J. Phycol. **38,** 273–283 (2002)

PRIMARY PRODUCTION OF CRUSTOSE CORALLINE RED ALGAE IN A HIGH ARCTIC FJORD[1]

Rodney D. Roberts

Cawthron Institute, Private Bag 2, Nelson, New Zealand

Michael Kühl,[2] Ronnie Nøhr Glud

Marine Biological Laboratory, University of Copenhagen, Strandpromenaden 5, DK-3000 Helsingør, Denmark

and

Søren Rysgaard

National Environmental Research Institute, Department of Lake and Estuarine Ecology, Vejlsøvej 25, DK-8600 Silkeborg, Denmark

Crustose coralline algae occupied ~1%–2% (occasionally up to 7%) of the sea floor within their depth range of 15–50 m, and they were the dominant encrusting organisms and macroalgae beyond 20 m depth in Young Sound, NE Greenland. In the laboratory, oxygen microelectrodes were used to measure net photosynthesis (P) versus downwelling irradiance (E_d) and season for the two dominant corallines [*Phymatolithon foecundum* (Kjellman) Düwel *et* Wegeberg 1996 and *Phymatolithon tenue* (Rosenvinge) Düwel *et* Wegeberg 1996] representing > 90% of coralline cover. Differences in P-E_d curves between the two species, the ice-covered and open-water seasons, or between specimens from 17 and 36 m depth were insignificant. The corallines were low light adapted, with compensation irradiances (E_c) averaging 0.7–1.8 μmol photons·m^{-2}·s^{-1} and light adaptation (E_k) indices averaging 7–17 μmol photons·m^{-2}·s^{-1}. Slight photoinhibition was evident in most plants at irradiances up to 160 μmol photons·m^{-2}·s^{-1}. Photosynthetic capacity (P_m) was low, averaging 43–67 mmol O_2·m^{-2} thallus·d^{-1} (~250–400 g C·m^{-2} thallus·yr^{-1}). Dark respiration rates averaged ~5 mmol O_2·m^{-2} thallus·d^{-1}. In ice covered periods, E_d at 20 m depth averaged ~1 μmol photons·m^{-2}·s^{-1}, with daily maxima of 2–3 μmol photons·m^{-2}·s^{-1}. During the open water season, E_d at 20 m depth averaged ~7 μmol photons·m^{-2}·s^{-1} with daily maxima of ~30 μmol photons·m^{-2}·s^{-1}. Significant net primary production of corallines was apparently limited to the 2–3 months with open water, and the small contribution of corallines to primary production seems due to low P_m values, low *in situ* irradiance, and their relatively low abundance in Young Sound.

Key index words: **Arctic; crustose coralline algae; microsensor; oxygen; photosynthesis-irradiance response primary production**

The high Arctic is an extreme environment for marine plants. The sea is covered by ice 9–10 months of the year, the sea floor temperature below 20 m depth is <0° C year around, and there are months of continuous darkness during winter (Rysgaard et al. 1998). Light attenuation by sea ice limits primary production, and consequently many ecosystem processes are closely tied to the few months of open water (Horner and Schrader 1982, Rysgaard et al. 1998, 1999). Detailed quantitative studies of ecosystem processes are being conducted at Daneborg in Young Sound, northeast Greenland (e.g. Rysgaard and Berg 1996, Rysgaard et al. 1998, 1999, Sejr et al. 2000, Glud et al. 2000, http://www.dmu.dk/LakeandEstuarineEcology/CAMP/). Measurements have been made of primary production by phytoplankton (Rysgaard et al. 1999), sea-ice microalgae, benthic microalgae, and brown macroalgae (Kühl et al. 2001, Rysgaard et al. 2001). Corallines are the dominant encrusting organisms on rocks that scatter the otherwise muddy sea floor in Young Sound, but the contribution of crustose coralline algae to primary production has not been determined.

Coralline algae are abundant and widespread from polar regions to the tropics (Johansen 1981, Steneck 1986). There are relatively few quantitative data on the growth and production rates of corallines (Lewis 1977, Jones and Woelkerling 1983, Chisholm et al. 1990, Garrabou and Ballesteros 2000). Corallines are slow growing algae (Johansen 1981) and are among the least productive plants in a particular environment (Goreau 1963, Marsh 1970, Littler and Murray 1974). In certain habitats, however, corallines can contribute significantly to primary production because of their sheer abundance (e.g. Lewis 1977, Littler et al. 1991). Quantitative data on the production rates or growth of corallines in polar waters is lacking. Adey (1970a, 1973) examined the effect of temperature and light on growth (marginal extension) and productivity of sub-Arctic corallines. Optimal growth occurred at temperatures of 9–15° C and declined above and below this range (Adey 1970a). Adey (1973) examined photosynthesis-irradiance relationships at various temperatures in the sub-Arctic coralline *Clathromorphum circumscriptum* and

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[1] Received 11 June 2001. Accepted 17 December 2001.

[2] Author for correspondence: e-mail mkuhl@zi.ku.dk.

found that plants used low light more efficiently at low temperatures (0–5° C) but maximum production rates were 30%–60% higher at elevated temperatures (10–20° C).

In this study we present the first comprehensive investigation of the production rates of high Arctic coralline algae. We describe the composition and abundance of the coralline flora and quantify photosynthesis-irradiance relationships for the two dominant coralline species during ice-covered and open-water seasons. Data on incident light and areal abundance are used to discuss the contribution of corallines to the carbon budget of the site.

MATERIALS AND METHODS

Location. The study was conducted at Daneborg in Young Sound, northeast Greenland. A detailed description of the site is given elsewhere (Rysgaard et al. 1996, 1998, Glud et al. 2000). Water temperature at depths >10 m is relatively constant (0 to −1.8° C). Salinity is reduced in surface waters during summer months but remains at ~34 psu in bottom waters year around. Young Sound is covered by ice for 9–10 months of the year. Sea ice begins to form in September and increases in thickness over several weeks to months to a maximum of ~1.6 m. The sea ice is usually overlain by snow, which further reduces light penetration. The snow cover melts and the sea ice thins during June; sea-ice breakout usually occurs in mid-July. When coralline specimens were collected in mid-June 1999, there was still an ~1.6-m thick ice cover with additional ~30 cm of snow on top. Sea-ice breakout occurred a month before samples from the open-water season were collected in mid-August 1999.

The sea floor at Daneborg is comprised predominantly of soft muddy sediments scattered with rocks (dropped from floating ice) and bivalve shells. The larger pebbles and boulders stand clear of the muddy sediment and offer a substratum for encrusting organisms. A small amount of additional substratum is made available by large barnacles and larger mollusk shells, but most shells and small rocks are not encrusted. The dominant encrusting organisms are crustose coralline algae, which occupy much of the available rock surface beyond ~17 m. Green, brown, and red foliose macroalgae are common in shallower waters, but their abundance declines rapidly with depth. Abundance data for corallines were collected over their full depth range at the study site. Species composition and production data relate primarily to material collected at Station B (74°18.59′ N, 20°14.39′ W) from depths of 15–18 m, with some additional material from Station A (74°18.59′ N, 20°15.04′ W, 36 m depth) and Station C (74°18.59′ N, 20°14.24′ W, 10 m depth). Station B was chosen as the primary study site because it represented the zone of maximum production (see Results and Discussion), allowed easy access through the sea ice, and was within diveable depths.

