

## Seasonal change in the optical properties of the permanent ice cover on Lake Bonney, Antarctica: Consequences for lake productivity and phytoplankton dynamics

**Abstract**—Geophysical and ecological dynamics within lakes of the McMurdo Dry Valleys, Antarctica, are controlled by the presence of permanent ice covers. Despite the importance of the permanent ice cover, there have been no studies that have examined specific couplings between changes in the geophysical properties of the ice covers and dynamic ecological processes within the underlying water column. Herein we present seasonal irradiance and primary production data from Lake Bonney, Taylor Valley, and we show that the phenomena of “ice whitening” is caused by changes in the scattering properties within the upper meter of the ice column and that the timing and extent of this phenomena exerts a predominant constraint on primary production and overall phytoplankton dynamics.

Lakes with permanent ice covers in the McMurdo Dry Valley region of Antarctica are end-members among the world’s spectrum of limnological entities. The globally unique permanent physical barrier at the interface between the atmosphere and the liquid water column influences many processes within the water column. Specifically, ice covers affect ecosystem-level processes including mixing (e.g., Armitage and House 1962; Wilson 1964; Spigel and Priscu 1998), sedimentation (e.g., Neddell et al. 1987; Anderson et al. 1993), and radiative transfer (e.g., Wharton et al. 1993; McKay et al. 1994; Howard-Williams et al. 1998). Time-varying geophysical properties of perennial ice covers have been examined in the past (e.g., Clow et al. 1988; McKay et al. 1994; Adams et al. 1998; Fritsen et al. 1998), as have the dynamics and physiological characteristics of microalgal populations within the highly stratified water columns that are found beneath the perennial ice (e.g., Goldman 1964; Koob and Leister 1972; Vincent 1981; Lizotte et al. 1996). However, specific links between changes in the geophysical properties of a permanent ice cover and variations in ecological processes within a lake have not generally been quantified.

Several studies have produced information pertinent to a quantitative examination of the interactions between ice geophysics and ecosystem-level processes. For instance, Priscu (1991), McKay et al. (1994), and Howard-Williams et al. (1998) found that the optical properties of permanent ice covers can vary over time-scales from hours to months, and Lizotte and Priscu (1992a, 1994) found that phytoplankton exhibit extreme shade adaptation in response to light levels, often averaging less than 1–2% of surface irradiances. In this report, we utilize in situ measurements to quantify the seasonal variability in irradiance fields in Lake Bonney, and we link these variations to geophysical changes in the ice cover. The optical properties of the ice cover are then related to seasonal patterns of water column primary production and

phytoplankton dynamics through a quantitative analysis of in situ primary production data and modeling.

Lake Bonney is located at the terminus of the Taylor Glacier in the Taylor Valley of southern Victoria Land, Antarctica (778°43’S, 162°23’E). The lake is 7 km long and 1 km at its widest point, with a narrow (~30 m) and shallow (12 m) region that separates the lake into distinct east and west lobes. The maximum depth in each lobe is ~40 m. Water column temperature, conductivity, and oxygen are highly stratified, owing to the presence of a 3–5-m permanent ice cover (which has virtually eliminated wind-driven mixing) and a paleolimnological history that has produced relatively freshwater overlying highly saline bottom water. The physicochemical characteristics, paleohistory, and current-day hydrology of the lakes in the McMurdo Dry Valleys have been published previously (e.g., Green and Friedmann 1993; Priscu 1998).

During August through December of 1995 and 1996, the ice thickness on both lobes averaged ~4.3 m, and the surface topography consisted of a series of ridges and troughs (~5–10 m wide; 10–20 cm deep) running parallel to the long axis of the lake. Small (~1-m diameter) accumulations of sediments and snow were often present within the troughs.

Downwelling and upwelling irradiances of photosynthetically active radiation (PAR) above the air/ice interface on the east lobe of Lake Bonney were monitored with Licor  $2\pi$  irradiance sensors (192SA) that were mounted and leveled at original heights of 1 m above the ice surface. PAR beneath the ice (10 m from the ice surface) was measured with a  $4\pi$  sensor (LiCor 193S). PAR within the ice was measured with additional  $4\pi$  irradiance sensors that were frozen into an auger hole (10 cm in diameter) at 1, 2, 3, and 4 m (relative to the ice surface) in August of 1995. Thermocouples were deployed in the ice at original depths of 0.5, 1, 2, and 3.5 m. Data from all sensors were collected at 20-min or 1-h intervals with Campbell data loggers. For the current analysis, 20-min data were averaged to yield 1-h readings.

From August 1995 to January 1996, phytoplankton productivity and biomass were measured in the water column of both lobes. Chlorophyll *a* concentrations and daily rates of primary production were determined using the fluorometric and  $^{14}\text{C}$  methodology, as described by Lizotte et al. (1996).

Figure 1 shows the mean daily flux of PAR as measured by irradiance sensors located above, within, and below the ice cover on the east lobe of Lake Bonney for the period between September 1995 and May 1996. The seasonal cycle of incident downwelling irradiance had a broad seasonal maximum during December and January; unfortunately, the record of incident and 10-m irradiance ended in February because of a battery failure (Fig. 1A). Similar seasonal cycles in incident irradiance have been measured throughout

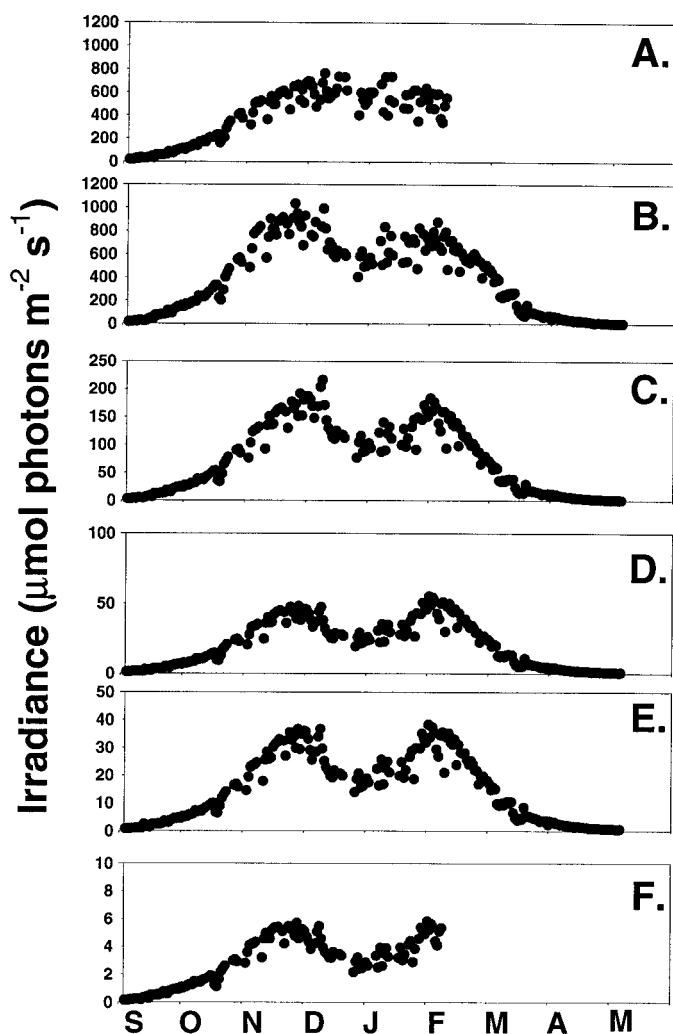


Fig. 1. Fluxes of PAR averaged over the diurnal cycle in the east lobe of Lake Bonney, Antarctica. Downwelling irradiance at the ice surface (A); scalar irradiance at 1 m (B), 2 m (C), 3 m (D), and 4 m (E) within the ice; scalar irradiance 10 m beneath the ice surface (F).

the McMurdo Dry Valleys, with local shading by topography and cloud cover contributing to the inter- and intralake variations in the irradiance received at the surface of the lake ice (Dana et al. 1998).

