralline red algae (Roberts et al., 2002) and (c) *Laminaria saccharina* (Borum et al., 2002). Data on benthic microalgae and crustose coralline algae are per unit area of algae-covered sediment surface while data on *Laminaria saccharina* are per unit area of thallus surface. Data on *Laminaria saccharina* are recalculated from weight-based values to thallus-area-based values by using a specific weight of 5.84 mg cm⁻² and recalculated from hourly to daily rates by assuming 24 h of production per day; photosynthesis continued at saturating levels up to irradiance levels of at least 250 μmol photons m⁻² s⁻¹.

causing enhanced and constant availability of light. The shift from darkness to higher irradiance and vice versa occurs gradually as sun height increases/decreases but also involves more sudden increases in irradiance as the ice cover breaks up or snow-covered ice is re-established.

Our studies followed the performance of various groups of benthic primary producers in Young Sound over the summer season from the last part of the ice-covered period throughout the open-water period, where most production takes place. During this period, photosynthesis/irradiance relationships of benthic microalgae, crustose coralline algae and *L. saccharina* followed normal patterns of saturation with no clear signs of photoinhibition up to irradiances of 120, 80 and 250 μmol photons m⁻² s⁻¹, respectively (Fig. 9.7). All algal groups measured at Young Sound showed compensation irradiances (E_c) and irradiances at onset of saturation (E_k) in the low end of the range reported for marine algae, thereby indicating adaptation to low light levels (Kirk, 1994; Table 9.3). Crustose coralline algae had the lowest E_c and E_k values and thus demonstrated the most efficient adaptation to low light levels. The other photosynthetic parameters did not show clear differences among algal groups (Table 9.3). Rates of respiration and photosynthesis of *L. saccharina* were quantified on a dry-weight basis (in addition to area-based values) and a comparison of these data with ranges reported for other macroalgae allowed evaluation of the adaptive capacity of *L. saccharina*. Respiration rates were in the low end of the typical range reported for macroalgae (Markager & Sand-Jensen, 1994) and maximum photosynthetic rates were within the reported range for polar macroalgae (Kirsch & Wiencke, 1995); so *L. saccharina* can indeed adapt to the harsh Arctic conditions.

Photosynthesis parameters of benthic diatoms and coralline algae did not vary markedly among water depths (Glud et al., 2002; Roberts et al., 2002). In contrast, the photosynthetic characteristics of *L. saccharina* changed systematically with depth (Borum et al., 2002). Pigment content, respiration rate, light utilisation efficiency and maximum photosynthetic rate all increased significantly with depth while compensation irradiance and irradiance at onset of saturation declined (Fig. 9.8). The larger pigment content and light utilisation efficiency in combination with the reduced compensation and saturation irradiances all

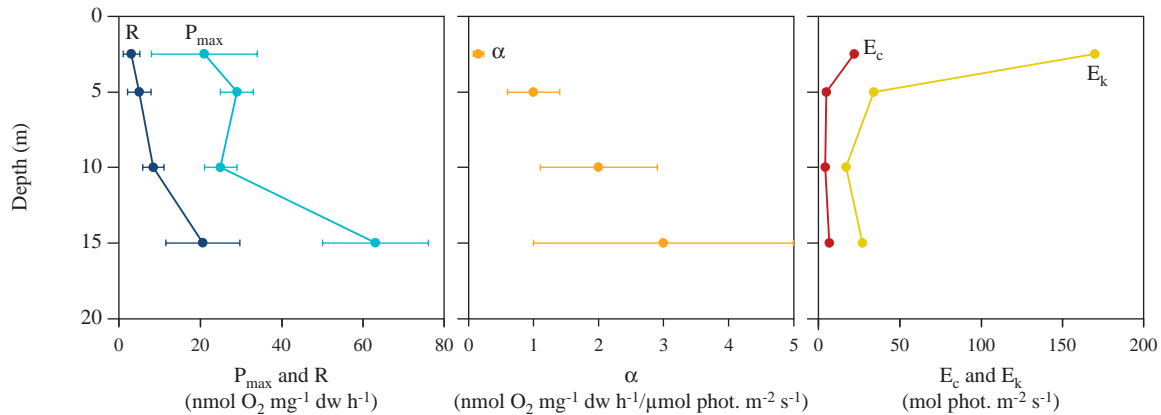


Figure 9.8 Photosynthesis parameters versus depth for *Laminaria saccharina* during the open-water period (August): R (respiration rate), α (photosynthetic efficiency), P_{\max} (max. photosynthetic rate), E_c (compensation point), E_k (saturation point).

contribute to more efficient utilisation of the reduced light supplies. A more efficient photosynthetic apparatus requires production and maintenance of higher pigment content and enzymatic activity, which also create higher respiratory costs. In fact, low temperature may be an advantage and a prerequisite for survival in the long dark period, as it keeps respiratory costs low (Borum et al., 2002).