Collection and storage of material. In June 1999, divers collected random samples of coralline-coated rocks from 15 to 18 m depth and also searched this depth range for additional visually distinctive species. Divers searched extensively at 10–12 m depth but found only a single coralline specimen. Additional material was collected by grab from 36 m depth. Specimens were placed in black plastic bags under water to prevent exposure to high irradiance and low salinity in surface waters or after emersion. Specimens collected in June 1999 were held at the adjacent field laboratory at near *in situ* levels of temperature (0 ± 1° C) and irradiance (<5 μmol photons·m^{-2}·s^{-1}) in aerated seawater (collected from near the sea floor). Temperature was measured with an electronic thermistor thermometer (Omnitherm, Germany) connected to a strip chart recorder for continuous temperature recording. Light was quantified as downwelling quantum irradiance with an irradiance sensor connected to a meter (LiCor, Lincoln, NE, USA). Specimens collected in August were packed in near-bottom seawater, transported on ice to Aarhus University, Denmark, and stored in conditions as above before taken for measurements.

Species composition of corallines. Species were identified based on a key (Adey 1970b) and voucher specimens from the Botanical Museum, University of Copenhagen. The morphology of the reproductive structures is critical in identification of the species. A small proportion of corallines lacked conceptacles and therefore could not be identified. The species composition of the coralline flora was then quantified by measuring the areal coverage of each species on a random sample of 47 coralline-coated rocks and shells taken from 15 to 18 m depth. Specimens on rocks from Stations A and C were also identified.

The areal cover of corallines was estimated from three independent video surveys of the sea floor. The first was a transect swum from 22 m depth to 4 m depth. All coralline-covered rocks passing beneath the camera's field of view were measured to generate % cover estimates for each of several depth zones. The second estimate was from video footage taken at 17 m and 36 m depths by a swimming diver with a video camera. The area of coralline-covered rocks was measured in 45 fields of view at each site. The third estimate used a video camera or digital camera set on a frame to film vertically onto the sea floor over a defined area. Image analysis was used to determine the proportion of each video quadrat occupied by corallines, and a correction factor applied to take account of corallines wrapped around the sides of rocks. The correction factor was obtained by comparing the visible corallines with the actual three-dimensional cover of corallines. The latter was determined by tracing coralline cover onto transparent film that could be wrapped around rocks and then measuring the total area by image analysis.

Production measurements. Net rates of photosynthesis and respiration were measured with oxygen microsensors in the laboratory at *in situ* temperature (±1° C). Specimens were placed in a thermostated laminar flow chamber constructed of clear plastic and allowed to acclimate for 90 min at near-saturation irradiance (15–40 μmol photons·m^{-2}·s^{-1}). The experimental apparatus was enclosed within a black plastic cover, or a darkened room, to exclude ambient light. Light intensity was controlled by use of a tungsten halogen lamp (Schott Glas, Mainz, Germany) and neutral density filters.

For microprofiling, an oxygen microsensor with low (<1%–2%) stirring sensitivity (Revsbech 1989) was mounted in a motorized micromanipulator (Märtzhauser, Wetzlar/LOT-ORIEL, Darmstadt, Germany). The microsensor was connected to a pA-meter (PA2000, Unisense A/S, Aarhus, Denmark), a chart recorder, and a T3200 PC (Toshiba, Tokyo, Japan) equipped with an A/D-data acquisition card (Computer Boards Inc., Middleboro, MA, USA) and a custom-built motor controller card. The net diffusive oxygen flux, J(x), was calculated from the slope of measured oxygen microprofiles within the diffusive boundary layer (DBL) using the formula (Jørgensen and Revsbech 1985) $J(x) = -D_0\, \delta C/\delta(x)$, where D_0 is the molecular diffusion coefficient of oxygen and C is the concentration of oxygen at depth x. Oxygen calibrations were made at experimental temperature and salinity by measuring the microsensor signal in a solution of sodium dithionite in seawater (zero oxygen) and in air-saturated seawater. The molecular diffusion coefficient of oxygen was taken from Broecker and Peng (1974) and corrected for experimental temperatures as described by Li and Gregory (1974).

After the equilibration period (see above), the microsensor tip was lowered toward the coralline surface with the aid of a horizontally mounted binocular microscope until O_2 readings showed that the sensor was sufficiently close to provide at least six subsequent readings, with a vertical interval of 5 μm, within the DBL. Initial profiling sampled three to nine locations on the same specimen (depending on the variability encountered) to assess spatial variability in oxygen production and to select a representative location for measuring the photosynthesis-irradiance relationship. After finding a representative location, the light was turned off for 6 min before photosynthesis-irradiance experiments commenced. Profiles proceeded from the lowest to the highest irradiance. An equilibration period of 6 min at each new light intensity provided 95 ± 2% (mean ± SE, $n = 6$) of final equilibration.

Irradiance measurements. Downwelling irradiance (E_d, 400–700 nm) was measured in the experimental setup by an underwater quantum irradiance sensor (LiCor LI-192SA) connected to a light meter (LiCor LI-1000). Irradiance was remeasured each time the oxygen profiling apparatus was moved. Downwelling light attenuation coefficients (K_d) for ice-covered seawater were determined by vertical profiles with the same equipment. To avoid artifacts caused by the presence of the access hole (Hansen et al., unpublished data), only profiles ($n = 5$) taken beyond the influence of the ice hole were used. To achieve this, a diver installed an ice screw and carabiner in the undersurface of the sea ice at least 10 m from the hole, and the light sensor was lowered from this point. K_d values for sea ice (1.6 m thick including 10–20 cm of snow cover) in June 1999 were determined by comparing synchronized recordings of ambient irradiance at the Daneborg field station (74°18.59′ N, 20°13.58′ W) and on the undersurface of the ice at Station A. K_d values for the water column during the open water season of August 1999 used the same method, with the underwater sensor on the sea floor at 20 m depth (Station B). Hourly year around readings of incident light (400–700 nm) at the Zackenberg Ecological Research Station (25 km NNW of Daneborg) were used to estimate production over extended periods.

Curve fitting of net photosynthesis (P) versus irradiance (E_d) curves. P-E_d curves were fitted by the function of Platt et al. (1980) modified by the addition of a respiration term (R):

$$P = P_s(1-\exp(-\alpha E_d/P_s))\exp(-\beta E_d/P_s) + R \qquad (1)$$

where E_d is the downwelling irradiance (400–700 nm), P_s is a scaling parameter defined as the maximum potential photosynthetic rate in the absence of photoinhibition, α is the initial slope of the light curve before the onset of saturation and provides a measure of the efficiency with which the plant uses light at low irradiance, and β is the slope of the light curve beyond the onset of photoinhibition. In the absence of photoinhibition ($\beta = 0$) we used the simplified equation

$$P = P_m(1-\exp(-\alpha E_d/P_m)) + R \qquad (2)$$

The maximal rate of production at light saturation is termed the photosynthetic capacity, P_m, and can be derived as (Harrison and Platt 1986)

$$P_m = P_s[\alpha/(\alpha+\beta)][\beta/(\alpha+\beta)]^{\beta/\alpha} \qquad (3)$$

The index of light adaptation (i.e. the irradiance at onset of photosynthesis saturation), E_k, was calculated as $E_k = P_m/\alpha$. The compensation irradiance, E_c, where the total rate of photosynthesis equals the total rate of respiration and no net exchange of oxygen is taking place, was calculated by solving the P-E_d curve equation for E_d when $P = 0$. All P-E_d curves were fitted with a nonlinear Levenberg-Marquardt regression algorithm.