The in-ice and beneath-ice irradiance had seasonal patterns that were strikingly different than that associated with incident irradiance (Fig. 1B,C). The single seasonal peak in irradiance at the surface of the ice during December and January was not evident in the ice or in the water column. Rather, mean daily irradiance within the ice and within the water column increased to a maximum in late November and then decreased in December and early January, whereupon the irradiance levels again increased to a second seasonal maximum in late January to early February (Fig. 1B,C). The seasonal maximum in mean daily irradiance ranged from  $\sim 1,000 \mu\text{mol photons m}^{-2} \text{ s}^{-1}$  at 1 m to  $\sim 40 \mu\text{mol photons m}^{-2} \text{ s}^{-1}$  at 4 m in the ice. Mean daily irradiance in the water column at 10 m ( $\sim 5\text{--}6$  m below the lower ice surface)

reached a seasonal maximum of only  $6 \mu\text{mol photons m}^{-2} \text{ s}^{-1}$  during both November and February. Therefore, when incident irradiance was at its seasonal maximum (during late December to early January; Fig. 1A), scalar irradiance in the ice and water column was depressed, being  $\sim 50\%$  lower than in November and February. The percentage of the incident downwelling irradiance reaching 10 m (a measure of PAR transmission through the ice), averaged 1.8% during the months of August, October, and November, and decreased to 0.8% by 1 January. This percentage then increased again to 2.1% by February. The  $\sim 50\%$  change in transmission translates into an absolute change of  $3 \mu\text{mol photons m}^{-2} \text{ s}^{-1}$  in the mean daily flux of PAR at 10 m. A decrease in the transmission of PAR in the austral spring also has been measured at Lakes Hoare (McKay et al. 1994), Vanda (Howard-Williams et al. 1998), and in previous years at Lake Bonney (Priscu 1991). However, the increase in ice transparency later in the season has not often been described, presumably because field operations in the McMurdo Dry Valleys typically end in January, owing to logistic constraints.

Air temperatures increased from  $-40^\circ\text{C}$  in September to  $0^\circ\text{C}$  in late November (Fig. 2A). Ice temperatures (Fig. 2B) increased in response to this seasonal warming, and the ice became isothermal at  $0^\circ\text{C}$  on 28 November. Once the ice became isothermal, it remained at  $0^\circ\text{C}$  throughout December and early February. Temperature measurements were not obtained past 4 February 1996. However, in previous years (1993 to 1995), the ice at Lake Bonney typically began to cool below  $0^\circ\text{C}$  by the end of February (Fritsen et al. 1998).

The mean daily albedo averaged 0.58 in August, September, and November and increased to 0.85 during January, when the transmission of PAR was at a minimum (Fig. 2C). Diffuse attenuation coefficients for scalar irradiances  $\{K_o = \ln[E_o(z) E_o(\Delta z)^{-1}] \Delta z^{-1}\}$  at depths between the scalar irradiance sensors (i.e., between 1–2, 2–3, 3–4, and 4–10 m) decreased with depth in the ice and exhibited some temporal variation (Fig. 2D). The ice at depths greater than  $\sim 2$  m was comprised of clear ice and ice with vertically oriented cylindrical bubbles, whereas the ice at and above  $\sim 2$  m contained numerous spherical bubbles and sediment inclusions (Adams et al. 1998). Therefore, the decrease in the attenuation coefficients with increasing depth can be attributed to differences in the geophysical properties of the ice as well as to the filtering of the longer wavelengths in the upper portions of the ice, which makes the attenuation coefficients of PAR at depth more indicative of attenuation coefficients for wavelengths in the blue region of the PAR spectrum.

An apparent diffuse attenuation coefficient ( $K^*$ ) between the incident downwelling irradiance and the scalar irradiance at 1 m was calculated in the same manner as was that of the  $K_o$  (see above) in order to evaluate the change in the attenuation characteristics of the upper 1 m. Note that this value is not strictly a diffuse attenuation coefficient because of the difference in the geometry of the irradiance measurements; however, the calculation illustrates that attenuation between the two sensors exhibited a large change over the 1995–1996 season. Also, note that irradiance values at 1 m were typically larger than were the incident values (because of differences in the geometry of the measurements), which re-

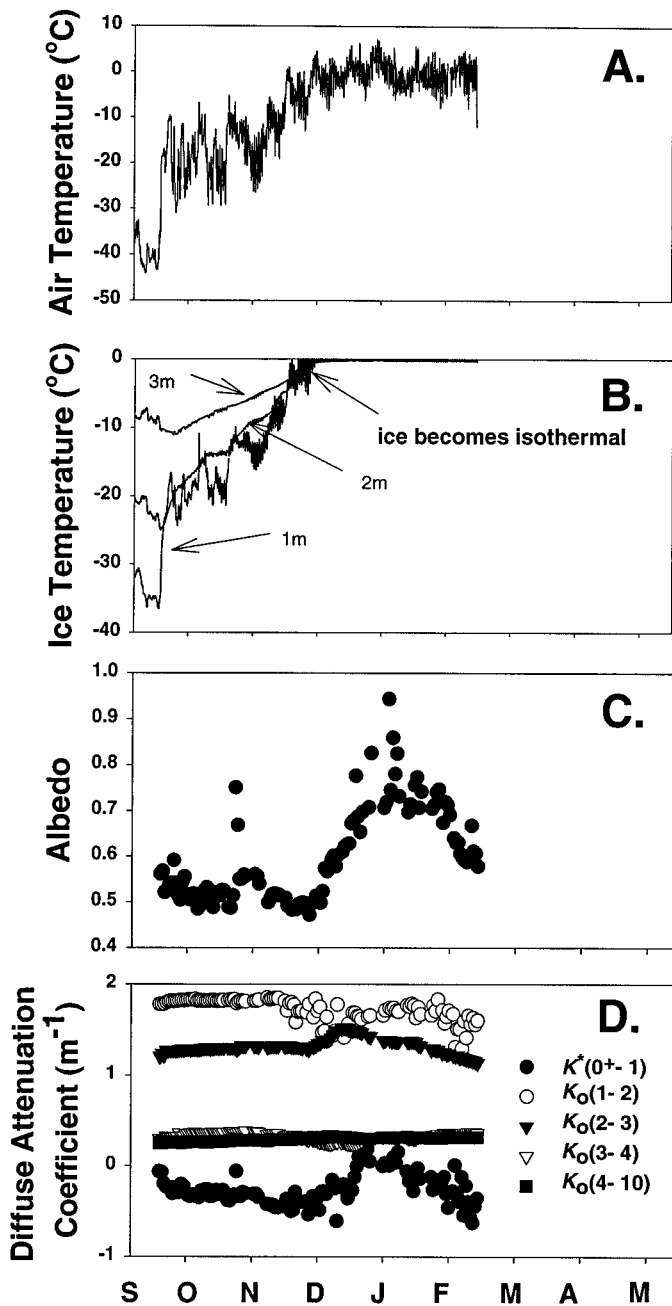


Fig. 2. Temperatures in the air (A) and at 1, 2, and 3 m in the ice cover (B). Mean daily albedo of PAR above the ice (C) in the east lobe of Lake Bonney, Antarctica, and the diffuse attenuation coefficients over depth intervals indicated in meters from the air/ice interface (D). Note that  $0^+$  is used to designate the position just above the air/ice interface.

sulted in negative calculated values of  $K^*$  for large portions of the season.

