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Author(s): Jon A. Sperling
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ALGAL ECOLOGY OF SOUTHERN ICELANDIC HOT SPRINGS IN WINTER[1]

JON A. SPERLING
Department of Biology, Queens College (C.U.N.Y.), Flushing, New York 11367

Abstract. A survey of algal habitats of southern Icelandic hot springs (Hengill-Ölfus district) was made between December 15, 1968, and January 20, 1969. Carbon-14 primary productivity was measured in experiments designed to compare the role of direct solar radiation on algal habitats of different aspect and inclination. Incident light (0.4–0.7 μm) energy on December 20, was 23.1, 3.3, and 5.1 g-cal/cm^2·day for south-facing 60° slopes, north-facing 60° slopes, and horizontal surfaces, respectively. Primary productivity for algal cores incubated (in vials) in these positions was 1110, 260, and 1130 mg C/m^2·day. Coincidence of productivity of south-facing and horizontally-incubated cores suggested that the latter received far more illumination than was indicated by light meter readings. Similar results were noted for incubations carried out on January 8, 1969.

Submersed algal habitats exhibited a dramatic cutback from their summer appearance. Residual populations of *Mastigocladus laminosus* Cohn were found up to 55°C in quiet waters. Healthy mats of *Phormidium corium* (C.A. Ag.) Gomont, *Lyngbya martensiana* Menegh. and *Mastigocladus* occurred locally in south flowing effluents (41°–31°C) in moderate to fast flow. The aerial blue-green algal community bordering the hot springs appeared unchanged from that of the summer.

The cryptic persistence of *Mastigocladus* on submerged rock from habitats (55°–40°C) having a swept bare appearance was demonstrated in the laboratory. This finding obviates the suggestion that nonthermal overwintering niches might serve as seeding sources for the large-scale resumption of growth in the spring.

Eight of the 14 PVC substrates left for 15 days in thermal effluents showed signs of colonization, which indicated that the 24-h compensation point for this period had been exceeded.

Key words: Algae; algae, blue-green; algae, thermophilic; algae, winter survival; algal ecology; Iceland; Icelandic hot springs; Mastigocladus; *photosynthetic efficiency; primary productivity; winter light in high latitudes.*

INTRODUCTION

Knowledge of the winter ecology of the Icelandic thermal algae is based on limited observations in the field (Schwabe 1936), on calculated light values for a hypothetical Icelandic hot spring with respect to the compensation point of a nonthermophilic blue-green alga, *Phormidium foveolarum* (Harder, in Tuxen 1944), and on experiments conducted in Yellowstone hot springs where opaque filters were used to simulate Iceland's short winter days (Brock and Brock 1968). These investigators concur that for a period of about 2 mo around the winter solstice there is insufficient light for algal growth, and that beginning about early November the algae disappear from the hot springs to return again between late January and early spring. It has been suggested that the seeding source for this return are algae that have survived in a dried and possibly frozen state, in nonflowing thermal waters, or in cooler zones of the thermal effluents (Castenholz 1967, 1969*a*).

The author made an algal survey of southern Icelandic hot springs during the summer of 1966. Investigations to ascertain the importance of direction and angle of exposure (inclination from the horizontal) of the algal habitat were done between December 15, 1968, and January 20, 1969.

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STUDY AREA

Hengill-Ölfus district, 64 N lat (Army Map Service 1961).

1. Hofmannaflöt, 64° 02′ N, at the SW base of Dalafell.

   Site 12. An unnamed rheotherm, about 25 m due north of a large borehole drilling rig (at that location since 1952) at the end of the unpaved road. Effluent on a steep slope (30°–70°). Site facing S 15° W.

   Site 9. The most westerly of several small, closely-spaced rheotherms, about 100 m ENE of the road terminus at the borehole drilling site, joining with a larger effluent to form a tepid pool 8–10 m in diameter. Site facing S 10° E.