Statistical analyses. Differences in P-E_d curve parameters (P_m, E_k, α, and E_c) between seasons and coralline species were compared by two-way ANOVA and differences between depths by one-way ANOVA. Homogeneity of variances was assessed with Levene's test and normality from probability plots of residuals (Kirby 1993). The proportion of the variability in P-E_d curve parameters explained by each term in the ANOVA models was determined by magnitude of effects calculations following the methods of Graham and Edwards (2001). Negative variance components were remedied by the "pool of the minimum violator" technique (Graham and Edwards 2001).

RESULTS

Coralline species. Four species of crustose coralline algae were identified from 15 to 18 m depth (Station B), but only two were abundant. *Phymatolithon foecundum* contributed 56% of the coralline abundance (by areal coverage) and *Phymatolithon tenue* a further 35%. *Lithothamnion glaciale* Kjellman 1883 was present on only 2 of 48 rocks examined, and its abundance (7%) was probably overestimated by the chance inclusion of one very large specimen that contributed over 90% of the areal coverage for this species. The parasitic coralline *Kvaleya epilaeve* Adey et Sperapani 1971 was found on only one rock (0.03% of areal coverage). About 2% of corallines were unidentifiable because they lacked reproductive structures or other diagnostic characteristics. The single coralline specimen found at 10 m depth (Station C) was *Phymatolithon tenue*, and the three specimens collected from 36 m depth (Station A) were all *Phymatolithon foecundum. Phymatolithon tenue* could be recognized in remote images from 30 m depth by its very large conceptacles and was common at this depth.

Abundance of corallines with depth. Corallines were limited to a depth range of ~15–55 m (Fig. 1). Within this zone, they covered ~1%–2% of the sea floor along the depth transect, with the exception of a more densely populated area at around 30 m depth, where coverage averaged 6.6% (Fig. 1). No corallines were seen on video footage from <12 m depth or at 60 m depth. Diver observations confirmed the lack of corallines in shallow water, with extensive searching at 10–12 m turning up only one small specimen of *Phymatolithon tenue.* The coverage of rocks by corallines was variable. Most rocks with corallines has more or less complete cover on the upper surface, but some had areas of bare rock or (less commonly) of noncoralline encrusting red algae. The underside of rocks was bare, and some rocks that protruded above the sediment had not been colonized by encrusting organisms at all.

Microenvironment of corallines. Our microsensor measurements showed a dynamic oxygen microenvironment, which was mainly regulated by the incident irradiance at

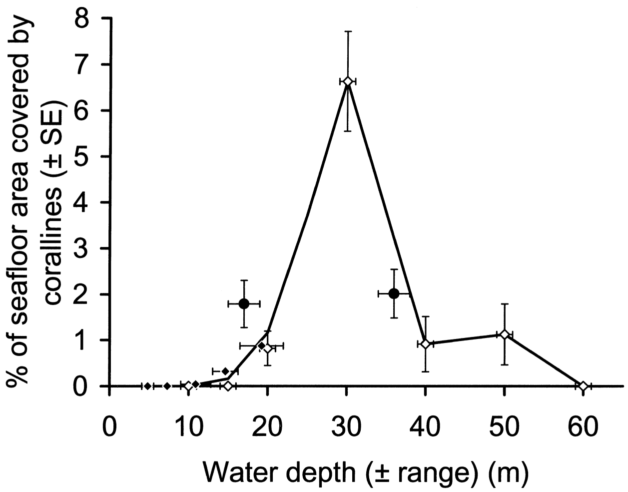

FIG. 1. Abundance (% cover) of coralline algae (all species combined) along a shore normal transect at the study site. Video A (●) and video B (◆) data were from video footage taken by a diver swimming above the sea floor. Quadrats (◇) were sea floor images from a remotely operated camera mounted in a frame. The solid line averages the available data at each depth.