The large change in albedo, the relatively large change in  $K^*$ , and the relatively minor change in  $K_o$  values deep in the ice serve to illustrate that the major seasonal change in the ice optical properties occurred in the upper portion (less than 2 m) of the ice. These results, in combination with the temperature records, illustrate that the initial change in optical

properties occurred when the ice reached  $0^\circ\text{C}$ . Furthermore, the measured decrease in the transmission of PAR into and through the ice in conjunction with the increase in albedo demonstrates that changes in scattering properties account for the initial change in irradiance fields during the austral spring (see also McKay et al. 1994). The fact that there were changes in scattering properties is also consistent with the seasonal change in the visual appearance of the ice cover, which has been referred to as a "whitening" of the ice (Goldman et al. 1967; Howard-Williams et al. 1998).

Increased scattering in these ice covers has been proposed to be the result of the formation of melt features called Tyndall figures and fine fracturing (Mae 1975; McKay et al. 1994). However, other scattering features have recently been discovered in the ice, and these appear to be seasonally dynamic as well. For instance, hoarfrost has been found on the upper surface of spherical bubbles within the upper 2 m of the ice, and horizontal fractures were found along the basal plane of ice crystals in the lower portions (2–3 m) of the ice, where liquid water had filled cylindrical bubbles and has frozen (Adams et al. 1998).

Surface melting and liquid water drainage from the ice above freeboard would also enlarge the interstices between the crystal boundaries, which would allow air to intrude into the ice cover, which would in turn produce scattering features. Increased scattering at crystal boundaries has been observed during November (see fig. 8.23 in Fritzsche and Bormann 1995) and during the formation of candling features, features that are apparent on the surface of ice covers that have substantial surface topography (see fig. 7 in Wharton et al. 1993). Melting of ice at the crystal boundaries along with water migration may be similar to that described in sea ice, in which brine drainage from above the hydrostatic level decreases irradiance transmission in the austral summer (Buckley and Trodahl 1987).

Note that decreases in irradiances below sea ice in both the Arctic and Antarctic have also been documented during the austral spring and summer. However, these decreases have been attributable primarily to increases in absorption caused by the growth of microalgae in the sea-ice matrices (e.g., Maykut and Grenfell 1975; Palmisano et al. 1987; Arrigo et al. 1991). Although cyanobacterial communities do grow within the interior of these permanent ice covers (Priscu et al. 1998; Fritsen and Priscu 1998), they do not grow to concentrations that would cause the observed changes in the ice cover's bulk optical properties (Fritsen and Priscu 1998). Furthermore, an increase in absorption is inconsistent with the observed change in the surface albedo.

The specific physical mechanism that produces the temporal variation in scattering in the ice has yet to be described unequivocally, though it is readily apparent that the initial change coincides with the point when the ice becomes isothermal at its melting point. The increase in transmission during the latter half of the summer, however, occurs when the thermal structure of the ice remains constant at  $0^\circ\text{C}$ , indicating that the change in the optical properties is not a function of temperature alone. Surface and internal melting (Fritsen et al. 1998) may be filling the scattering features (e.g., fine fractures, hoarfrost, vapor inclusions) during this time (McKay et al. 1994; Howard-Williams et al. 1998).

Irradiance values in the lake also respond to additional factors besides the ice-whitening phenomena. For instance, cloud cover and the surrounding topography as well as changes in the distribution of snow and sediment deposits alter the transmission of PAR through these ice covers (McKay et al. 1994). However, our analysis, in conjunction with prior modeling scenarios (McKay et al. 1994) and anecdotal observations (Goldman et al. 1967; Howard-Williams et al. 1998), suggests that the basic seasonal changes in the flux of PAR in the lake are set by the seasonal solar radiation cycle and the geophysical changes associated with the ice-whitening phenomena. Spatial and temporal variations from this basic seasonal pattern are likely to result from the intermittent and more random effects of cloud cover, snowfall, and sediment deposition.

The reduction in mean daily irradiance of  $3 \mu\text{mol photons m}^{-2} \text{s}^{-1}$  at 10 m in the water column (Fig. 1F) is minor in absolute terms; however, the phytoplankton in these permanently ice-covered lakes are highly shade adapted and are sensitive to minor fluctuations in irradiances below their saturation values of  $\sim 10\text{--}30 \mu\text{mol photons m}^{-2} \text{s}^{-1}$  (Lizotte and Priscu 1992a; Neale and Priscu 1998). Therefore, even seemingly minor changes in mean daily irradiances are likely to be significant to the lake's primary production.

During the initial portion of the austral growing seasons of 1995 (between mid-September and January), depth-integrated chl *a* values typically increased twofold in the west lobe and sevenfold in the east lobe of Lake Bonney (Fig. 3B). Depth-integrated rates of primary production increased  $\sim 8\text{--}10\text{-fold}$  in each lobe between mid-September and the first week in December (Fig. 3C). When mean daily irradiance decreased in the water column in January (Figs. 1, 3A), depth-integrated primary production also decreased by 11 and 16% in the west and east lobes, respectively (Fig. 3C). Similar decreases in primary production were measured in the east lobe of Lake Bonney between November 1990 and January 1991 (Fig. 3C). A decrease in depth-integrated primary production was also observed in December of 1991; unfortunately, rates were not determined later in the 1991–1992 season. When combining data from the austral springs of 1990, 1991, and 1995, it is apparent that water column primary production is highly correlated with the transmission of PAR through the ice (Fig. 3D), which is consistent with assertions that light is the primary constraint on photosynthesis by the phytoplankton (Lizotte and Priscu 1992a, 1994), and the optical properties of the lakes exert stringent controls on the ecosystem (Howard-Williams et al. 1998).