   Site 10. The shallow (about 40-cm maxi-

TABLE 1. Physicochemical data from incubation, colonization experiment, and collection sites

Site	pH	Temperature, °C[a]	Alkalinity,[b] total (ppm)	Hardness,[b] Ca/total (ppm)	Cl^- (ppm)	SiO_2^- (ppm)	Specific conductivity[c]
3a	6.9	40	195	125/155	25	55	4200
92	6.9	33	110	65/n.d.[d]	60	52	4000
93	9.6	50	155	15/n.d.	n.d.	n.d.	1050
12	7.5	37	90	75/85	15	n.d.	3100
4	7.2	25	210	135/175	25	n.d.	4200
9	7.0	37	150	85/105	25	n.d.	3700
10	7.4	25	185	115/150	20	n.d.	3900
5	8.2	36	115	60/65	80	n.d.	5600
104	6.7	50	210	120/190	15	100	6200

[a] Temperature at primary productivity and PVC substrate incubation sites.
[b] Total alkalinity and hardness as $CaCO_3$.
[c] Specific conductivity in mho/cm at 25°C.
[d] n.d. = no data.

mum depth) tepid pool immediately below site 9.

Site 3a. The most westerly of three closely-spaced rheotherms located about 160 m ENE of the road terminus. Springs issuing on a slope of 10°–25°. Site facing S 10 E.

Site 4. Several meters due west of site 3a, in the runoff of a rheotherm issuing on a gentle slope about 80 m directly north of 3a.

2. Gufudalur, 64° 02′ N.

Site 92. An unnamed rheotherm descending the steep (nearly vertical) north bank of the Varmá, and located about 150 m WNW of the one-lane wooden bridge crossing the Varmá.

Site 93. Runoff from a borehole on the farm premises at Gufudal. The effluent descends a short, steep north slope and enters into the Saudá.

3. Klambragil, 64° 03′ N (upper Reykjadalsá).

Site 104. In the Reykjadalsá, in moderate to swift flow. In the immediate vicinity of a small wooden building ("hut"). Flow approximately level.

4. In the town of Hveragerdi. 64° 00′ N.

Site 5. A fast-flowing warm stream formed by the overflow of a swimming pool ("sundlaug" on map). Steep banks block this site from receiving direct solar radiation in early winter.

Physicochemical data for the above sites is presented in Table 1.

Materials and Methods

Water samples were collected in washed polyethylene bottles (125 ml). No more than 4 h elapsed between collections and water analyses. Total alkalinity was determined titrimetrically against the methyl orange indicator (American Public Health Association 1965). Hardness and chloride-ion concentration were measured titrimetrically by modifications of the EDTA and mercuric nitrate methods, respectively (Hach Chemical). A Wheatstone bridge (Solu bridge, RB3, Industrial Instruments) was used to measure specific conductance. A glass combination electrode connected to a portable meter (pH-180, Beckman Instruments) was used to determine pH. Temperature was measured with a mercury bulb thermometer. From some of this data the total carbon dioxide was obtained nomographically (American Public Health Association 1965).

Light

Light readings were taken with a Weston illumination meter (model 756, Weston Instruments). Directional illumination was determined at each light reading by holding the light target of the meter due south and due north at inclinations of 60° from the horizontal and horizontally. Illumination curves were established for 17 days. Total foot-candle values for these curves were determined by planimetry and converted to $g\text{-}cal/cm^2 \cdot day$ using the following conversion factors: 6700 foot-candles = 1 g $cal/cm^2 \cdot day$ under cloudless conditions (Kimball 1924), and 7000 foot-candles = 1 g $cal/cm^2 \cdot day$ under cloudy conditions (Reifsnyder and Lull 1965) (Table 2).

The spectral sensitivity of the photovoltaic cell exceeded the visible light range (0.4–0.7 μm) by 11% (Weston Instruments 1969). The illumination values reported are corrected to include only the visible spectrum. Other weather data were obtained from reports of the Icelandic Weather Bureau (Vedráttan 1961–1969) (Table 2).