Differences in photosynthetic characteristics between ice-covered and open-water seasons were insignificant in coralline algae but apparent in *L. saccharina*. By the end of the long period of darkness in June, the new leaf blade of *L. saccharina* had low

respiration rates, low compensation and saturation irradiances and relatively high maximum photosynthetic rates and was hence well adapted to the low light levels under the ice cover. During the open-water period in August, the compensation irradiance increased, probably in response to the increased ambient irradiance.

Active fluorescence measurements *in situ* using the, saturation pulse method, generated snapshots of the *in situ* acclimation of the photosynthetic apparatus by producing “rapid light curves” (RLC) within 1–2 min or, light curves, (LC) over longer time periods (c. 30 min). RLCs reflected the *in situ* acclima-

Table 9.3 Photosynthetic parameters of benthic diatoms, crustose coralline red algae and *Laminaria saccharina* measured by net O_2 production: R (respiration rate), α (photosynthetic efficiency), P_{\max} (max. photosynthetic rate), E_c (compensation point), E_k (saturation point). Data on O_2 production of benthic diatoms and crustose coralline algae are related to the surface of the algal community. For comparability of data, production rates of *L. saccharina* were recalculated from hourly biomass-specific rates (shown in parenthesis) to diurnal rates related to thallus surface area. In this conversion we used the following information on area-specific biomass: June: 5.08 (new thallus), 6.58 (old thallus) and August: 6.17 (new thallus) $mg\ dw\ cm^{-2}$ (J. Borum, unpublished data), and multiplied by 24 to obtain diurnal rates. Results from various depths and seasons are represented as averages for benthic diatoms but as ranges for corallines and *Laminaria*.

Algal group/sp.	Depth (m)	Month	R $mmol\ O_2\ m^{-2}\ d^{-1}$ ($nmol\ O_2\ mg^{-1}\ dw\ h^{-1}$)	P_{\max} $mmol\ O_2\ m^{-2}\ d^{-1}$ ($nmol\ O_2\ mg^{-1}\ dw\ h^{-1}$)	α $mmol\ O_2\ m^{-2}\ d^{-1}/\mu mol\ phot\ m^{-2}\ s^{-1}$ ($nmol\ O_2\ mg^{-1}\ dw\ h^{-1}/\mu mol\ phot\ m^{-2}\ s^{-1}$)	E_c $\mu mol\ phot\ m^{-2}\ s^{-1}$	E_k	Source
Diatoms	10, 20, 30	Jun, Aug	-10.96	85	2.6	4.5	32.9	Glud et al. (2002)
Corallines	17, 36	Jun, Aug	-4.8	43–67	4.2–6.3	0.7–1.8	7–17	Roberts et al. (2002)
<i>L. saccharina</i>	2.5, 5, 10, 15	Jun, Aug	-4.6–31 (-3–21)	31–180 (21–85)	0.2–13.7 (0.15–5)	2–22	15–170	Borum et al. (2002)