The combination of irradiance, ice temperature, and seasonal primary production data illustrates the fact that primary production is reduced in the water column when the ice cover whitens and that the ice cover whitens when it warms to near  $0^\circ\text{C}$ . Hence, the seasonal change in optical properties of the ice follows a pattern that appears to be driven by thermal forcing. The correlation between ice temperature and initial ice whitening provides a direct coupling between the local climate, the ice optical properties, and primary production in the lakes. We have not yet compiled enough long-term field data that illustrates the sensitivity of phytoplankton production to interannual variations in the ice geophysical properties that are driven by local climate var-

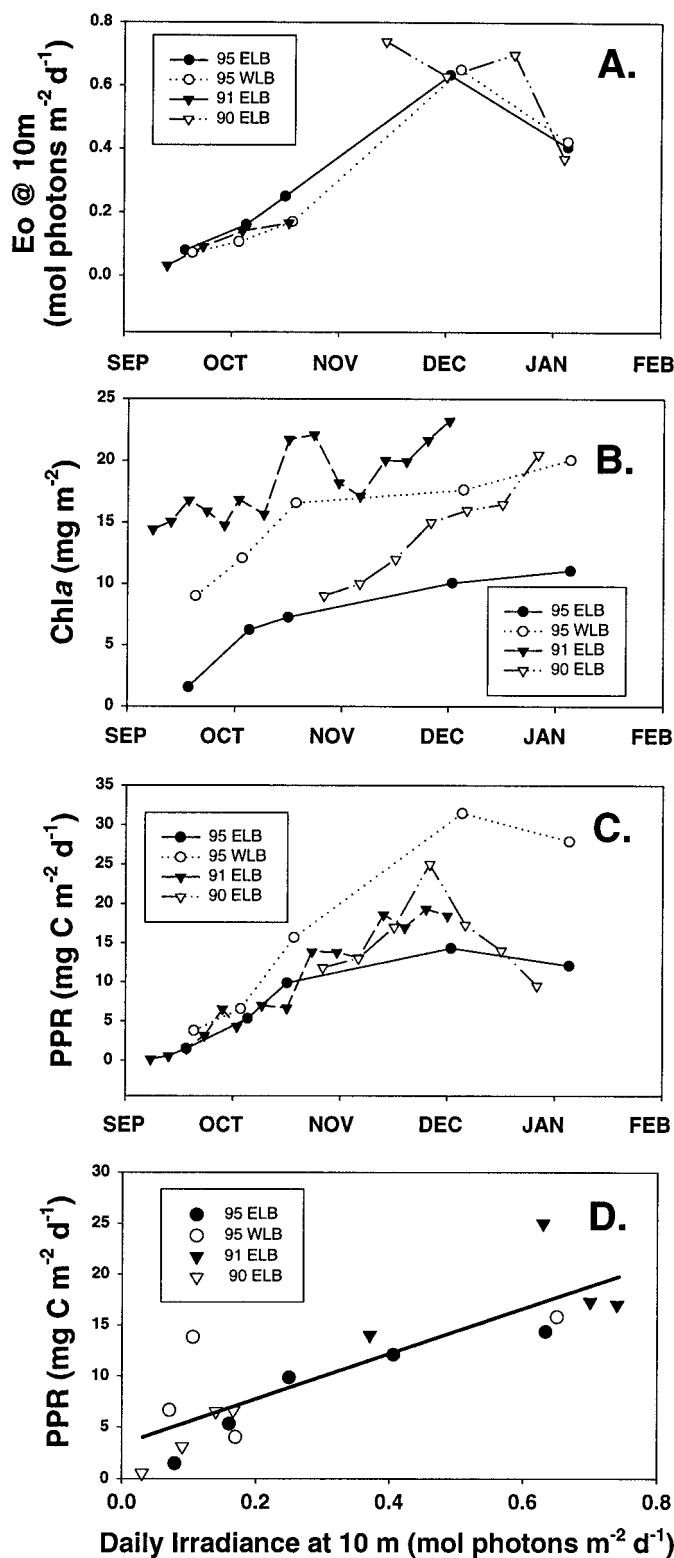


Fig. 3. Daily integrated PAR at 10 m (A), depth-integrated chl *a* (B), and daily primary production rates (PPR) during 24-h in situ incubations in Lake Bonney (C) in 1990, 1991, and 1995. ELB = east lobe; WLB = west lobe. (D), Relationship between depth-integrated rates of primary production and daily irradiance of PAR at 10-m depth [slope of the least-squares regression =  $22.17 \text{ mg C m}^{-2} \text{d}^{-1} (\text{mol photons m}^{-2} \text{d}^{-1})^{-1}$ ;  $r^2 = 0.7204$ ].



iations. However, published data on the photophysiology of the Lake Bonney phytoplankton and the ice optical properties presented herein can be scaled using a first-order modeling analysis. Our modeling analysis is designed to invoke a minimum number of variables in order to illustrate the consequences of ice whitening on the production and accumulation of phytoplankton carbon (C). This approach is simplistic but has the heuristical advantage of highlighting the seasonal phenomena of ice whitening and its potential constraints on phytoplankton productivity.

Primary production and growth of phytoplankton directly under the ice (5 m) and near the chemocline (10 m) in the east lobe of Lake Bonney were simulated, assuming that photosynthesis resulted in the production of new algal biomass and that the production of new algal biomass was supported by phosphate. The role of phosphate as a nutrient that constrains phytoplankton growth in Lake Bonney is supported by both direct experimentation and resource-ratio considerations (Sharp 1993; Priscu 1995; Lizotte et al. 1996).

Potential rates of new biomass production supported by the available light energy ( $P$ ;  $\mu\text{g C liter}^{-1} \text{ h}^{-1}$ ) were calculated from the hyperbolic-tangent relationship between in situ irradiances and in situ biomass-specific photosynthetic rates and the stock of phytoplankton C,  $C_p$  ( $\mu\text{g C liter}^{-1}$ ), such that

$$P = C_p [P_m^b \tanh(E_o \alpha / P_m^b)],$$

where  $E_o$  is the in situ flux of PAR,  $P_m^b$  is the light-saturated maximum rate of photosynthesis, and  $\alpha$  is the slope of the light-limited portion of the photosynthesis versus irradiance (PE) response curve (Jassby and Platt 1976). Coefficients describing these in situ relationships for phytoplankton populations from discrete depths within Lake Bonney have been previously reported by Lizotte and Priscu (1994). In particular, the coefficients used for modeling photosynthetic rates were taken from their table 1, where in situ photosynthetic efficiencies for the chrysophyte population from 10 m averaged  $0.0055 \mu\text{g C } (\mu\text{g chl } a)^{-1} \text{ h}^{-1} (\mu\text{mol photons m}^{-2} \text{ s}^{-1})^{-1}$  (range, 0.0040 to 0.0073), while the photosynthetic efficiencies of the cryptophyte population immediately below the ice averaged  $0.0015 \mu\text{g C } (\mu\text{g chl } a)^{-1} \text{ h}^{-1} (\mu\text{mol photons m}^{-2} \text{ s}^{-1})^{-1}$  (range: 0.0012 to 0.0047). Photosynthesis in both populations saturated at irradiances between 10–50  $\mu\text{mol photons m}^{-2} \text{ s}^{-1}$  and the maximum rates of photosynthesis were 0.05 and 0.2  $\mu\text{g C } (\mu\text{g chl } a)^{-1} \text{ h}^{-1}$  for the populations at 5 and 10 m, respectively (Lizotte and Priscu 1994). Chlorophyll *a*-specific coefficients were normalized to C, assuming a chl *a*:C ratio of 0.02.

Irradiances in the water column were modeled from incident irradiance values recorded at the surface of the ice (Fig. 1A) and assuming either a constant percentage of transmission value (i.e., no change in the ice optical properties) or a seasonal change in the percentage of transmission in order to produce the seasonal irradiance cycle shown in Fig. 1. PAR in the water column was then modeled, assuming an exponential decrease with depth using an attenuation exponent of  $0.1 \text{ m}^{-1}$  for the water, which is representative of Lake Bonney water (Lizotte and Priscu 1992b; Howard-Williams et al. 1998).