TABLE 2. Light energy (g-cal · cm^{-2} · day^{-1}) of the visible spectrum (0.4–0.7 μm) on horizontal and south- and north-inclined surfaces during 17 winter days in Iceland

Date	North (60° inclination)	South (60° inclination)	Horizontal	Vedráttan[a] 1968–1969
Dec. 20/68	3.3	23.1	5.1	6.0
Dec. 24	3.0	10.7	4.8	6.0
Dec. 25	4.5	22.3	5.6	5.0
Dec. 26	4.3	20.0	5.8	7.0
Dec. 27	6.7	8.9	7.1	4.0
Dec. 28	2.3	2.5	2.9	3.0
Dec. 29	1.0	1.1	1.6	3.0
Dec. 30	1.1	1.2	1.3	2.0
Dec. 31	0.8	0.9	1.0	1.0
Jan. 1/69	1.2	1.3	1.5	1.0
Jan. 2	4.0	4.4	4.8	5.0
Jan. 3	4.4	18.6	6.5	9.0
Jan. 4	5.3	26.7	6.7	10.0
Jan. 5	4.9	27.1	6.2	8.0
Jan. 6	7.1	35.6	8.9	10.0
Jan. 7	6.3	41.7	7.9	11.0
Jan. 8	7.6	39.9	8.7	11.0
$\bar{x}$ 17 days	4.0	16.8	5.1	6.0

[a] Light data uncorrected for the visible spectrum.

Measurement of primary productivity

Primary productivity of thermophilic algae was measured using the method of Brock (1967). Algal cores were removed from their mats with a no. 8 (1.76 cm^2) steel cork borer and placed in vials (20-ml screw cap). A thick, colorless, gelatinous base found in mats at site 3a (cf. results) was not included in the incubations. About 7 min was allowed for temperature equilibration following which the contents of an ampoule (1.0-ml fluid volume) containing 5 μCi $NaH^{14}CO_3$ was added to each vial. An experiment was designed to compare the primary productivity of uniform algal populations situated at selected angles of exposure at times when direct solar radiation was available. Closely spaced vials (in pairs) were placed in the thermal effluent and positioned (1) to face due south at an inclination of 60°, (2) to face due north at an inclination of 60°, and (3) to lie horizontally. The counts from vials darkened with aluminum foil were 1% to 3% those of light-incubated samples. An Abney level (Keuffel & Esser) was used to verify the resting angle of the vials and to determine stream slope and inclination of the illumination-meter light target. Except during transport the vials were kept in refrigerated storage (about 5 mo) prior to being processed for counting.

Processing involved separation (under a dissecting microscope, of the algal layer from a thin adhering base comprised chiefly of empty sheaths and inorganic detritus. The algae were then homogenized using a piston-type Teflon pestle mounted on a variable speed motor, vacuum filtered on 5.1-cm glass-fiber filters (Gelman, type E), rinsed once with 5.0-ml 0.01 N HCl to remove adsorbed isotope, and dried to a constant dry weight in a glass desiccator. Radioactivity was measured in a gas flow proportional counter which had a carbon-14 counting efficiency of about 19%. Computational procedures for primary productivity followed recommendations set forth by Wetzel (1965) and Leach (1970).

Estimation of chlorophyll and phaeophytin

Chlorophyll *a* determinations were performed on the processed cores immediately following counting. The surface layers of the filters were removed under a dissecting microscope, homogenized in 90% acetone, and refrigerated for 48 h to complete the extraction. The samples were then centrifuged, filtered, adjusted to 10-ml volume and read spectrophotometrically (model DB-G, Beckman Instruments). Chlorophyll *a* was computed using the equation of Odum et al. (1958) for narrow-band pass spectrophotometers.

An estimation of the phaeophytin was made following the method of Moss (1967*a, b*). A calibration curve to correct for chlorophyll degradation to phaeopigments was constructed using extracts of laboratory cultured *Mastigocladus*, and data for *Anabaena cylindrica* (Moss 1967*a*) (Fig. 1). The endpoints (average of two processed cores) of acidified chlorophyll (which brings about total degradation to phaeophytin) samples from the incubation cores fell between endpoints for *Mastigocladus* and *Anabaena cylindrica.* Calibration curves were drawn for sites 3a and 92. This method gave the ratio of chlorophyll to phaeophytin, not absolute concentrations. The latter were found by applying the absorption ratios, 430:410 nm (Sperling 1972), to a nomograph (Moss 1967*b*). Primary productivity and chlorophyll data allowed the computation of photosynthetic efficiency (mg C/h · mg Chl *a*).

