

Plankton ecology in an ice-covered bay of Lake Michigan: utilization of a winter phytoplankton bloom by reproducing copepods

Henry A. Vanderploeg, Stanley J. Bolsenga, Gary L. Fahnenstiel, James R. Liebig & Wayne S. Gardner
*Great Lakes Environmental Research Laboratory, National Oceanic & Atmospheric Administration,
2205 Commonwealth Blvd. Ann Arbor, MI 48105-1593, USA*

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Abstract

Plankton ecology was examined during the 1986 winter in Grand Traverse Bay, a 190 m deep, fjord-like bay on Lake Michigan. Before ice cover, algal concentration was low and uniformly distributed with depth, as it is in open Lake Michigan. During ice cover (February and March), a bloom of a typical winter-spring phytoplankton community developed in the upper 40 m, resulting in a 4 to 7-fold increase in feeding rate of adult *Diaptomus* spp. High algal concentration and zooplankton feeding persisted after ice melt (April). During and after ice cover, lipid concentrations of *Diaptomus* dropped rapidly from 34% of dry weight to 17% because of egg production. High incident photosynthetically active radiation (PAR), high (45–50%) PAR transmittance of the ice due to little snow on the ice, and water column stability were probably responsible for the bloom. High ice transparency may be a common feature of large lakes and bays, where strong winds blow snow cover off the ice, or at low latitudes where snowmelt due to occasional rains and warm temperature is common. Winter reproducing calanoid copepods use these blooms to increase their reproductive output.

Introduction

Little is known about the ecology of plankton of large north temperate lakes during winter, especially under ice cover. Very few studies have been done on the Great Lakes because of unsafe conditions in winter, when ice surfaces can be unstable and dynamic (Bolsenga *et al.*, 1988). A major factor determining phytoplankton production under ice is the presence of snow cover on the ice, because a few centimeters of snow can limit transmittance of photosynthetically active radiation (PAR) to levels less than 10% (Bolsenga & Vanderploeg, 1992). In areas of modest to abundant snowfall, which includes much of north tem-

perate North America and Europe, the usual pattern seen on small lakes is that ice forms, and the blanket of snow of varying depth which accumulates on the ice severely attenuates PAR transmittance for much of the winter (Bolsenga & Vanderploeg, 1992). Following deposition of the blanket of snow, there is typically an extreme drop of photosynthesis with a replacement of phototrophic phytoplankton by heterotrophic flagellates (Rodhe, 1955; Wright, 1964; Allen, 1969). In some shallow eutrophic lakes, the lack of photosynthesis plus respiratory demand from sediment can lead to anoxia and fish kills (Greenbank, 1945). In contrast, in lakes in central Japan, where snowfall is rare and the sky usually clear, blooms