Potential rates of new biomass production supported by phosphate,  $P'$  ( $\mu\text{g C liter}^{-1} \text{ h}^{-1}$ ) were simulated as a function of the inorganic phosphate concentration ( $P_i$ ), the half-saturation constant for phosphate uptake ( $K_p$ ), and the maximum photosynthetic rate such that

$$P' = C_p P_m^b [P_i / (K_p + P_i)].$$

Phosphate concentrations in the epilimnion of Lake Bonney have been measured between 0.05 and 0.7  $\mu\text{M}$ , and they generally decrease with distance above the major nutricline located at  $\sim 15$  m from the ice surface (Priscu 1995). The half-saturation constant for phosphate uptake and growth has not been determined within lakes of the McMurdo Dry Valleys. Therefore, a constant value of 0.05  $\mu\text{M}$  is used for comparative analysis only.

Realized rates of new C production were calculated as the minimum of either  $P$  or  $P'$  to ensure that new biomass production only occurred when sufficient nutrients and light were available. Biomass and inorganic phosphate concentrations were calculated at 1-h time intervals to avoid overshoot problems that became apparent during simulations with larger time steps when nutrients become depleted. Inorganic phosphate depletion as a result of new C production was calculated assuming the Redfield C:P ratio (106:1, mol: mol).

Simulations with transmission of PAR changing throughout the season (to simulate ice whitening) resulted in phytoplankton C increasing from 7.5  $\mu\text{g C liter}^{-1}$  in early August to 135  $\mu\text{g C liter}^{-1}$  on 1 April (i.e., net production of 127.5  $\mu\text{g C liter}^{-1}$ ) at 10 m when phosphate concentrations were initially set at 0.1  $\mu\text{M}$  (Fig. 4A). When ice whitening was not simulated (i.e., % transmission held constant), the 10-m population also reached 135  $\mu\text{g C liter}^{-1}$ ; however, this biomass was attained approximately 2 months earlier, in the beginning of February (Fig. 4A). Biomass accumulation was limited to 135  $\mu\text{g C liter}^{-1}$  during both simulations, because phosphate became a limiting factor. When phosphate concentrations were increased to 1  $\mu\text{M}$  at 10 m, biomass accumulation decreased in response to ice whitening from 288 to 153  $\mu\text{g C liter}^{-1}$  (Fig. 4A; a decrease of 46.8%), and phosphate never became limiting in either case.

Net annual production of C at 5 m was reduced by 19.8%, from 22.2 to 17.8  $\mu\text{g C liter}^{-1}$  (Fig. 4B) when simulated with ice whitening. Phosphate never became a limiting factor during either of the simulations of algal production at 5 m. The predicted decrease in production at 5 m was moderate compared with those predicted at 10 m. This was because irradiances were predicted to be near those that saturate photosynthesis of the 5-m population during both simulations. Therefore, an increase in irradiances at 5 m in response to the absence of ice whitening should only cause a moderate increase in C production at this depth.

The twofold difference in efficiencies of light utilization between the 5- and 10-m populations resulted in predictions of slower phytoplankton growth at 5 m compared with that predicted at 10 m, despite irradiances being higher at 5 m in the water column in both scenarios (i.e., with and without ice changes in % transmission). Therefore, algal growth was inverted and populations were predicted to develop a deep-chl *a* maxima during the early portions of the season, even

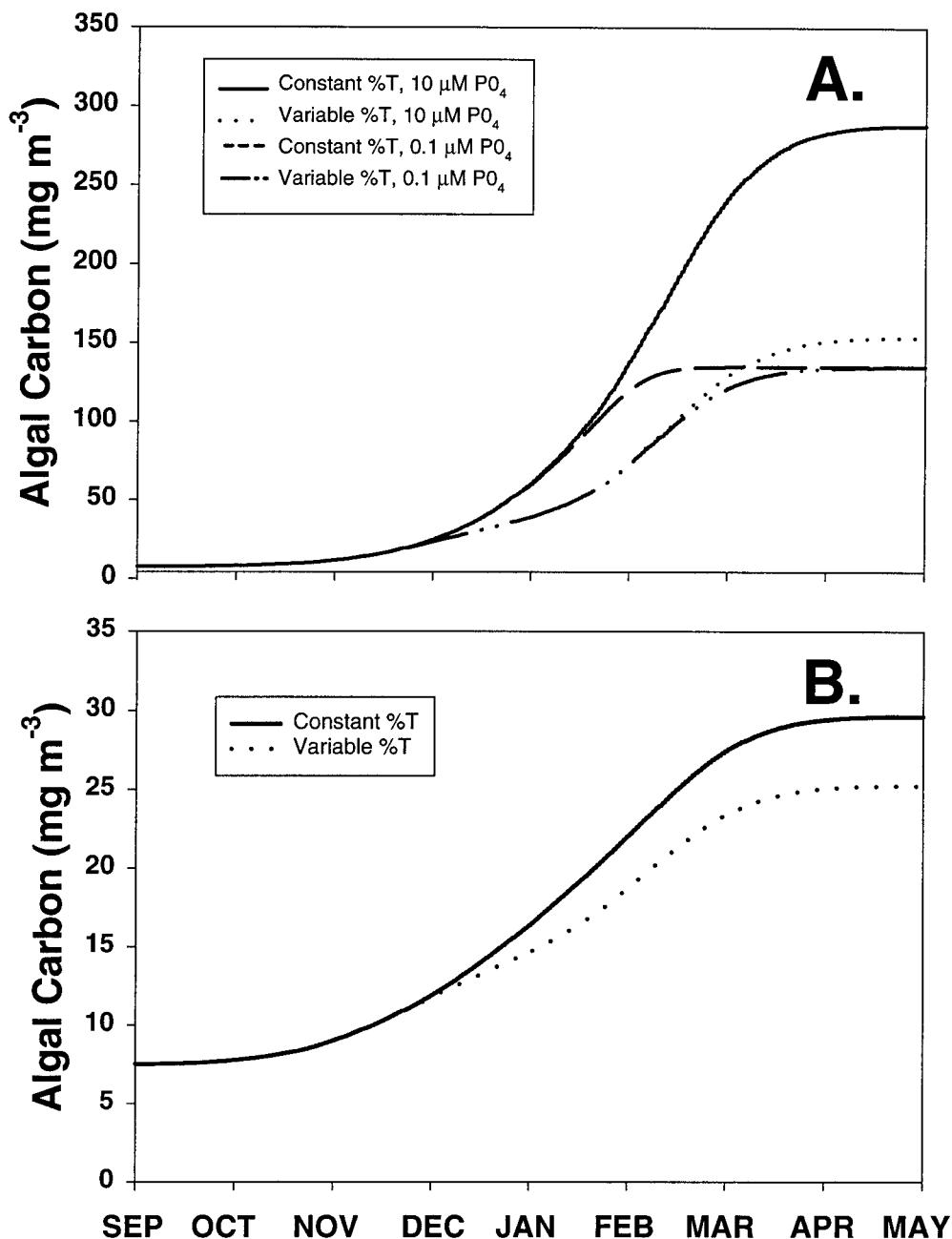


Fig. 4. Simulated phytoplankton biomass (expressed as C), illustrating the potential effects of constant or variable transmission of PAR throughout a growing season. The panels show the production and accumulation at 10 m (A) with phosphate concentrations of 0.1 or 1.0  $\mu\text{M}$  and at 5 m (B) with a phosphate concentration of 0.1  $\mu\text{M}$ .

in the absence of P-limitation. The prediction of the formation of a deep photosynthesis maximum resulted from the differences in light utilization, which may explain the seemingly paradoxical development of productivity maxima in the deeper layers of the lake early in the growing season in the absence of P-limitation (Lizotte et al. 1996).