Colonization experiment

An experiment to test the ability of algae to grow or colonize during the short-day season was performed between December 25, 1968, and January 8, 1969. Thin sheets (1 mm) of white polyvinyl chloride (PVC) were cut into 6-cm × 11-cm cards for use as algal substrates. To induce colonization the cards were roughened with coarse sandpaper, and half of one side was rubbed with algae taken from site 3a and allowed to dry overnight. *Mastigocladus* is notable for its ability to endure long periods of desiccation (Castenholz 1969*a*). Fourteen cards were subjected to various rates of flow, inclinations with respect to

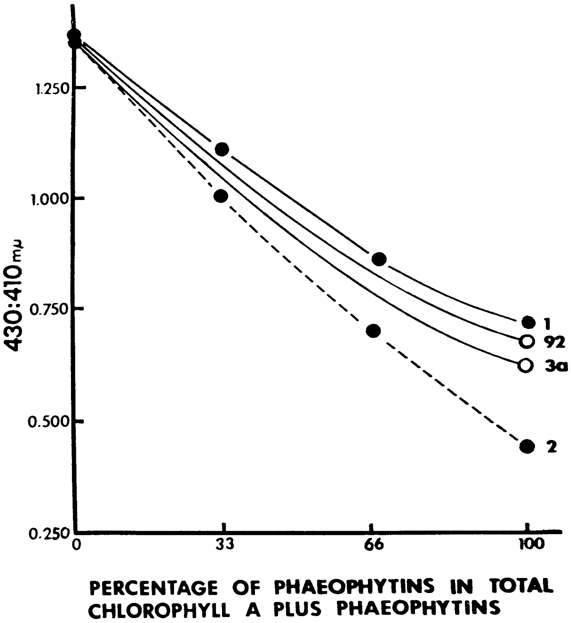

FIG. 1. Calibration curves (solid lines) made from extracts of cultured *Mastigocladus laminosus* (1), and from collection sites 3a and 92 (author's data). Broken line (2) made from extracts of cultured *Anabaena cylindrica* (data of Moss 1967*a*).

the sun, temperatures, chemical conditions and seeding sources. Each card was secured by a 15-mm nail passed through it and hammered into the streambed. The cards were placed with their innoculated halves in downstream position and removed after 15 days.

Results and Discussion

Algal communities of the incubation sites

A diverse thermal algal community occurred in the turbulent south-facing runoff at site 3a. In the summer of 1966 the author noted this runoff to be nearly choked with algae (chiefly *Phormidium* spp.) for a distance of 20–25 m from the source and over a temperature gradient of 44°–35° C. In mid-December temperature at the source was 40° C and the algae occurred in broken patches within 15 m of the source. The community consisted chiefly of *Phormidium corium* (C.A. Ag.) Gomont, with *Mastigocladus laminosus* Cohn and *Plectonema nostocorum* Bornet present in far lesser amounts.

The vertical profile of cores taken at site 3a consisted of an upper dark-green layer of *Phormidium corium* 0.5–1.0 mm thick in a healthy vegetative condition. A few empty cells were noted. Underlying the photosynthetic layer was a zone of empty light-orange-colored sheaths which were continuous with the living filaments of the photosynthetic layer. Below this was an easily separated thick (up to 1.5 cm) semiopaque, gelatinous layer of dead filaments, empty sheaths, particulate matter, and apochlorotic bacteria (Flexibacteriales).

Lyngbya martensiana Menegh. occurred in nearly pure stands in the very steep south-facing runoff at site 92. It occupied the runoff to the outermost margin of the flow over a gradient of 39°–30° C. The *Lyngblya* zone was 2.0–2.8 mm thick and merged gradually into a lighter zone of empty sheaths, dead filaments, and inorganic detritus 1.0–1.8 mm thick.

Other thermal algal communities

The headwaters of the Reykjadalsá at Klambragil had been previously visited by the author in August 1966. At that time a *Mastigocladus*-dominated community occupied about 1 km of the river over a gradient of 55°–35° C. The *Mastigocladus* mat was 6 cm thick in places, although only the upper 1.0–2.0 mm was green and contained living algae. This region was revisited on December 23, 1968, and January 6, 1969. Remnants of the algal mat persisted in still water zones up to 55° C. These were yellow-brown and yellow-green and probably contained mostly dead cells. The stoney river bottom had a scoured appearance. Stones were taken at 50° C from a zone of rapid flow and kept for several months in dried storage. When the stones were placed in fresh Gorham's medium (no. 11) and incubated at 45° C, *Mastigocladus* appeared within 2 wk.