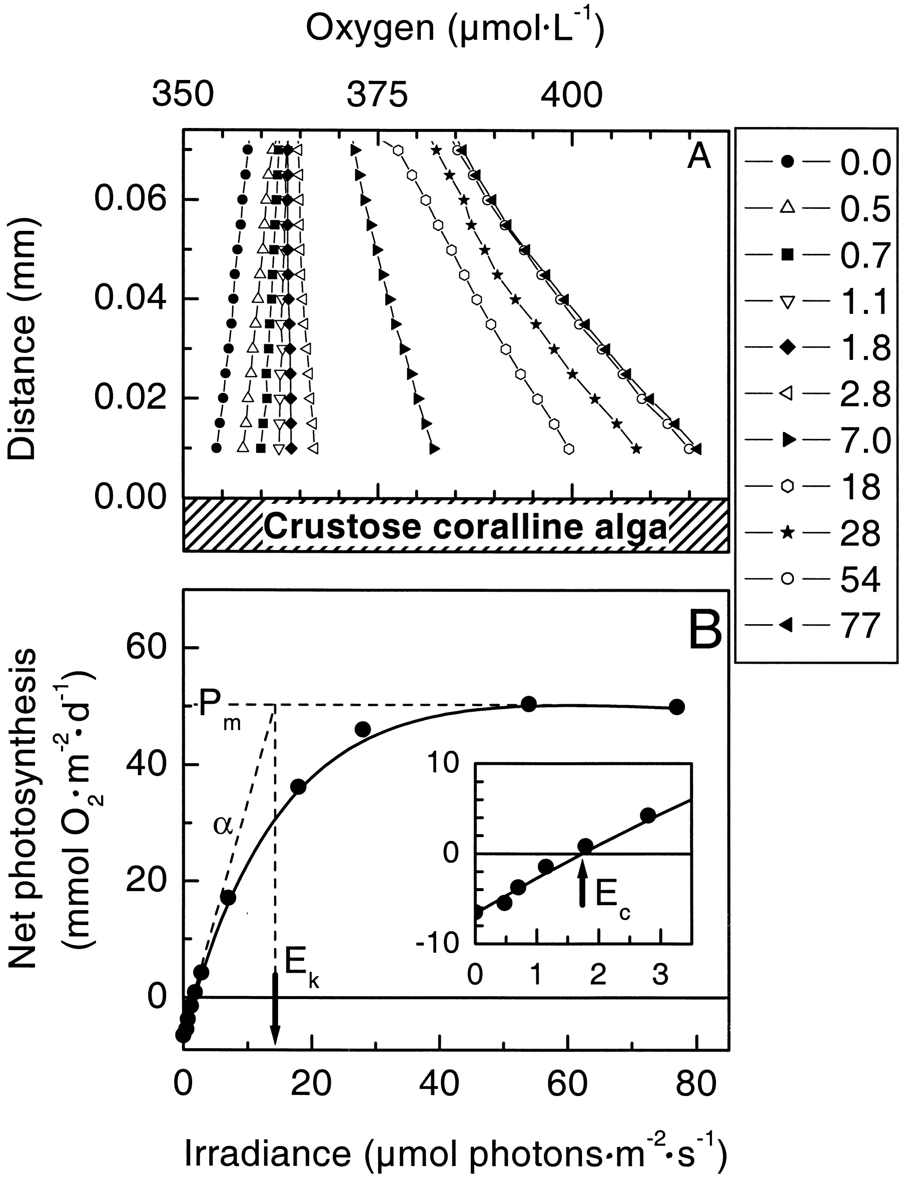

FIG. 2. Oxygen microenvironment and net photosynthesis as a function of irradiance on a coralline alga (*Phymatholithon foecundum*). (A) Profiles of O_2 concentration over the coralline surface. Each profile represents a single irradiance (denoted by numbers in the legend) in units of µmol photons·m^{-2}·s^{-1}. If the profiles were continued upward, they would converge at the O_2 concentration of the mixed water column. From each profile, the net photosynthesis can be calculated (see Materials and methods for more details). (B) Plot of irradiance (E_d) against net O_2 production rate (P). The solid line is a fitted curve following Eq. 1 in Materials and methods (r^2 = 0.9996). P-E_d curve parameters are illustrated and were calculated as described in Materials and methods.

the surface of the investigated corallines (Fig. 2A). In darkness, slightly lower oxygen levels were found on the coralline surface due to relatively low dark respiration activity. Even at very low irradiance, photosynthetic oxygen production affected the oxygen level, and above ~2 µmol photons·m^{-2}·s^{-1} the oxygen levels at the coralline surface showed supersaturation in comparison to the overlying water. The microsensor measurements showed that a thin DBL of <0.1–0.2 mm thickness was imposed by the experimental conditions. Calculations of diffusive fluxes over the DBL enabled quantification of dark respiration rates and net photosynthesis rates as a function of irradiance (Fig. 2B). Analysis of this (and many similar) P versus E_d curves showed low compensation irradiances and photoadaptive indices (Table 1).

Variability in photosynthesis rate within corallines. Profiles at several locations on a specimen were made before choosing a representative point for the P-E_d curve measurements. The variability in rates across the surface of a specimen was as great as the variability between species or between rocks (Fig. 3). There was no clear difference in the rates of net photosynthesis between nonreproductive thallus tissue and conceptacle tissue (Fig. 3).

Photosynthesis versus irradiance. P-E_d curves and derived curve parameters for the two dominant coralline species in June (ice covered) and August (open water season) 1999 are shown in Figure 4 and Table 1. The corallines were clearly adapted to low light conditions, with low values for photosynthetic capacity (P_m), light compensation point (E_c), and index of light adaptation (E_k). P_m averaged 40–50 mmol O_2·m^{-2} thallus·d^{-1}. The higher average for *Phymatolithon foecundum* in June (Table 1) was largely due to a single exceptional specimen with a P_m of 101 mmol O_2·m^{-2} thallus·d^{-1}

TABLE 1. Summary of photosynthesis vs. irradiance curve parameters for the two dominant coralline species (*Phymatolithon foecundum* and *Phymatolithon tenue*) in June (ice covered) and August (open water) 1999.

P-E_d parameter	June		August		ANOVA data				
	P. foecundum	*P. tenue*	*P. foecundum*	*P. tenue*		Season	Species	Interaction	Error
Pm	66.9 ± 11.7	47.2 ± 4.08	45.2 ± 18.2	42.5 ± 11.4	F	2.591	1.854	1.060	
					P	0.133	0.198	0.324	
					ω^2	8.6	4.6	0.3	86.5
α	4.26 ± 0.84	4.20 ± 0.8	6.34 ± 1.0	5.10 ± 0.63	F	2.866	0.552	0.452	
					P	0.116	0.472	0.514	
					ω^2	11.5	0.0	0.0	88.5
E_k	16.7 ± 2.43	12.5 ± 2.25	7.13 ± 0.75	8.36 ± 0.58	F	15.853	0.712	2.421	
					P	**0.002**	0.415	0.146	
					ω^2	46.5	0.0	4.5	48.9
E_c	1.53 ± 0.21	1.35 ± 0.33	1.82 ± 0.32	0.71 ± 0.15	F	0.420	5.913	3.078	
					P	0.529	**0.032**	0.105	
					ω^2	0.0	22.1	9.5	68.4

Values are mean ± SE, $n = 4$. Data from a two-way fixed-factor ANOVA (degrees of freedom = 1, 12) are shown at right, with significant differences ($P < 0.05$) in bold type.

P_m, photosynthetic capacity (mmol $O_2 \cdot m^{-2}$ thallus$\cdot d^{-1}$); α, initial slope of P-E_d curve [(mmol $O_2 \cdot m^{-2}$ of thallus$\cdot d^{-1}$/(μmol photons$\cdot m^{-2} \cdot s^{-1}$)]; E_k, index of light adaptation; E_c, compensation irradiance (both in units of μmol photons$\cdot m^{-2} \cdot s^{-1}$). ANOVA data are F = F ratio, P = P value, and ω^2 = magnitude of effects (%). The magnitude of effects is the percentage of the variation in the response variable explained by each term in the ANOVA model.

(Fig. 4). Excluding this specimen, P_m values ranged from 27 to 63 mmol $O_2 \cdot m^{-2}$ thallus$\cdot d^{-1}$. E_c values were low for all corallines, ranging from 0.42 to 2.7 μmol photons$\cdot m^{-2} \cdot s^{-1}$. E_c values were significantly lower for *Phymatolithon tenue* than for *Phymatolithon foecundum*, but the absolute difference was marginal (Table 1). E_k values were low for all corallines (maximum of 21.6 μmol photons$\cdot m^{-2} \cdot s^{-1}$) and about 2-fold lower in August than in June (Table 1). Magnitude of effects calculations confirmed the relatively small influence of the season, species, and interaction terms in controlling the PE response of the corallines (Table 1). The error term was the dominant source of variation for all parameters except for E_k, where season explained 47% of the variation (Table 1).

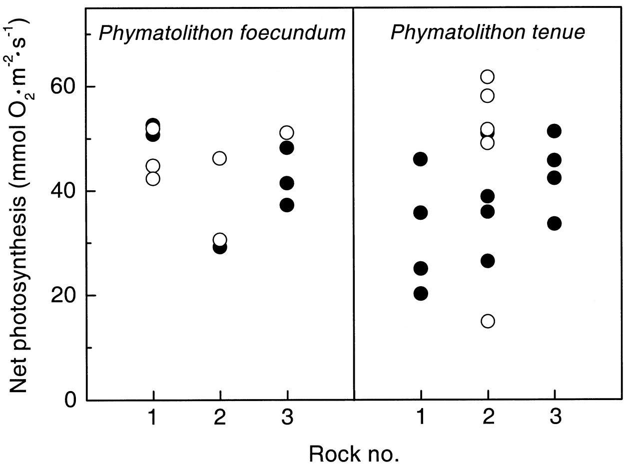

FIG. 3. The spatial variation in production rates across the surface of individual coralline algae. Data are from three rocks, each with one specimen of *Phymatolithon foecundum* and one specimen of *Phymatolithon tenue.* For each specimen, production measurements were made under constant irradiance at several locations on the surface of specimen. Some measurements were made over nonreproductive thallus tissue (●) and others over conceptacles (○).

