Is there light after depth? Distribution of periphyton chlorophyll and productivity in lake littoral zones

Yvonne Vadeboncoeur[1,3], Shawn P. Devlin[1,4], Peter B. McIntyre[2,5], and M. Jake Vander Zanden[2,6]

[1]Department of Biological Sciences, Wright State University, 3640 Colonel Glenn Highway, Dayton, Ohio 45435 USA
[2]Center for Limnology, University of Wisconsin, 680 North Park Street, Madison, Wisconsin 53706 USA

Abstract: Periphyton and phytoplankton contribute to the base of lake food webs, and both groups of microalgae are influenced by resources and physical forcing. Spatial variation in light availability interacts with the physical dynamics of the water column to create predictable depth gradients in resources and disturbance that may differentially affect periphyton vs phytoplankton. We characterized the depth distribution of chlorophyll and productivity of periphyton on sediments (epipelon) and phytoplankton in the euphotic zones of 13 oligomesotrophic lakes that span a large size gradient (0.017–32,600 km^2). Epipelic chlorophyll usually increased with depth in the epilimnion. Light was the primary driver of the consistent within-lake patterns in periphyton productivity across this lake-size gradient. In 5 lakes, epipelic periphyton exhibited a unimodal distribution of productivity with depth in the photic zone, but no evidence of photoinhibition was found for periphyton. Rather, patterns in sediment N and P and observed changes in biofilm structure were consistent with determination of epipelic biomass by disturbance at depths ≤1 m in the smaller lakes and by light limitation at depths >1 m. Further quantification of the effects of disturbance on epipelon is needed. Nonetheless, our data demonstrate that the perceived high spatial variability in periphyton biomass and productivity is not an impediment to development of robust models of whole-lake primary production that include both phytoplankton and periphyton.
Key words: periphyton, light, microphytobenthos, phytoplankton, epipelon, disturbance, phosphorus, C:N, North Temperate Lakes, Wisconsin, Lake Tanganyika, Lake Tahoe

Within ecosystems, different functional groups of primary producers partition resources in time and space, and in so doing, create a dynamic mosaic of resource availability for higher trophic levels. Until recently, lake ecologists focused on phytoplankton as the primary basal resource, engendering a perception that lake food webs are simple, linear, and largely dependent on planktonic primary production. Increased understanding of the energetic importance of littoral periphyton to a wide variety of fish species has developed synchronously with better integration of periphyton into studies of lake ecosystems (Vadeboncoeur et al. 2002, 2003, Karlsson et al. 2009). Many synthetic assessments have been made of the influences of among- and within-lake resource gradients on phytoplankton biomass and production (Wetzel 2001, Reynolds 2006). Similar syntheses for periphyton are lacking, in part because of the perception that benthic habitat heterogeneity is a strong determinant of sediment algal dynamics (MacIntyre et al. 1996).

The physical heterogeneity of littoral zones gives rise to spatial variation in periphyton biomass and productivity, especially where macrophytes provide a temporally variable and structurally complex substratum for periphyton (Wetzel 1964, Kahlert et al. 2002). However, many lakes either have patchily distributed macrophytes or lack them altogether. Lake bottoms typically are dominated by expanses of soft sediments. Despite the physical extent and relative homogeneity of soft-sediment habitat, the role of periphyton on soft sediments (epipelon) is both underappreciated and poorly described (Lowe 1996, MacIntyre et al. 1996). Epipelic algal communities are exposed to predictable variation in disturbance, light, and nutrients as a function of water-column depth. The influence of gra-

E-mail addresses: [3]yvonne.vadeboncoeur@wright.edu; [4]Present address: Department of Biological and Environmental Science, University of Jyväskylä, P.O. Box 35, FIN-40014, Jyväskylä, Finland, shawn.devlin@gmail.com; [5]pmcintyre@wisc.edu; [6]mjvanderzand@wisc.edu

DOI: 10.1086/676315. Received 15 August 2013; Accepted 24 December 2013; Published online 31 March 2014.
Freshwater Science. 2014. 33(2):524–536.

dients in resources and physical forcing with depth are well described for phytoplankton (Reynolds 2006), but the structuring effects of these gradients on periphyton in lakes remains largely unquantified (Lowe 1996).