Mastigocladus and an unidentified coccoid blue-green alga occurred as dark-green films on rock, wood and plastic milk containers from 36°–30° C, under slow to turbulent conditions at site 5. In still-water zones yellow-brown mats were noted. Scraping this material revealed a dark-green film of *Mastigocladus* beneath.

Mastigocladus encased in siliceous sinter occurred abundantly under rapid flow in many streams descending the south face of Dalafell. On December 20, 1968, many of the streams were yellow to pale green. On January 8, following a period of sunny weather, the streams were bright green. This coloration extended from 35°–20° C.

Site 93 was the only north-facing effluent investigated. *Mastigocladus* occurred as a thin (less than 0.5 mm) dark-green slime on sinter under moderate to rapid flow between 50°–40° C.

A seeding source for the spring return

There was little change in appearance between summer and winter populations of aerial algae along the margins of the thermal effluents. *Mastigocladus* and *Phormidium* spp. occurred in the hotter zones of the aerial environment. The cryptic presence of *Mastigocladus* under rapid flow near its upper thermal limit, as well as remnant populations in quiet

TABLE 3. Solar radiation (g-cal · cm^{-2} · day^{-1}) in Iceland for selected days covering a 6-mo period

Date		References			Date		References		
		Tuxen[a]	Einarsson[b]	Vedráttan[c]			Tuxen	Einarsson	Vedráttan
December	23	0.1	—	(4.7)	April	7	250	395	(264.4)
	30	0.5	6			14	295	446	
January	6	1.4	10	(12.3)		21	350	495	
	13	2.5	15			28	390	545	
	20	4.5	24		May	5	430	593	(395.0)
	27	7.3	36			12	465	640	
February	3	11	54	(57.0)		19	500	684	
	10	15	76			26	525	715	
	17	24	105		June	2	540	740	(312.0)
	24	40	135			9	555	754	
March	3	65	167	(140.0)		16	570	759	
	10	100	206			23	580	758	
	17	135	248						
	24	175	294						
	31	205	344						

[a] For a "schematic" hot spring. [b] Total radiation under clear sky. [c] $\bar{x}$ daily total radiation for the month (1961–1969).

waters obviate the need for other overwintering niches which might serve as seeding sources for the late winter–spring return.

Radiation in Iceland in winter

The effect of seasonal light change is of greater importance at higher latitudes and appears to be the only major external factor to influence the hot spring biota of Iceland (Schwabe 1936). Two aspects of the winter light regime in high latitudes are the importance of diffuse lighting on horizontal surfaces and the importance of direct sunlight on surfaces tilted toward the south (Geiger 1957).

Light data for Iceland from several sources show wide discrepancies (Table 3). Tuxen's (1944) calculated values for direct radiation reaching a hypothetical Icelandic hot spring on selected days from December through June omit diffuse radiation and subtract for light lost through refraction. Einarsson's (1966) values for total clear sky radiation are significantly higher. Under the prevailingly diffuse Icelandic winter light regime, radiation reaching algal communities in level surface habitats is largely undiminished by refraction and should approximate values recorded by the Icelandic Weather Bureau (Vedráttan 1961–1969; tables 2, 3).

Since 1957 the Icelandic Weather Bureau in Reykjavik has maintained two Eppley pyranometers (180° pyrheliometers). A "50-junction" type is used during the winter months. It is positioned in a high and relatively free location, but the panorama is obstructed at solar altitudes below 2° on the southern and southeastern horizon (Einarsson 1966). The percentage error loss in sensitivity under cloudless sky increases as solar altitude decreases, e.g., is 2% at 50°, 3% at 30° and 5% at 15° (The Eppley Company 1964). At 5° this error might be of the order of 10% and be perhaps 20% at 2°–3° (Drummond, *pers. comm.*). It would appear that clear sky radiation in winter is higher than that recorded by the Icelandic Weather Bureau.