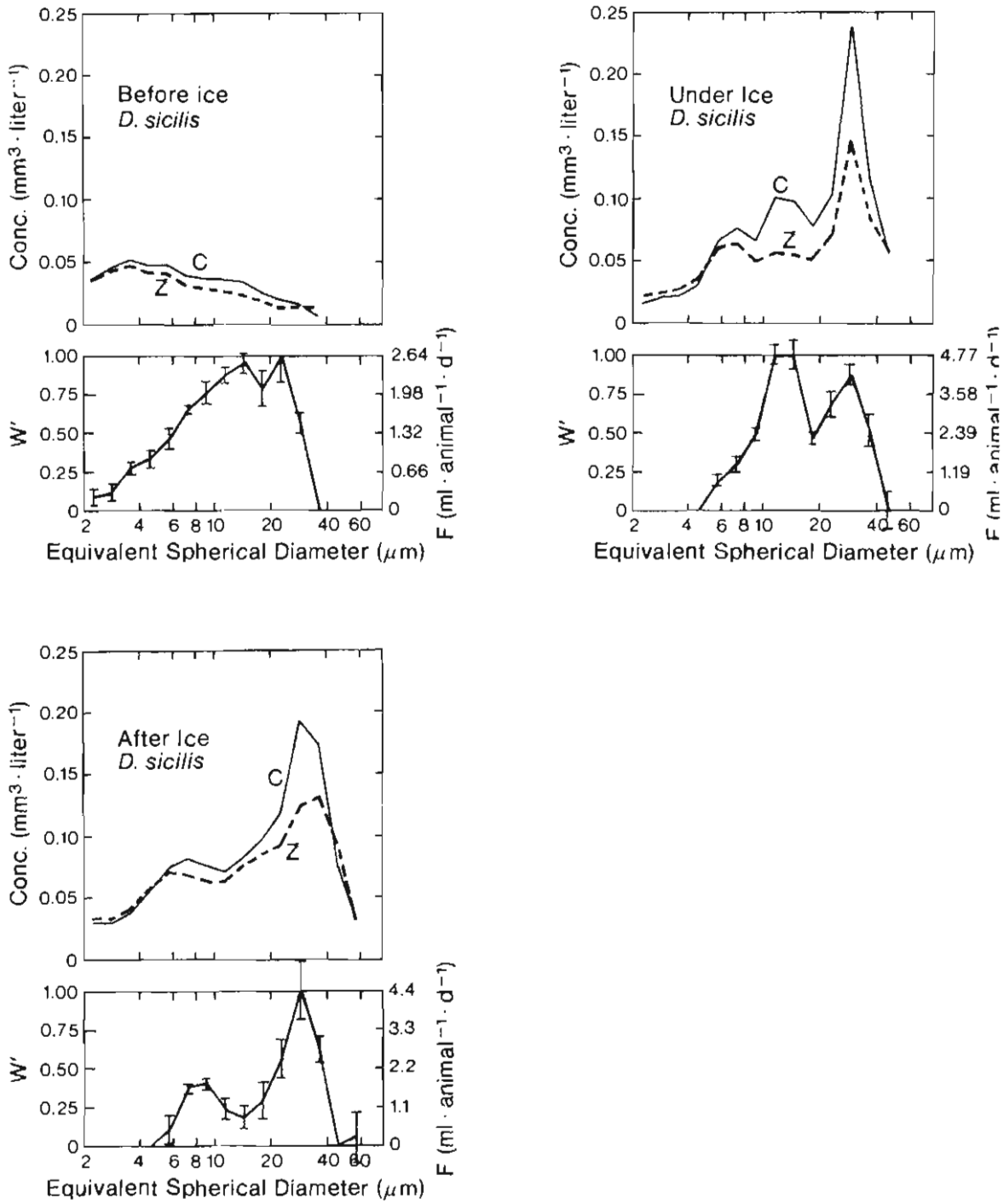


Fig. 1. Particle-size spectra and feeding of *Diaptomus sicilis* before, during, and after ice cover. C and Z, respectively, denote partic concentration in control and experimental (with zooplankton) bottles at the end of the feeding experiment.

Physiological condition of phytoplankton

To determine whether the under-ice phytoplankton community was a physiologically active phototrophic assemblage, we determined ^{14}C photosynthesis, constructed a photosynthesis-irradiance curve, and used a differential solvent extraction technique to determine photosynthetic end products (Fahnenstiel *et al.*, 1989).

Results and discussion

Phytoplankton concentration

Particle and chlorophyll concentrations were low in January before the formation of ice (Fig. 1 & Table 1). During ice cover (March) a bloom of algae occurred between approximately 2 and 64 m (Fig. 2). Visual examination of the ice did not reveal the presence of algae growing in the ice (Conover *et al.*, 1986). The bloom was verified as a general feature of the bay by similar values of *in vivo* fluorescence at Station B of Bolsenga *et al.* (1988), located 6 km to the north of Station A. A typical spring assemblage was found, and *Fragilaria crotonensis* Kitton, *Tabellaria Ehrenberg* spp. and *Cryptomonas erosa* Ehrenberg were dominants. High chlorophyll persisted into the post-ice period (April). During the season of our study, the water column is approximately isothermal (Auer *et al.*, 1976) because of wind mixing and the late formation of ice. Therefore, particle and chlorophyll concentrations during the pre-ice and post-ice cruises should be fairly uniform with depth throughout much of the water column.

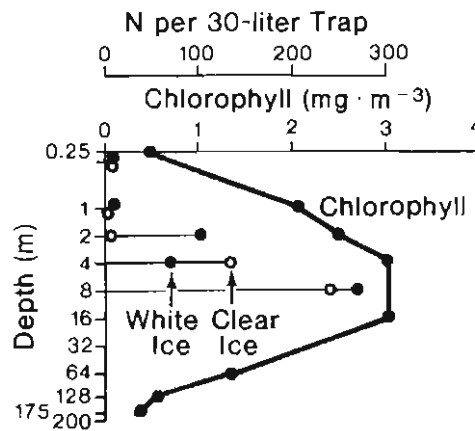


Fig. 2. Chlorophyll concentration and fine scale depth distribution of zooplankton determined with casts of the Schindler trap. A geometric sampling scheme was used to emphasize vertical structure near the ice surface. *In vitro* fluorescence measurements on raw water samples showed that chlorophyll concentrations at 8 and 32 m were respectively 100 and 88% of the maximum value observed at both 4 and 16 m.