We compared P-E_d curve parameters for *Phymatolithon foecundum* collected in June from 17 m and 36 m depth. Although corallines from 36 m had lower average values for P-E_d curve parameters, they were within the range encountered for corallines from 17 m depth, and none of the parameters differed significantly between the depths (Table 2). Magnitude of effects analysis showed that depth explained 32% of the variation in P_m values but less than 10% of the variation in other PE-curve parameters. The effect on P_m was exaggerated by the exceptionally high P_m value for one plant at 17 m depth (Fig. 4)

Given the minor differences in the P-E_d curve parameters between coralline species, seasons, and depths (Fig. 4, Tables 1 and 2), a generalized P-E_d curve was fitted to the P-E_d data (Fig. 5) for the purposes of estimating production at the site. The generalized P-E_d curve (based on 191 profiles from 20 individual P-E_d curves) had a P_m of 48.9 mmol $O_2 \cdot m^{-2}$ thallus$\cdot d^{-1}$, E_k of 12.7 ·mol photons$\cdot m^{-2} \cdot s^{-1}$, α of 3.84, and E_c of 1.30 μmol photons$\cdot m^{-2} \cdot s^{-1}$. The dark respiration rate was 4.8 mmol $O_2 \cdot m^{-2}$ thallus$\cdot d^{-1}$. Photoinhibition was evident in the generalized P-E curve ($\beta = 0.166$) and in most of the P-E_d curves for individual specimens (Fig. 4).

Irradiance and production rates. Attenuation of downwelling irradiance by the June 1999 sea ice (1.6 m thick) was high, with K_d values averaging 3.19 m^{-1} (Table 3). Water beneath the sea ice was relatively clear, with K_d values averaging 0.09 m^{-1} (Table 3). Much higher attenuation coefficients were recorded for the water column during the open water season (average K_d values of 0.194 and 0.197 m^{-1} for two methods of

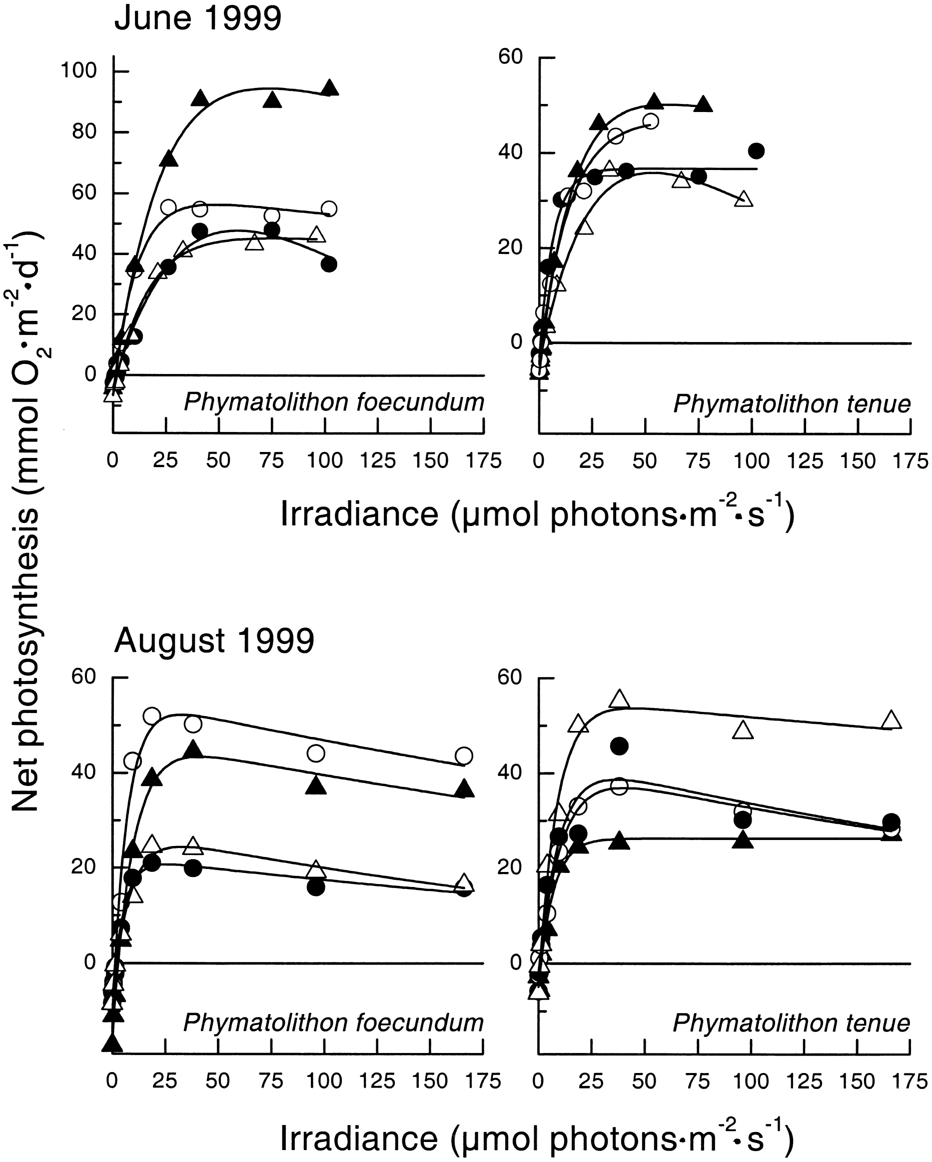

FIG. 4. Net photosynthesis (P) versus irradiance (E_d) curves for individual specimens (denoted by the different symbols) of the two dominant coralline species in June (1.6 m sea-ice cover) and August (open-water season). Solid lines are fitted curves based on Eq. 1 in Materials and Methods. $r^2 > 0.98$ for all but one curve ($r^2 = 0.93$).

estimation) (Table 3). K_d values for both sea ice and the water column showed considerable variation on a scale of hours to days (data not shown).

Irradiance at 17 m depth under full ice cover averaged ~1 µmol photons·m^{-2}·s^{-1}, with daily maxima of ~1–4 µmol photons·m^{-2}·s^{-1} (Tables 4 and 5). The average irradiance was around the light compensation point (E_c) of the corallines (Tables 1 and 2), indicating that production is negligible under full ice cover (1.6 m thick), even with summer light levels and near the minimum water depths occupied by corallines.