Investigators commonly accept 50% of the visible spectrum (0.1–0.4 μm) to be useful in photosynthesis (Rabinowitch 1951). This value may be higher for low altitude direct radiation where there is a shift in spectral quality toward the longer wavelengths, e.g., a red enhancement that continues into the far red end of the short-wave spectrum (Gates 1966). Monochromatic light studies have revealed a synergistic enhancement of photosynthesis in plants simultaneously receiving far-red (0.68–0.72 μm) and shorter wave (0.62 μm) illumination (Govindjee 1963). Gabrielsen (1960) showed that plants receiving direct radiation with the sun at 9° 20′ photosynthesized at a rate 14% above plants receiving the same quantity of direct illumination with the sun at 60°. Under strongly diffusing stratocumulus clouds the total short-wave spectrum useful in photosynthesis increases to 60%–65% (Szeicz 1966).

Although the winter light regime in Iceland is predominantly diffuse, there is a clear relationship between hours of bright sunshine and total radiation for the month of December (Fig. 2). The difference between December 1962 (1.7 g-cal · cm^{-2} · day^{-1}) and December 1968, the time of this study, (4.6 g-cal · cm^{-2} · day^{-1}) may have biological significance.

Clear sky radiation and south facing slopes

Gessler (in Dirmhirn 1964) calculated that clear sky radiation received by south-facing slopes of 30° and 45° at 60° N latitude on December 21 to be 5.1 and 6.7 times that received by horizontal surfaces.

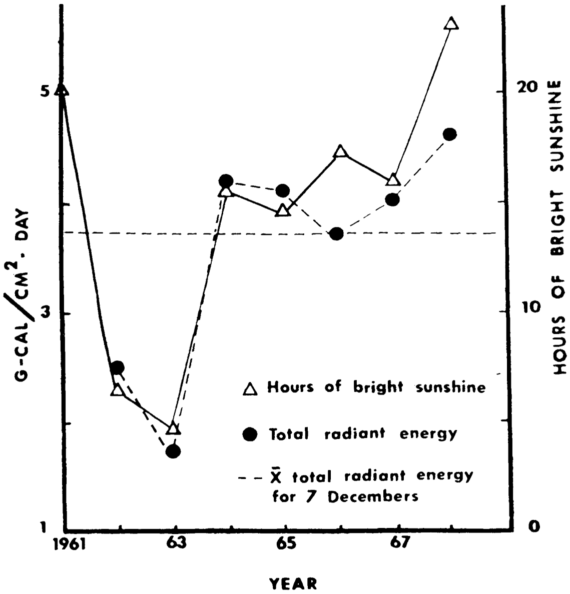

FIG. 2. The relationship between hours of bright sunshine and total radiant energy (g-cal · cm^{-2} · day^{-1}) for December (1961–1968). Data from Vedráttan (1961–1968).

These calculations are in agreement with the findings of this study (Table 2).

In this study light meter readings were taken with the target of the meter inclined at 60° because that angle is roughly between the inclination required for maximal reception of direct solar radiation about the time of the winter solstice in Iceland, e.g., about 86°, and the average inclination of many effluents noted in the Hveragerdi thermal field.

Daily radiation values obtained in this study for horizontal surfaces and north- and south-facing slopes are compared with values recorded for the same dates by the Icelandic Weather Bureau (Table 2). Values for north-sloping and horizontal surfaces were in close agreement with those of the weather bureau. On sunny days values for south-facing slopes were 2½ to 4 times greater than those reported by the weather bureau, whereas on cloudy days the figures were in close agreement.

The mean daily energy reaching south-facing slopes with 60° inclination between December 24, 1968, and January 8, 1969, was 16.6 g-cal · cm^{-2} · day^{-1}. This was about 3 and 4 times the energy received by a horizontal surface and a 60° north-facing slope, respectively. This value is roughly equivalent to a continuous illumination of 0.8 klx. The compensation point of shade-adapted *Chlorella pyrenoidosa* is 0.3 klx (Steeman Nielsen and Jorgensen 1968).

It is not implausible that saturating light intensities could be attained on south-facing slopes during the brief winter days. The growth saturating light intensity of shade and low temperature (31° C) acclimatized *Oscillatoria terebriformis* is about 350 foot-candles (3.7 klx) (Castenholz 1969*b*). However, although values as high as 1500–2000 foot-candles were recorded during the incubations, production values of south- and north-facing slopes were roughly proportional to the amount of light received at those sites.