The photosynthetic characteristics of the under-ice phytoplankton community (Fig. 3) were similar to those of the phytoplankton community during the early period of the spring (April) diatom bloom offshore open Lake Michigan during the same year (Fahnenstiel *et al.*, 1989). Significant ice cover is rare on open Lake Michigan, and none occurred that year. Both communities were characterized by significant photoinhibition (low I_{β}) and low light saturation parameter I_{K} , indicating that both communities were adapted to relatively low light levels, as is typical of the spring bloom in Lake Michigan. As with the spring bloom of the open lake, most of the photosynthate was incorporated into polysaccharides

Table 1. Food concentration and feeding of *Diaptomus sicilis* at 4 m depth before, during and after ice cover expressed as volume of particles consumed or chlorophyll (Chl) ingested. Water column was approximately isothermal on all dates.

Time	Temp. (°C)	Food concentration		Food consumption	
		Particles (mm ³ l ⁻¹)	Chl (μg l ⁻¹)	Particles (10 ⁶ μm ³ d ⁻¹)	Chl (ng d ⁻¹)
Before (Jan. 17, 1986)	1.5	0.440 ± 0.022	0.546 ± 0.020	0.499 ± 0.024	1.03 ± 0.01
During (Mar. 11, 1986)	1.0	1.01 ± 0.02	3.68 ± 0.03	2.11 ± 0.24	6.63 ± 0.29
After (Apr. 16, 1986)	2.2	1.30 ± 0.03	2.76 ± 0.09	1.65 ± 0.47	9.72 ± 0.53

P_S^B	P_M^B	α	I_k	β	I_{β}	r^2
2.23	1.57	3.89	0.40	0.41	5.44	0.91

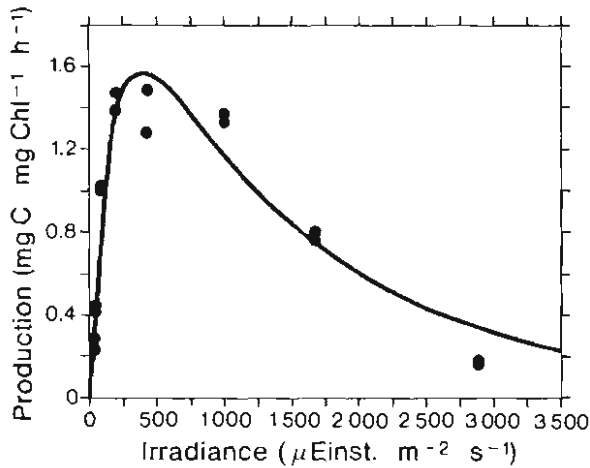


Fig. 3. Photosynthesis-irradiance characteristics of the under-ice phytoplankton community in Grand Traverse Bay sampled from 4 m depth on March 11, 1986; P_S^B = maximum photosynthetic rate in absence of photoinhibition ($\text{mg C mg Chl}^{-1} \text{ h}^{-1}$), P_M^B = maximum light saturated rate (same units as P_S^B), α = initial linear slope at low irradiances ($\text{mg C mg Chl}^{-1} \text{ Einst}^{-1} \text{ m}^{-2}$), $I_k = P_M^B/\alpha$ = light saturation parameter ($\text{Einst m}^{-2} \text{ h}^{-1}$), β = negative slope at high irradiances (same units as α), and $I_{\beta} = P_M^B/\beta$ = index of photoinhibition (same units as I_k). r^2 = proportion of variance explained by regression.

(38%) and small molecular weight compounds (34%) with less incorporation into lipids (17%) and proteins (11%).

Zooplankton feeding and distribution

Feeding rate, expressed either as particles or chlorophyll consumed, of *Diaptomus sicilis* on 4 m seston increased from the pre-ice to under-ice period: a 2-fold increase in particle concentration led to a 4-fold increase in particle consumption, and a 7-fold increase chlorophyll led to 6-fold increase in chlorophyll consumption (Table 1). Curiously, chlorophyll concentration was lower during the post ice cruise but chlorophyll ingestion increased. We do not know if this increase

represents a different physiological status of the zooplankton or some factor associated with size morphology or physiological status of the phytoplankton (Vanderploeg, 1990); however, the similarity of particle-size spectra on these two dates and the similarity of physiological status of under-ice algae to spring bloom algae in Lake Michigan would point to the physiological status of *D. sicilis*. Chlorophyll and particle consumption of *D. sicilis* in Grand Traverse Bay were similar to values reported for similar food concentrations in Lake Michigan during winter and spring (Bowers, 1980; Vanderploeg, 1981).