Predicted irradiance levels at 17 m depth during the open water season averaged ~9 µmol photons·m^{-2}·s^{-1}, with a maximum of ~46 µmol photons·m^{-2}·s^{-1} (Table 5). Data collected at 20 m depth over 2 days in mid-August (Table 4) gave corresponding values at 17 m depth averaging ~15 µmol photons·m^{-2}·s^{-1}, with daily maxima of ~54 µmol photons·m^{-2}·s^{-1}. Thus, during the open water season corallines in the shallow part of their depth range (around 17 m depth) received average irradiance levels roughly equal to their E_k values (Table 1) and maximum irradiance levels that would saturate photosynthesis (Figs. 2, 4, and 5).

Modeled data showed that the production of corallines at 17 m depth was closely tied to the annual cycle of sea-ice cover (Fig. 6). Irradiance was low, and net oxygen production was negative under 1.6 m of sea-ice in early June. Irradiance and production rose sharply as sea ice thinned and broke out. Maximum production occurred in July, after which production gradually declined along with the seasonal decline in light to be near zero by the end of September (Fig. 6). The highest daily averages for production at 17 m depth were ~35 mmol O_2·m^{-2} coralline thallus·d^{-1} or

TABLE 2. Photosynthesis vs. irradiance (P-E_d) curve parameters for *Phymatolithon foecundum* from 17 m and 36 m depth in June 1999.

			ANOVA data		
P-E_d parameter	17 m	36 m		Depth	Error
P_m	66.9 ± 11.7	40.2 ± 3.82	F	0.073	
			P	0.073	
			ω^2	31.7	68.3
α	4.26 ± 0.84	3.19 ± 0.87	F	0.073	
			P	0.332	
			ω^2	1.4	98.6
E_k	16.7 ± 2.43	13.1 ± 3.71	F	0.073	
			P	0.258	
			ω^2	6.6	93.4
E_c	1.53 ± 0.21	1.18 ± 0.18	F	0.073	
			P	0.243	
			ω^2	7.8	92.2

Values are mean ± SE, n = 4. Data from a one-way fixed-factor ANOVA (degrees of freedom = 1, 6) are shown at right.

P_m, photosynthetic capacity (mmol $O_2 \cdot m^{-2}$ thallus d^{-1}); α, initial slope of P-E_d curve [(mmol $O_2 \cdot m^{-2}$ thallus$\cdot d^{-1}$/(µmol photons$\cdot m^{-2} \cdot s^{-1}$)]; E_k, index of light adaptation, E_c, light compensation point (both in units of µmol photons$\cdot m^{-2} \cdot s^{-1}$). ANOVA data are F = F ratio, *P* = P value, and ω^2 = magnitude of effects (%). The magnitude of effects is the percentage of the variation in the response variable explained by each term in the ANOVA model.

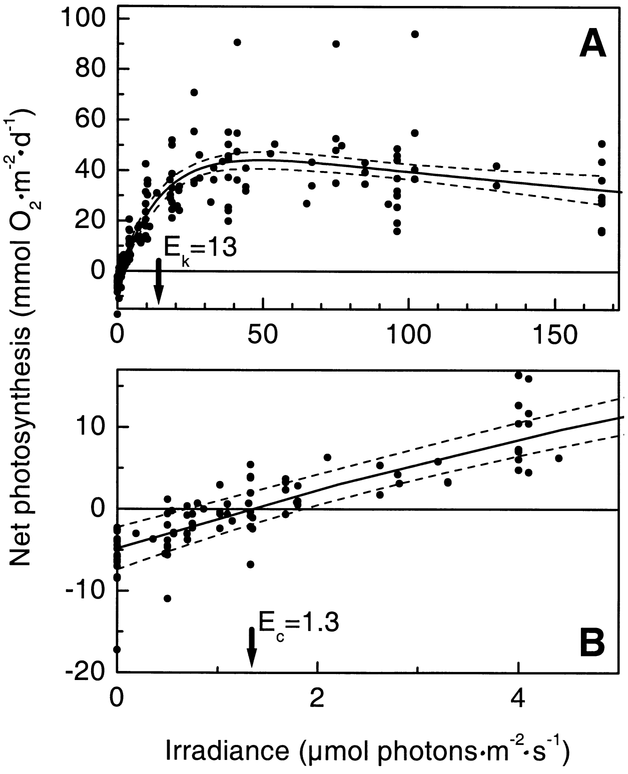

FIG. 5. A generalized photosynthesis-irradiance curve for corallines at the study site. The solid line is the fitted curve (r^2 = 0.79) based on Eq. 1 in Materials and methods, with P_s = 57.99 ± 5.37, α = 3.84 ± 0.470, β = 0.155 ± 0.070, and R = −4.80 ± 1.31 (mean ± 95% confidence interval). The dotted curves are 95% confidence intervals for the fitted curve. The black circles are the raw data to which the curve is fitted. The data represent P-E_d curves for 20 individual specimens, totaling 191 oxygen profiles.

~200 g $C \cdot m^{-2}$ coralline thallus$\cdot yr^{-1}$. This is close to the maximum modeled production rates (P_m) for the corallines (Fig. 5) of ~50 mmol $O_2 \cdot m^{-2}$ thallus$\cdot d^{-1}$ or ~300 g $C \cdot m^{-2}$ thallus$\cdot yr^{-1}$. However, P_m values would be attained only near mid-day during the open water season and only in water <20 m deep. The average production rate at 17 m depth over the 4-month period from June to September 1999 was ~12 mmol $O_2 \cdot m^{-2}$ thallus$\cdot d^{-1}$ or ~70 g $C \cdot m^{-2}$ coralline thallus$\cdot yr^{-1}$.

The low abundance of corallines (Fig. 1) limits their contribution to primary production. At 17 m depth the corallines covered about 1% of the sea floor (Fig. 1), giving maximum production rates of ~0.44 mmol $O_2 \cdot m^{-2}$ sea floor$\cdot d^{-1}$ or ~2.6 g $C \cdot m^{-2}$ sea floor$\cdot yr^{-1}$, and average rates during June to September were 4-fold lower than maximum rates. Thus, even in the shallow part of their depth range, the average production from corallines over the four summer months from June to September was only ~0.23 g $C \cdot m^{-2}$ of sea floor.

Decreased irradiance in deeper water (Table 5) would reduce coralline production despite the peak in coralline abundance at ~30 m depth (Fig. 1). In the deeper part of the coralline's range, irradiance levels were extremely low during both the open-water and ice-covered seasons (Table 5). Average irradiance levels at both 35 m and 50 m depth (Table 5) were below the measured light compensation point of the corallines (Tables 1 and 2). At 50 m depth, predicted irradiance levels were higher in the ice-covered season than the open-water season because the higher clarity of the ice-covered water column offset the strong attenuation of light by the sea ice.

TABLE 3. Attenuation coefficients for downwelling irradiance (K_d) for the water column during open-water and sea-ice covered seasons and for sea ice in the summer of 1999.