Note that if the chl *a*:C ratio were increased, predicted rates of light-limited biomass production would change in direct proportion. Therefore, when chl *a*:C is doubled to 0.04, then rates of biomass production increase in direct pro-

portion. Because of uncertainty in the stoichiometry of C and pigments, our model results are tentative. Furthermore, the model does not account for losses of algal organic C as a result of respiration and grazing, which are unknown at this point in time. Importantly, the model has utility in demonstrating the effects of the ice-whitening phenomena on lake productivity.

The combination of field studies and numerical analysis illustrates that the temporal change in the ice cover's optical properties are of a magnitude that may affect the overall

dynamics of water column phytoplankton photosynthesis. The exact geophysical processes responsible for initial ice whitening, which are followed by increases in light transmission, need to be identified. The simulation analysis further shows that these effects are likely to manifest themselves differently between the vertically stratified populations simply because of differences in light utilization and growth, which may be constrained by other factors, such as temperature or nutrients (Lizotte et al. 1996). Ice whitening will also affect nutrient distributions in the water column through its control on photosynthesis and phytoplankton growth. Specifically, our analysis suggests that decreased production rates caused by ice whitening should extend the time period during which nutrients are not limiting for phytoplankton growth on a time scale of months. Alternatively, the absence or delay of ice whitening, which could be caused by cold air temperatures in the spring, may result in an incremental increase in production and a more rapid depletion of nutrients. This would then lead to extended time periods during the austral summer and autumn, when energy availability to phytoplankton greatly exceeds nutrient availability.

Our study shows that a large portion of the season's photosynthetically active radiation enters the water column of this permanently ice-covered lake 2 months before and after the summer solstice (~21 December). It should be noted that the seasonal peak in light transmission into the lakes following the summer solstice coincides with a time when limnological studies typically end owing to logistical constraints. Given the fundamental ecological implications of our results, the ice-whitening phenomena is likely to be the primary factor determining annual variations in production, nutrient dynamics, and trophic structure within the lakes of the McMurdo Dry Valleys. This phenomena should be explicitly recognized when examining historical limnological data from these lakes, long-term limnological studies of phytoplankton dynamics, or other limnological processes related to radiative transfer in the permanently ice-covered lakes in Antarctica.

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## Influence of fish kairomones on the ovipositing behavior of *Chaoborus* imagines

**Abstract**—The phantom midge, *Chaoborus*, is a dipteran, the larvae of which occur in many freshwater habitats and are known to be vulnerable to predation by fish. The hypothesis was tested that ovipositing imagines of *Chaoborus* use chemical cues to detect predatory fish and avoid depositing eggs into waterbodies containing fish kairomones. The experimental setup consisted of cages with two small water-filled plastic containers, in which *Chaoborus* imagines could oviposit. One container was connected to a flow-through system holding fish kairomones, while the other container (the control) was connected to a flow-through system without fish kairomones. Three different *Chaoborus* species were tested: two pond-dwelling species, *Chaoborus crystallinus* and *C. obscuripes*, which do not coexist with fish, and a lake-dwelling species, *C. flavicans*, which does coexist with fish. The imagines of the two pond-dwelling species showed an ovipositing preference for fish-free water. No significant difference in ovipositing preference was found for the lake-dwelling species (*C. flavicans*). The present experiment suggests that in addition to direct predatory effects, adult oviposition behavior may contribute to the lack of local coexistence between fish and pond-dwelling *Chaoborus*.

Predation is often thought to be limited to direct, lethal effects of predators, although more recent data suggest that indirect effects can be equally important. Indirect effects include trophic linkage effects and those caused by behavioral and chemical interactions (Kerfoot and Sih 1987). Many indirect effects in freshwater communities are mediated by chemical communication, and a large number of organisms have been shown to respond in a variety of ways to chemicals or kairomones released by their predators (Havel 1987; Dodson 1989; Adler and Harvell 1990; Larsson and Dodson 1993).

Many aquatic insects have terrestrial adult stages that must return to the water to oviposit, and the selection of oviposition sites can be an important feature in determining freshwater community structure. The presence of fish could indirectly structure these communities by influencing adult choice of oviposition sites. Therefore, selection should favor adults with oviposition behavior that yields the highest juvenile survival. This particular research topic has largely been ignored by aquatic ecologists (*but see* Resetarits and Wilbur 1989; Kats and Sih 1992).



The phantom midge *Chaoborus* is a dipteran. Its larvae inhabit many freshwater habitats and are known to be vulnerable to predation by fish (Wright and O'Brien 1982). Some *Chaoborus* species have adaptations that enable them to coexist with fish. For example, *C. flavicans*, a lake-dwelling species, exhibits diel vertical migration in response to the presence of fish (Dawidowicz 1990; Tjossem 1990). In contrast, the larvae of *C. americanus*, a pond-dwelling species, do not respond to chemicals from fish, whereas the larvae of *C. punctipennis*, a lake-dwelling species, do (Barendonk and O'Brien 1996). These results suggest that the larvae of lake-dwelling species, such as *C. flavicans*, have evolved a behavioral adaptation to the presence of fish, whereas the larvae of pond-dwelling species, such as *C. crystallinus*, have not evolved such an adaptation or have lost the response. Therefore, it would be of selective advantage for adults of these pond-dwelling species to actively avoid oviposition in waterbodies with high fish densities.

Petranka and Fakhoury (1991) have demonstrated selective oviposition behavior by *Chaoborus*, but the mechanisms underlying this oviposition behavior are largely unknown, and their experimental design could not determine whether chemical or mechanical cues were important. Furthermore, they could not determine what species showed the selective oviposition behavior, although circumstantial evidence suggested that the lake-dwelling species *C. albatus* showed an oviposition preference for the fish-free pools. As the presence of fish chemicals has been shown to influence *Chaoborus* larvae and other zooplankton in a variety of ways (Dodson 1989), the goal of this study was to determine if chemicals alone can influence oviposition behavior of *Chaoborus* imagines. Three different species were tested—two pond-dwelling species, *C. crystallinus* and *C. obscuripes*, which do not coexist with fish, and a third, *C. flavicans*, which is found in lakes where fish are present. Therefore, one would predict that the two pond-dwelling species should show stronger reactions to fish kairomones than the lake-dwelling species. Selection should favor adults that avoid egg laying in a habitat where offspring would suffer higher mortality.

*Chaoborus* larvae were collected from two ponds and a lake in Schleswig-Holstein, Germany. *C. obscuripes* and *C. crystallinus* were taken from fishless ponds near Plön and *C. flavicans* from Plußsee, which contains a large planktivorous fish population (Kremser pers. comm.).

The larvae were well fed with young *Daphnia magna* and held under a 20:4 light:dark photoperiod, at  $24 \pm 1^\circ\text{C}$ , to prevent dormancy of the *Chaoborus* pupae (Bradshaw 1970; Ratte 1979).