D. sicilis' W' vs. equivalent spherical diameter (ESD) curves (Fig. 1), or particle-size selection curves, were similar to those reported for a complete annual cycle in Lake Michigan (Vanderploeg, 1981). *D. sicilis* was able to utilize the pea

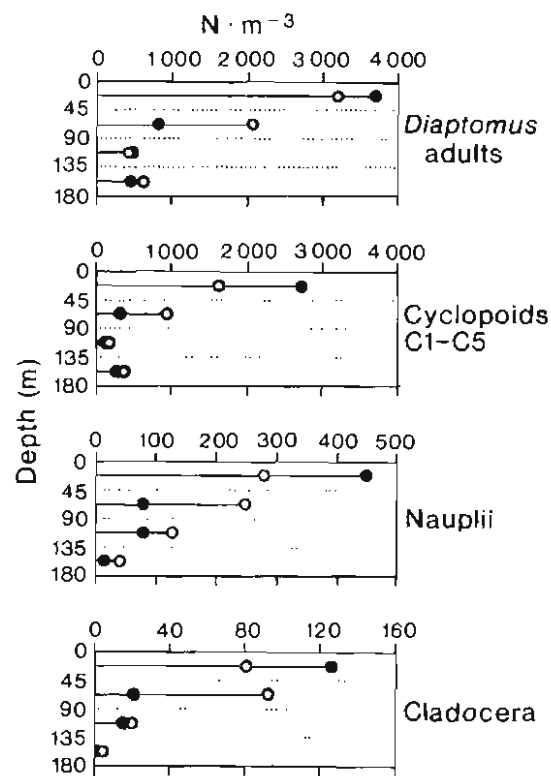


Fig. 4. Concentration of zooplankton in 45 m thick section of the water column as measured with an opening and closing net lowered through a hole in clear ice (open circles) or in slush ice (closed circles).

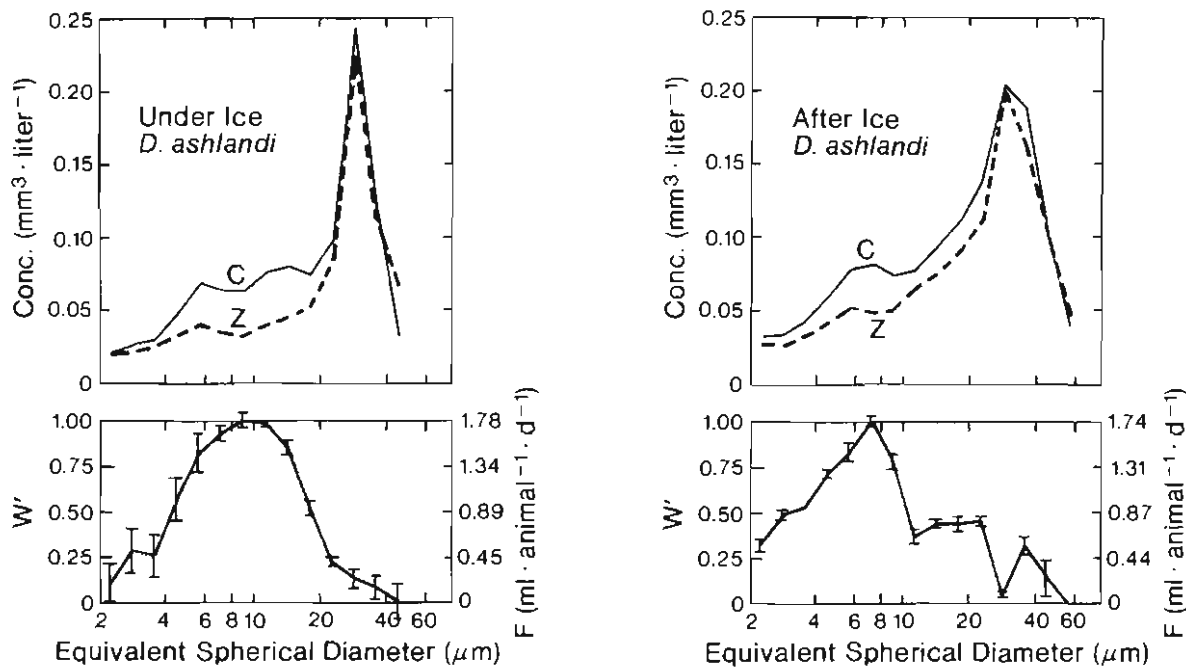


Fig. 5. Particle-size spectra and feeding of *Diaptomus ashlandi* during and after ice cover. Symbols same as Fig. 1.

in the particle-size spectrum occurring at $30\ \mu\text{m}$, whereas *D. ashlandi* did not efficiently use this peak (Fig. 5). *D. ashlandi* evidently selected smaller particles. This result is consistent with small copepods remotely detecting smaller algae more efficiently than large copepods (Price & Paffenhofer, 1985) and the inability of small copepods to handle or ingest certain large unicellular or colonial algae (Vanderploeg *et al.*, 1988).