Primary productivity

Although light values for south-facing slopes were several times higher than those of horizontal surfaces and north-facing slopes, primary productivity of horizontally incubated cores approximated that of cores tilted southwards (Table 4). Horizontally incubated cores probably received more light than was indicated from the light meter readings because the sides of the incubation vials scatter direct radiation which then reaches the core rim and undersurface. In contrast, the photovoltaic cell is a one-

TABLE 4. Data for primary productivity, chlorophyll, and photosynthetic efficiency from carbon-14 incubation sites on December 20, 1968 (site 3a), and January 8, 1969 (site 92)

Site	Core facing	Mg C/m² · day	Mg Chl *a*/m²*	Mg Chl a/m²**	Mg C/mg Chl *a** per m²/day	Mg C/mg Chl *a*** per m²/day
3a	South, inclined 60°	1110	92	130	11.10	8.54
3a	North, inclined 60°	260	102	151	2.24	1.72
3a	Horizontal	1130	92	138	10.61	8.15
92	South, inclined 60°	1330	163	325	5.30	4.07
92	North, inclined 60°	200	99	204	1.27	0.98
92	Horizontal	1110	139	264	5.46	4.20

* Chlorophyll values obtained by the method of Moss (1967*b*) and photosynthetic efficiencies derived from those values.
** Chlorophyll values obtained by the method of Odum et al. (1958) and photosynthetic efficiencies derived from those values.

sided light receptor, and is slightly sunk in its mount, a condition which at very low solar altitudes would result in some rim shading. Cores incubated in south-facing and horizontal vials at both sites floated. The vials were shifted to return the cores to the proper angle. Primary productivity of southerly- and horizontally-exposed cores were close to values reported by Brock (1970) for Yellowstone hot springs in summer.

The effect of light diminution in winter on algal growth has been noted in hot springs of Temperate latitudes, e.g., Brock and Brock (1969) for Yellowstone (44° 30′ N) and Stockner (1967) for Yellowstone and Mt. Rainier (46° 44′ N). Growth in winter was shown to be limited, but algal biomasses were essentially unchanged from summer values. Stockner (1967) observed that denuded mat areas in Yellowstone hot springs failed to show colonization after 15 days. In the present study, 8 of the 14 PVC substrates showed some sign of colonization. These were either south or horizontal facing. Two of the substrates (at 40° C) showed conspicuous colonization by *Mastigocladus*. The algae were scattered over the cards' surface with several clumps measuring up to 1.5 mm in diameter. A single north-facing card was uncolonized. The results indicated that the 24-h compensation point on horizontal and south-facing surfaces had been exceeded.

Chlorophyll a *and photosynthetic efficiency*

The fact that cores from both incubation sites were identically processed but that only those from site 92 showed high amounts of phaeophytin *a* (Sperling 1972) suggested that most of the phaeophytin was present when the cores were taken and that minimal degradation of chlorophyll *a* had occurred in storage and processing.

The highest value for chlorophyll *a* obtained by Odum's method, which includes all acetone soluble pigments contributing to the absorption maximum for chlorophyll at 665 nm, was 325 mg/m^2, and 163 mg/m^2 by the method of Moss (Table 4). Maximal summer values for chlorophyll *a* obtained by Brock and Brock (1966) in Iceland (at 48° C) and in Yellowstone (at 56° C) were 500 mg/m^2 and 830 mg/m^2, respectively.

Photosynthetic efficiencies at site 3a were about twice those of site 92 (Table 4). Chlorophyll *a* concentrations at the latter site were greater although much higher values for chlorophyll degradation were also found. Hourly photosynthetic efficiencies of south-facing cores at site 3a were 3.2 and 2.4 mg $C \cdot h^{-1} \cdot mg^{-1}$ Chl *a* using chlorophyll values by the methods of Moss and Odum, respectively. These values were for the 3-h incubation period only, which constituted about 85% of the entire illumination period. They approximate photosynthetic efficiencies of natural lake populations of phytoplankton, and cultures of Chlorophyta and Cyanophyta (Strickland 1960).

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