The experimental setup consisted of five 60- × 60- × 100-cm (height) cages. Each cage was illuminated by an Osram Cyclolux lamp with a light intensity of  $36.8 \mu\text{mol m}^{-2} \text{s}^{-1}$ .

Each cage contained a hatching aquarium (30 × 10 × 20 cm [height]). The top of the aquarium was covered with a tilted glass pane leaving only a small gap (Fig. 1). Previous experiments showed that this hatching aquarium design prevented ovipositioning into the aquarium after the imagines had emerged. In front of each hatching aquarium were two adjacent 20- × 30- × 15-cm (height) black plastic containers

(Fig. 1a), as Yap et al. (1995) showed that *Aedes albopictus* preferred dark-colored jars for oviposition sites. The black containers and the hatching aquarium in each cage were randomly positioned, but their relative positions were kept the same, therefore not allowing an orientation stimulus by light or the wall of the room (Fig. 1b). Each plastic container was connected to one of two independent flow-through systems. Each flow-through system consisted of a reservoir of 36 liters with filtered fishless pond water, outside the cages, five black containers in series, one in each cage, and a peristaltic pump (Fig. 1b). The flow rate of the pumps was  $1.5 \text{ liters h}^{-1}$ . Two rudd (*Scardinius erythrophthalmus*) and two sticklebacks (*Pungitius pungitius*) were placed in one of the large containers. None of the tested *Chaoborus* species originated from the fishless pond where I obtained the experimental water. The black plastic containers and the hatching aquaria were gently aerated for 1 h a day, causing a surface disturbance of the water that prevented the growth of a bacterial film. Previous observations showed that the imagines could be trapped by such a surface film.

One hundred twenty *Chaoborus* pupae were placed in each hatching aquarium. It was impossible to determine the sex of the live pupae without damaging them; therefore, I assumed that the sexes for each replicate were randomly distributed. The experiment was run for 8 d. Once a day, dead pupae were removed and replaced with live ones. Starting the experiments with pupae had two advantages: (1) pupae are less likely to be damaged during handling than adults, and (2) the use of pupae ensured that copulation took place soon after emergence of the imagines. During copulation, the genitalia of the females should still be soft, which is an essential prerequisite of successful mating events in many dipteran species (Parma 1971). After mating, all females oviposited in one of the plastic containers.

Egg rafts were collected daily at noon and placed into a microtiter plate, to assess development time of individual egg rafts and fertilization status. In addition, this prevented later female attraction by egg rafts from earlier females. After all imagines had died, they were collected and preserved in alcohol, to determine the sex ratio for each cage.

Data from experiments with individual decisions are often essentially binomial data. Only in cases with high numbers of replicates (>50) will such data eventually approach a normal distribution (Sokal and Rohlf 1995). Therefore, I employed a two-tailed binomial exact test (SPSS vers. 6.1) to examine the differences of the data distributions. The probabilities of the  $k$  tests were combined following the method of Stouffer et al. (1949; cited in Folks 1984) rather than the method by Fisher (1954). The method after Stouffer et al. was used to combine the probabilities of the  $k$  tests. Rice (1990) stated that the Fisher method is unsuitable as a consensus test because it is more sensitive to data that refute a common  $H_0$  compared with the data that support it. Stouffer et al.'s method lacks this bias. In this test, each of a group of  $k$   $P$ -values is transformed to a corresponding standard normal variable ( $z_p$ ). A test of  $H_0$  is carried out by calculating  $Z = z_{p(\text{average})}/(1/\sqrt{k})$ . The fifth replicate of the experiment with *C. obscuripes* was not included in the analysis because of the low number of data.

In the experiments with *C. crystallinus* and *C. obscuripes*,

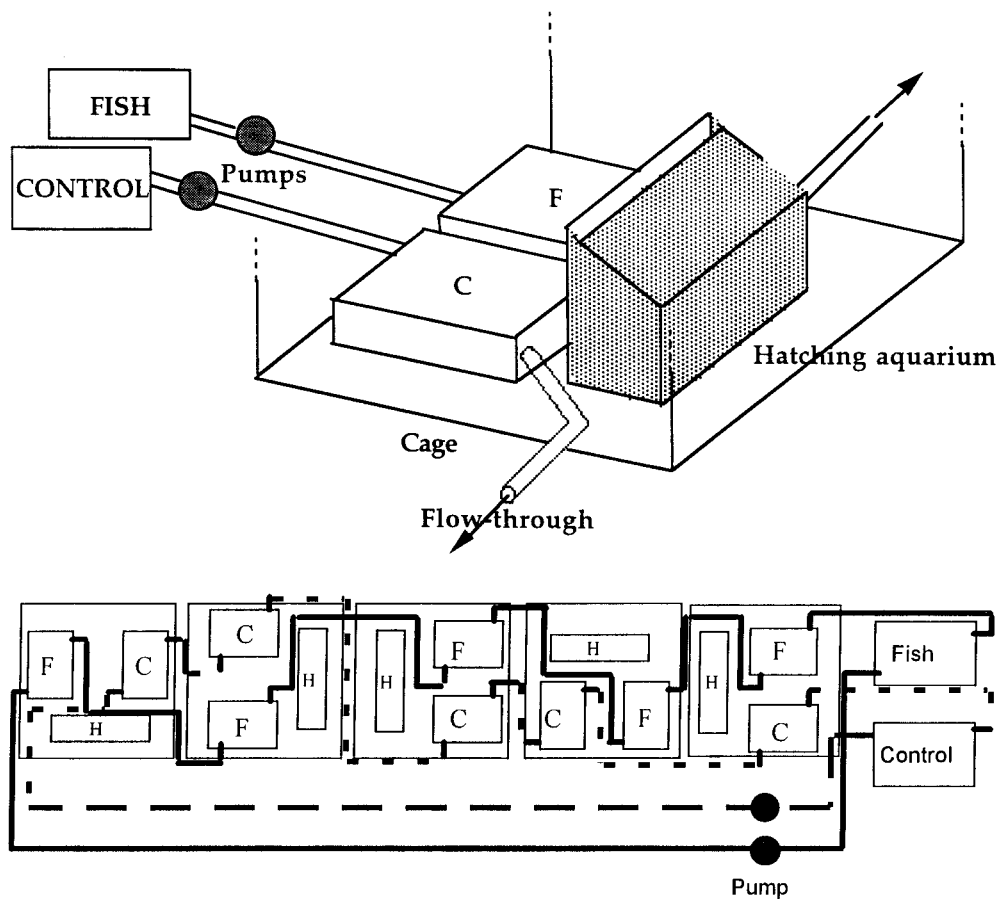


Fig. 1. (a) Design of the experimental setup. The positions of a hatching aquarium and the black containers within the cages are shown. (b) Diagram of the experimental setup showing the positions of the hatching (H) aquaria and the black containers within the cages. The black lines are the flow-through system for the fish-conditioned water (F), and the dashed lines are the flow-through system for the control water (C).

males emerged earlier, with 56.3% (SE = 3.7%;  $n = 5$ ) and 73.3% (SE = 6.5%;  $n = 5$ ) of the populations being males, respectively. After 1–3 d, nearly all imagines had emerged from the hatching aquarium and started to mate. The males caught a female when she flew into the swarm; copulation took place in flight and lasted 1–2 s. In contrast, *C. flavicans* copulation took place at the wooden frame of the cage; 47.8% (SE = 3.4%;  $n = 5$ ) of the emerged *C. flavicans* imagines were males. In the experiment with *C. crystallinus*, 94.3% (SE = 6.3%;  $n = 5$ ) of all egg rafts were fertilized and hatched, while for *C. obscuripes* and *C. flavicans*, the numbers were 86.6% (SE = 2.5%;  $n = 5$ ) and 85.7% (SE = 7.2%;  $n = 5$ ), respectively. These high fertilization rates indicate that the cage design was appropriate for successful *Chaoborus* mating.