Zooplankton cannot take advantage of the under-ice bloom unless they occur at the same depth as the bloom. Both the detailed and overall profiles of depth distribution suggest that much of the zooplankton community is at the correct

depth to utilize the bloom, at least at noon (Figs 2 & 4). We would intuitively expect that the portion of community below the bloom would move upwards when light intensity decreased as night approached. This hypothesis is consistent with the observation that the zooplankton community beneath the clear-ice (Figs 2 & 4) was found at a greater depth than the community beneath white ice.

Lipids and reproduction

From the pre-ice cruise in January to the post-ice cruise in April, lipid stores in *D. sicilis* declined

Table 2. Reproduction and lipid concentration of *Diaptomus sicilis* before, during and after ice cover.

Time	Carrying eggs (%)	Carrying eggs or ripe (%)	Total lipid per dry wt. (%)	Triacylglycerol per dry wt. (%)
Before (Jan. 17, 1986)	16	36	34.2 ± 3.1	27
During (Mar. 11, 1986)	76	84	29.5 ± 2.8	22
After (Apr. 16, 1986)	56	72	17.5 ± 1.0	11

(Table 2). The decrease in lipid concentration while food consumption was increasing is consistent with use of lipids for reproduction since reproduction, as measured by egg carrying or egg carrying plus ovary ripeness, increased during the ice and post-ice period. A similar seasonal pattern of reproduction and lipid concentration was seen in open Lake Michigan (Vanderploeg *et al.*, 1992). Laboratory experiments have shown that lipid concentrations can fall in reproducing *D. sicilis* under satiating food concentrations (Vanderploeg *et al.*, 1992). Thus, the under-ice and post-ice blooms of phytoplankton were used by physiologically active zooplankton to increase their reproductive output and, possibly, survival.

Ecological implications

The under-ice bloom in Grand Traverse Bay preceded the spring bloom in open Lake Michigan since chlorophyll concentrations at a 100 m deep offshore station in southern Lake Michigan were approximately uniform with depth and had values of 0.93, 1.70, and 2.41 $\mu\text{g l}^{-1}$ on January 23, April 4 and 17, respectively (Fahnenstiel *et al.*, 1989; G. L. Pernie, personal communication). The under-ice bloom may be regarded as a special case of Sverdrup's (1953) critical-depth model of spring bloom initiation or Smetacek & Passow's (1990) extension of Sverdrup's model. The ice on Grand Traverse Bay permitted 45–50% of the incident PAR to reach the water column and the ice surface stabilized the water column sufficiently to prevent turbulence from removing algae from the photic zone. In the Sverdrup model of the spring bloom, the thermal gradient of the mixed depth prevented downward mixing. In the under-ice bloom, the thermal gradient was presumably small; however, wind induced mixing was removed. This is consistent with the observation that spring bloom formation is encouraged by low winds and high incident solar radiation (Smetacek & Passow, 1990).

Because many freshwater calanoid copepods overwinter as physiologically active adults that

feed actively and reproduce during winter and spring, clear ice cover can augment reproductive output of these calanoids by setting up bloom conditions before the spring bloom. However, snow does accumulate on the ice, it is likely that the algal concentration will be low under ice and that the spring bloom subsequent of ice loss may be delayed. In contrast to March 1986, Landsat imagery indicated that in March 1985 nearly 100% of the ice surface was covered with snow (Bolserga & Vanderploeg, 1992). Thus ice cover in 1985 may have been a detriment to zooplankton production.

The potentially mixed consequences of ice cover to plankton production may affect the recruitment of larval whitefish, which depend on copepodite and adult copepods as their primary food source in April and May (Freeberg, 1985; Taylor *et al.*, 1987). The hypothesis that emerges is that ice cover enhances egg survivorship (Freeberg, 1985; Taylor *et al.*, 1987) and is beneficial to larval recruitment if the ice is clear, but detrimental if covered with snow. We believe that more work is necessary to understand the importance of winter to the annual production cycle. Winter is an important time for freshwater calanoid copepods because they reproduce then or later in spring. These copepods are important to a wide variety of larval fishes, and they are important grazers throughout much of the year in north temperate lakes, especially oligotrophic lakes (Vanderploeg, 1990).

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