Water body	Observation period	Estimation method	Estimated K_d (mean ± SD m^{-1})	*n*
Water column				
during open water	15 to 16 Aug 1999	Sensors in air and 20 m depth	0.197 ± 0.033	45
	30 July to 12 Aug 1999	Underwater profiling	0.194 ± 0.026	5
Sea-ice (1.6 m thick)	11 June to 2 July 1999	Sensors in air and under ice	3.19 ± 0.34	471
Water column				
under sea-ice cover	11 June to 2 July 1999	Profiles clear of ice-hole effects	0.09 ± 0.004	5

Table 4. Measured downwelling irradiance (400–700 nm) at 17–20 m depth during the open water and under full sea-ice cover (1.6 m thickness).

Season	Depth (m)	Observation period	Irradiance measure	Underwater irradiance	Ambient irradiance
				μmol photons·m^{-2}·s^{-1}	
Open water	20	15 to 16 Aug 1999	Daily maxima	31–32	950–975
			Average	8.6	345
Full ice cover	17	11 June to 3 July 1999	Daily maxima	1.2–4.1	1250–1300
			Average	1.1	550

DISCUSSION

Crustose corallines are the dominant encrusting algae and are the most abundant macroalga beyond 20 m depth at the investigated site. However, we showed that they occupied only 1%–2% (rarely up to 7%) of the sea floor area and their contribution to primary productivity appeared to be very small.

Corallines are adapted to low light and have low photosynthetic capacity. The P-E_d responses of the two dominant coralline species at Daneborg were attuned to low light levels. Our measured E_k and E_c values were lower than those of most other algae (Kirk 1994) but comparable with those of other macrophytes and microalgae from low light polar environments (Kirk 1994, Kühl et al. 2001). The corallines showed low rates of net photosynthesis with P_m values of ~50 mmol $O_2 \cdot m^{-2}$ thallus·d^{-1} or ~300 g C·m^{-2} thallus·yr^{-1}. These rates are comparable with rates reported for crustose corallines in some tropical (Chisholm et al. 1990) and temperate locations (Littler and Murray 1974) but are lower than most rates reported for other crustose corallines (Adey 1973, Littler and Doty 1975, Wanders 1976, Littler et al. 1991, Kaspar 1992) or foliose macroalgae (e.g., Littler and Murray 1974, Krause-Jensen and Sand-Jensen 1998). However, similarly low P_m values were recorded for the brown alga *Laminaria saccharina* in the Young Sound (Kühl et al. 2001).

Coralline algae occur over a huge range of irradiance regimes. At the lower extreme the corallines include the deepest known benthic algae, occurring at depths of well over 200 m (Steneck 1986). Adey (1970a) found that *Phymatolithon tenue* [formerly *Leptophytum laeve* (Strømfelt) Adey] grew well at low light intensities of 20–50 lux, but the ability of marine macrophytes to store photosynthates for use during prolonged darkness (Drew 1983, Steneck 1986, Dunton 1990) may influence these data.

Production of corallines at Daneborg is limited by light. In addition to their low photosynthetic capacity, the production rates of corallines at Daneborg are limited by irradiance. Irradiance levels sufficient to produce P_m values are only experienced during the open-water season and only in water less than ~20 m depth. Sea-ice cover strongly attenuates light, effectively limiting coralline production to the 2- to 3-month period of open water. The relatively deep water inhabited by the corallines and the relatively high K_d values during the open-water season meant that most corallines in Young Sound never experienced irradiances of more than a few μmol photons·m^{-2}·s^{-1}.

Low abundance limits the contribution of corallines to primary productivity. Despite the generally low P_m values of crustose coralline algae, their local contribution to productivity is sometimes magnified by their sheer abundance (e.g. Littler et al. 1991). This was not the case at Daneborg, where corallines occupied only 1%–2% (exceptionally up to 7%) of the sea floor within a relatively narrow depth range of ~15–50 m. The low abundance of corallines results from the limited amount of hard substrata (mostly scattered rocks) that protruded above the fine sediment characteristic of Young Sound (Glud et al. 2000). The peak in coralline abun-

Table 5. Predicted downwelling irradiance (400–700 nm) at various depths during the open-water season (based on 1732 measurements between 8 July and 30 September 1999) and under full sea-ice cover (1.6 m thickness; based on 745 measurements between 1 and 15 June 1999).

Season	Irradiance measure	Incident irradiance (μmol photons·m^{-2}·s^{-1})	Irradiance at depth of		
			17 m	35 m	50 m
Open water	Average	302	8.96	0.258	0.013
	Maximum	1298	45.6	1.31	0.068
	Minimum	0.006	0.000	0.000	0.000
Full ice cover	Average	592	0.795	0.157	0.041
	Maximum	1392	1.99	0.394	0.041
	Minimum	53.7	0.071	0.014	0.004

Predictions are based on light attenuation coefficients from Table 3 and hourly records of incident PAR at nearby Zackenberg (see Materials and methods). Seventeen and 50 meters are approximate minimum and maximum depth limits of corallines at the study site (see Fig. 1).

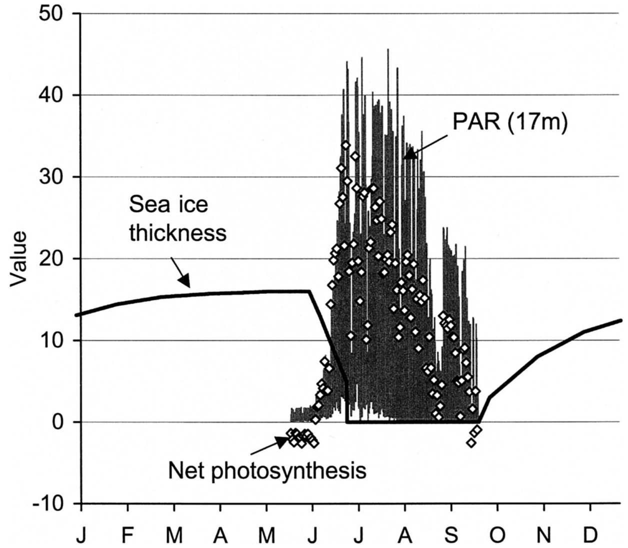

FIG. 6. Annual cycle of sea-ice cover (thick line) and its effect on irradiance levels (gray lines) and net photosynthesis of corallines (◇) at Station B, 17 m depth. Sea-ice thicknesses (shown as meters ×10 on the figure) are from Rysgaard et al. (1998) but assuming breakout when ice thins to 30 cm. Hourly irradiance levels (μmol photons$\cdot$m$^{-2}\cdot$s^{-1}, 400–700 nm) at 17 m depth are based on incident photosynthetically active radiation (PAR; in air) and K_d values from Table 3. For simplicity it was assumed that the K_d of sea ice did not vary with its thickness and that the water column K_d value switched from the "ice-covered" to the "open-water" value when sea ice broke out. Daily averages of net photosynthesis (mmol $O_2\cdot m^{-2}$ thallus$\cdot$d^{-1}) of corallines at 17 m depth are based on the fitted P-E_d curve in Figure 5. Production was estimated only during the period studied (June to September inclusive). x axis ticks mark the middle of each month.

dance at ~30 m depth resulted from a higher abundance of large surface rocks and was probably a feature local to the specific transect rather than a consistent feature at this depth throughout Young Sound.