After 2 d, the first imagines in the experiment started to lay eggs in one of the two black containers. The pond-dwelling species *C. crystallinus* and *C. obscuripes* laid significantly fewer egg rafts in the container with fish water compared to the control (Table 1). As the sex of the pupae was not determined, one replicate for both of the species contained a relatively high percentage of males, and hence the total number of oviposited eggs was considerably lower than

in the other replicates. *C. flavicans*, the lake-dwelling species, tended to prefer the containers with fish kairomones compared to the control, although this preference was not significant (Table 1). *C. crystallinus* laid an average of 64.8% of all egg rafts in the control containers, while *C. obscuripes* laid 65.7% and *C. flavicans* laid 38.5% of their egg rafts in the control containers. Females laid only one egg raft and died soon after ovipositing. At 24°C, hatching occurred approximately 3 d after laying; the developmental time of the egg rafts was the same for all species in all treatments.

This study clearly shows that the imagines of the pond-dwelling species *C. crystallinus* and *C. obscuripes* can use fish kairomones to assess the quality of oviposition sites, whereas the imagines of the lake-dwelling species *C. flavicans* do not show any preference in their ovipositing behavior. Therefore, while direct predatory effects contribute to the lack of local coexistence between fish- and pond-dwelling *Chaoborus* (von Ende 1979), the results of this study indicate that adult oviposition behavior may also play an important role in influencing *Chaoborus* species distribution. The tendency of the pond-dwelling species of *Chaoborus*

Table 1. Number of egg rafts in control and fish containers. Summary statistics are for the binomial exact test for each replicate and standard normal variable  $z_p$  for the consensus combined  $P$ -value test after Stouffer et al. (1949; cited in Folks 1984).

Taxon	Number of egg rafts in control container	Number of egg rafts in fish containers	Binomial exact test	$z_p$ (average)	Combin. after Stouffer et al.
<i>C. crystallinus</i>	33	18	0.0251	1.43	$P < 0.05$
	22	9	0.0311		
	33	19	0.0714		
	36	21	0.0637		
	12	7	0.3593		
<i>C. obscuripes</i>	12	3	0.035	1.12	$P < 0.05$
	12	3	0.035		
	11	5	0.210		
	11	7	0.481		
	1*	1	1.000		
<i>C. flavicans</i>	12	19	0.282	0.91	$P > 0.05$
	1	9	0.021		
	5	11	0.210		
	10	8	0.815		
	8	9	1.000		

\* Data not included in the analysis.

imagines to avoid habitats with fish has probably evolved in response to fish preying on the aquatic stages of these taxa.

As the design of this experiment effectively rules out the possibility that imagines could use visual or mechanical cues, chemical cues appear to be the mechanism used by *Chaoborus* to detect fish. An alternate interpretation of these results could be that mature females prefer to oviposit in water similar to the water in which they were born (i.e., water with or without fish chemicals). The only difference between the control and the fish water was the added fish chemicals; the water itself was obtained from the same pond for both treatments, and none of the organisms originated from that particular pond. Furthermore, the results suggest that fish kairomones are nonvolatile, contact oviposition inhibitors rather than volatile cues. Although the fish-conditioned water and control containers were placed next to each other, it is unlikely that volatile fish kairomones would be distributed into the air in such a sharp gradient that *Chaoborus* imagines could assess water quality of the containers while flying.

Many dipterans have contact chemoreceptors on various body appendages, including the tarsi (Stadler 1984). Petranka and Fakhoury (1991) suggest that *Chaoborus* may chemically sample water with their tarsi while positioning themselves at the water surface to oviposit. By contrast, Weber and Tipping (1993) suggest that for *Culex* species, chemoreceptors in the mouth parts may be used to assess water quality, as they observed preoviposition drinking by imagines. I observed such drinking behavior for *Chaoborus* as well, but it is uncertain which one of the proposed sensory structures the *Chaoborus* imagines use to assess water quality.

Unlike me, McPeck (1989) did not find that the fishless lake species (pond-dwelling species) of *Enallagma* damsel-

flies discriminated between fishless and fish-containing lakes. In his examination of the dispersal of adult *Enallagma* damselflies, two species found as larvae in fishless lakes and two other species found as larvae in lakes supporting well-developed fish communities all dispersed very few adults to adjacent lakes. In contrast, another species found in lakes that winterkill, and thus contain fish only periodically, dispersed large numbers of adults to adjacent lakes. He attributed species differences in the propensity to disperse to the constancy of the fish and fish-containing condition of the lakes inhabited by those damselfly species. The same may be true for *C. flavicans*, the lake-dwelling species, which generally lives in lakes with well-developed fish communities. Assuming this species has a low propensity to disperse (relative to a pond-dwelling species), this could explain the lack of any oviposition preference for *C. flavicans*. However, few data are available on the dispersal abilities of the different *Chaoborus* species (for *C. albatus*, see Lindquist and Deonier 1942); thus, further work is necessary to test this hypothesis.

This study has shown the behavioral avoidance of water containing fish kairomones by ovipositing *C. crystallinus* and *C. obscuripes*. The role of fish in structuring freshwater communities through direct predation is well documented (e.g., Zaret 1980; von Ende 1979). This study suggests a different mechanism for how predators may influence the composition of freshwater communities. Hanski and Ranta (1983) described how *Daphnia* in rock pools exist as metapopulations, and the same may be true for pond-dwelling species of *Chaoborus*. The presence of fish in a particular pond may affect not only the local pond, by discouraging oviposition, but may also increase emigration to neighboring ponds. This emigration would increase abundance and thus influence the population genetic structure of neighboring

ponds. This nonconsumptive effect of the predator may result in far-reaching (watershed-scale) direct and indirect effects since the prey are only to a small degree removed from the system. *Chaoborus* pond-dwelling species live in a fluctuating, unpredictable habitat, with a relatively short persistence time (compared to lakes). One can view ponds in the landscape as "patches of a metapopulation"; these patches are permanent and temporary ponds that periodically dry out or freeze solid from year to year. This last fact might explain why 35% of the individuals tested oviposited into the fish water, since many species that live in such unpredictable habitats show a wide variation in habitat selection behavior (Krebs 1994).

The data presented indicate that for pond-dwelling species of *Chaoborus*, selection may act at the adult stage, so that they behave to avoid fish. For the lake-dwelling species of *Chaoborus*, selection may occur at the larval stage, promoting alternative antipredator behaviors such as vertical migration and reduced movement frequency to avoid fish (Dawidowicz 1990; Berendonk and O'Brien 1996), assuming that fish predation is the ultimate cause for selective ovipositing and vertical migration in *Chaoborus*.

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