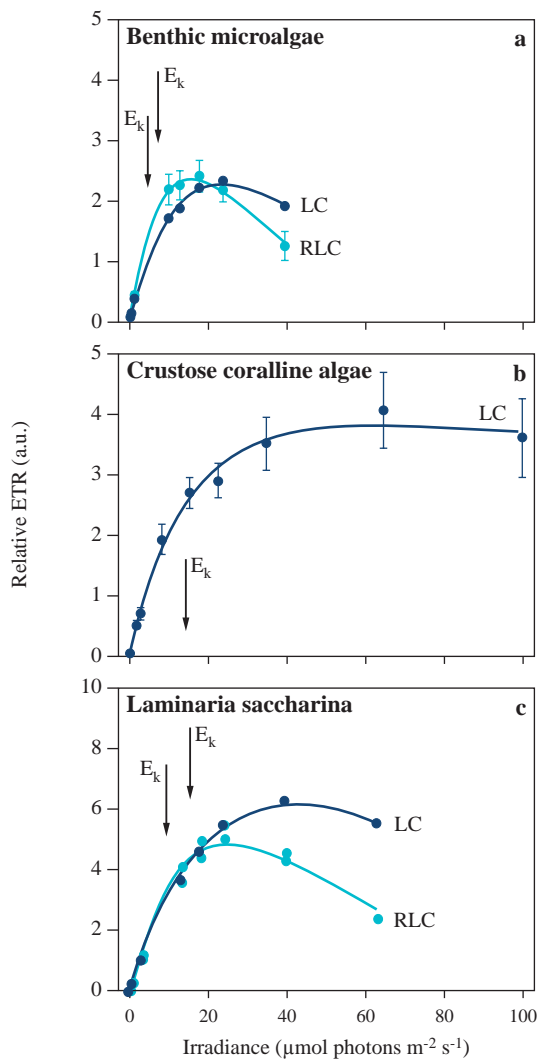


Figure 9.9 Light curves (LC) and rapid light curves (RLC) of (a) benthic diatoms (Kühl et al., 2001), (b) crustose coralline red algae (Kühl et al., 2001) and (c) *Laminaria saccharina* (Kühl et al., 2001).

tion of the phototrophs to ambient light because the short illuminations of each light level (10 s) did not allow any acclimation to the applied light levels during measurement. In contrast, the longer illumination period of each actinic light level used in LCs allowed the photosynthetic apparatus to acclimate during the measurement. Consequently, RLCs and LCs differed markedly within each algal group (Fig. 9.9). RLCs showed lower light saturation points than did LCs, indicating inhibition and/or downregulation of photosynthesis at high light levels while LCs showed no such effect (Fig. 9.9; Table 9.4). The apparent short-

Table 9.4 Light compensation point (E_c) and light saturation point (E_k) for benthic diatoms, crustose coralline red algae and *Laminaria saccharina* measured by net O_2 production, PAM Rapid light curves (RLC) or Light curves (LC). Unit: $\mu\text{mol photons m}^{-2} \text{s}^{-1}$. Data from June 1999 at 10 m depth (diatoms and *L. saccharina*). Based on Kühl et al. (2001).

Algae	E_c	E_k	Method
Diatoms		4.6	RLC
		6.9	LC
Corallines	1.6	17	Net O_2 prod.
		11	RLC
<i>L. saccharina</i>	1.9	12.8	Net O_2 prod.
		7.3	RLC
		12.5	LC

term acclimation to increasing irradiance as measured by LCs reversed to the initial characteristics of the light curve within 15–20 min after irradiance returned to ambient intensity. Our results clearly demonstrated that all the phototrophs were able to acclimate reversibly within minutes to moderate changes in light levels. This result also implies that light curves based on longer illumination periods, such as those used for measuring photosynthesis versus irradiance curves via oxygen production, may not reflect the actual photosynthetic capacity under *in situ* conditions but rather the potential to acclimate to the experimental conditions imposed on the organisms.

However, an important consequence of our observations is that all benthic primary producers seem able to optimise their photosynthetic performance during the season. Traditional measurements of light curves using longer exposure times in combination with detailed measurements of *in situ* irradiance are thus still necessary for the study of photosynthetic capacity and calculation of productivity over longer time scales. Last, but not least, although correlations can be made (e.g. Kühl et al., 2001), active fluorescence measurements are not easily converted to quantitative measures of photosynthesis in terms of oxygen production or carbon fixation. Thus, direct extrapolation from the photosynthetic acclimation patterns observed with active fluorescence techniques to similar patterns in benthic primary production is a risky business.

At higher irradiance levels and/or under higher UV stress, photoinhibition may take place, and this process is not necessarily reversible. Besides studies of

macroalgae, e.g. by Hanelt and co-workers (Hanelt, 1998; Hanelt et al., 1997), photoinhibition and UV effects on benthic primary producers in the Arctic have not, to our knowledge, been published. Future studies should explore the environmental limits for short-term reversible acclimation among benthic primary producers in the Arctic. A more detailed dataset of benthic primary production over a complete year is still lacking. Such a study could address the important question of how the phototrophs cope with the long period of darkness and would help strengthen the estimate of carbon cycling due to benthic phototrophs. The research logistics available makes Young Sound an excellent location for such a study.

Our studies of benthic primary production in Young Sound revealed that the various photosynthetic groups are well adapted to cope with the extreme Arctic environment in terms of low temperature, long periods of darkness or continuous light. Benthic primary production is a major component in the carbon budget of the Young Sound ecosystem (Glud et al., 2002) as will be addressed further in Chapter 11. As part of the studies in Young Sound, new techniques for *in situ* measurements of photosynthetic performance and productivity were developed and applied. With these techniques, it is now possible to undertake a range of detailed *in situ* studies of surface-associated photosynthesis in the Arctic – a research area, which, despite the great importance of benthic primary production in coastal Arctic ecosystems, is severely underexplored.

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