The maximum depth limit of corallines in Young Sound may be determined by the availability of light or suitable substrate. The proportion of sediment volume contributed by rocks drops from 12.8% at 36 m depth (Station A) to only 2% at 60 m depth (Glud et al. 2000), coinciding with the maximum depth limit of corallines. Irradiance levels at 50 m depth were ~0.004% of surface illumination in the open water season and ~0.007% during ice cover in June.

The minimum depth limit of corallines in Young Sound is probably not determined by light. Both *Phymatolithon foecundum* and *Phymatolithon tenue* occupy cold and relatively deep water (Adey 1970a). However, the minimum depth at which *P. tenue* is found decreases in colder water (Adey 1970a), and this species was abundant in 3–9 m of water in Labrador (Adey 1970a). We recorded only slight inhibition of photosynthesis at irradiances of up to 166 μmol photons$\cdot$m$^{-2}\cdot$s^{-1}, suggesting that these corallines could occupy shallower water without sustaining significant damage. We speculate that the minimum depth limit of corallines in Young Sound is due to ice scouring (Gutt et al. 1996, Conlan et al. 1998), walrus feeding disturbance (Oliver et al. 1985), and overgrowth by foliose macroalgae.

Contribution of corallines to primary production in Young Sound. Our study focused on Station B where water depth was 17 m. This site represents a best case scenario in terms of coralline productivity because it was the shallowest area where corallines were abundant. Production per unit area of sea floor would be much lower in the zone of peak abundance at 30 m depth due to the much lower ambient irradiance. Net production at the 17 m station from 1 June to 30 September 1999 averaged only 0.23 g C$\cdot$m^{-2} of sea floor. Production would be progressively lower if averaged over the whole year at 17 m depth, the full depth range of the corallines, and the sea floor at all depths in Young Sound. Even the maximum production rate we estimated for the corallines is low compared with pelagic primary production of ~10 g C$\cdot$m$^{-2}\cdot$yr^{-1} (Rysgaard et al. 1999). Thus, corallines make only a minor contribution to the overall primary productivity in Young Sound.

Adaptation to altered irradiance. Kühl et al. (2001) showed that macroalgae under sea ice are capable of acclimating their photosynthetic electron transport to changing irradiance within a matter of minutes. This is consistent with our microelectrode data that showed that 95% of final equilibration occurred within 6 min of changing to a new irradiance (see Materials and methods). After the 90-min initial acclimation period, the investigated specimens were fully acclimated at the time of measurement and gave an accurate picture of the P-E_d response of light-adapted corallines.

However, it is likely that corallines experiencing long-term darkness are capable of reducing their dark respiration rate. Dark respiration rates averaged ~5 mmol $O_2\cdot m^{-2}$ thallus$\cdot$d^{-1}. This was about 10% of P_m, which is within the normal range of 5%–20% found for macroalgae (e.g. Adey 1973, Littler and Murray 1974, Kaspar 1992). Corallines in Young Sound are, however, under sea-ice cover for 9–10 months of the year, which reduces irradiance to very low levels, and in most of their depth range the algae will therefore not experience light intensities sufficient to approach P_m. In these conditions, a respiration rate of ~5 mmol $O_2\cdot m^{-2}$ thallus$\cdot$d^{-1} cannot be sustained year around. Respiration rate could decrease in response to prolonged periods of low irradiance. A short-term postillumination enhancement of respiration followed by a decreasing dark respiration rate over time is found in many aquatic phototrophs (Falkowski and Raven 1997) but has to our knowledge not been investigated in crustose coralline algae. Further measurements of dark respiration, especially during winter, are needed to elucidate seasonal changes in dark respiration.

Spectral effects on the P-E_d response. Spectral light effects on photosynthesis in corallines may also contribute to the disparity between the P-E_d relationship measured in the laboratory and the observed depth distribution of corallines in Young Sound. We used a tungsten-halogen lamp, and in the experimental setup light passed through only 1–3 cm of water to reach the coralline specimen. On the sea floor, the corallines receive light that has passed through many meters of seawater (absorbing red light), containing dissolved and particulate matter (absorbing blue light). In the open-water season only 0.005% of surface light reaches the sea floor at 50 m depth. The spectral composition of this light will be quite different from that of light incident on the water surface and will primarily consist of light in the spectral region where the phycobilins of corallines absorb (560–600 nm).

Their pigment composition enables corallines to efficiently exploit those wavelengths that penetrate to deeper water. The utilization of other wavelengths supplied in our laboratory experiments may be more inefficient. Action spectra of photosynthesis in red algae thus show a low efficiency of blue and red light in fueling photosynthesis (Neori et al. 1988). If this is the case, then our laboratory measurements overestimate the light compensation point of the corallines and, consequently, underestimate productivity. The error may increase with depth as the spectral range of the light becomes narrower and the pigmentation of the corallines changes (Payri et al. 2001). Clearly, future studies of coralline primary production need to incorporate spectral light effects on P-E_d relationships.

CONCLUSION

The contribution of corallines to primary productivity at the high Arctic Young Sound is low, primarily because of their low abundance, their low photosynthetic capacity, and the low ambient irradiance levels in their habitat. As in many other marine habitats, corallines are the deepest macrophytes at this site and must operate at very small energetic margins to survive and grow at the extreme of their depth range. Yet even corallines from relatively deep water (36 m) had the ability to respond rapidly to irradiances orders of magnitude higher than they would experience *in situ*. This plasticity may serve them well in responding to windows of high light conditions to accumulate reserves for periods of prolonged darkness. In shallow water, production by corallines is closely tied to the open water season, so any change in the duration of that period will have a marked effect on their modest production. More detailed logging of the *in situ* irrradiance and spectral quality and studies of the ecophysiology of crustose coralline algae are needed to calculate more accurate budgets of coralline primary production, for example, with respect to regulation and magnitude of dark respiration and with respect to the dependence of P-E_d relationships on the spectral composition of light.

This study was part of the project *Changes in Arctic Marine Production* (http://www.dmu.dk/LakeandEstuarineEcology/CAMP/) and was funded by the Danish Natural Science Research Council (contracts 9700549, 9701839, 97000224, 9802967), the Commission for Scientific Research in Greenland (contract 602-53), and a BRAP grant from the New Zealand Ministry of Research Science and Technology. The hospitality of the Danish military division *Sirius* is gratefully acknowledged, as is the logistical help of the whole team in the summer 1999 expeditions to Daneborg. Peter Bondo Christensen, Mikael Sejr, Thomas Rasmussen, and Goran Ehlmé are thanked for their contributions to diving, field sampling, and data on coralline abundance. Jens Würgler Hansen is thanked for data on underwater light and ice hole effects. Susse Wegeberg is thanked for providing literature on Arctic corallines, access to voucher specimens, and confirmation of coralline identifications. Anni Glud (University of Copenhagen) and Preben Sørensen (University of Aarhus) are thanked for providing microsensors, technical assistance, and measuring equipment for the study. Thanks to Niels Peter Revsbech and Lars Riis Damgaard (University of Aarhus) for providing facilities and helpful advice and to Claire Taylor for tireless data processing. Joe Trodahl provided useful information on the complexities of light attenuation by sea ice, and Paul Gillespie gave helpful criticism of the manuscript.

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