Depth is a key factor determining ambient light intensity, nutrient availability, and the disturbance regime experienced by epipelon. Light availability declines with depth, and the rate of this decline varies among lakes depending on concentrations of phytoplankton and other light-absorbing substances in the water (Kirk 1994). Ambient light availability at depth determines photosynthesis rates (Vadeboncoeur et al. 2001) and controls the extent to which epipelic biofilms regulate nutrient retention in the sediments (Carlton and Wetzel 1988, Sundback et al. 2004, Genkai-Kato et al. 2012). Depth also determines the disturbance regime experienced by epipelon. Wave action can disrupt the sediment, resulting in reduced biomass in the wave zone and predictable changes in biofilm metabolism and nutrient retention with depth (Forehead and Thompson 2010). The effect of wave disturbance on sediments decreases rapidly with depth (Forehead et al. 2012), and the depth at which waves cease to be a strong structuring force depends upon lake size and the physical exposure of a particular site within a lake (Weatherhead and James 2001). Downslope transport of particles, including particulate nutrients, is a function of exposure and slope, but periphyton and the extracellular matrix excreted by algae stabilize littoral sediments (Mariotti and Fagherazzi 2012). These spatial patterns in light and disturbance and their emergent effects on sediment nutrient content are expected to be strong drivers of variation in periphyton biomass, species composition, and metabolism with depth (Lowe 1996).

Determining the drivers of within- and among-lake variation in phytoplankton distribution and metabolism has been a cornerstone of limnology that has yielded comprehensive understanding of one part of the energetic foundation of lake food webs (Reynolds 2006). No corresponding synthetic understanding of the determinants of variation in periphyton productivity and biomass exists. Periphyton and phytoplankton are composed of taxonomically similar groups of microalgae that are limited by light and nutrients, and both groups of microalgae are a critical energy source for higher trophic levels in lakes (Vadeboncoeur et al. 2003, Vander Zanden et al. 2011). We compared depth variation of sediment microalgae with those of their planktonic counterparts in 13 lakes. We measured benthic primary productivity and chlorophyll *a* along depth transects at multiple sites within each lake. We characterized variation in C and nutrient content of the surface layer of the sediments because we expected sediment nutrient content to determine and to reflect epipelic biomass. Our goals were to describe within- and among-lake variation in periphyton productivity with respect to light and depth across a large lake-size gradient and to compare light- and depth-related patterns between epipelon and phytoplankton in the same ecosystems.

METHODS

Study sites

We measured benthic and pelagic primary productivity and biomass in lakes in California, Wisconsin, and Michigan in North America and in Lake Tanganyika in Tanzania (Table 1). The lakes range in size from 0.017 to ~33,000 km^2, and all are characterized by low-to-moderate nutrient concentrations (Table 1). The USA lakes are dimictic, temperate lakes, and Lake Tanganyika is a meromictic tropical lake in the African rift valley. Four of the Michigan lakes were experimentally fertilized over the course of 3 y (Cottingham et al. 1998, Carpenter et al. 2001, Vadeboncoeur et al. 2001). The data presented here were collected for a variety of independent research projects. Therefore, the design is not balanced with respect to the number of sampling sites, times, or depths in each lake (Table 1). The data from the Michigan lakes were collected during summer (June 1–August 31) 1992–1995 (Vadeboncoeur et al. 2001). The Wisconsin lakes were studied during the summers of 2005–2007 (Devlin et al. 2013). The California lakes and Lake Tanganyika were sampled in July and August 2004.

All focal lakes except Lake Tanganyika are part of long-term research programs for which phytoplankton and water chemistry are monitored routinely. Phytoplankton data, total P (TP) concentrations, and light attenuation coefficients (k_d) contemporaneous with our benthic data were provided by researchers working on long-term research programs in the Michigan Lakes (Carpenter et al. 2001), the Wisconsin Lakes (North Temperate Lakes Long Term Ecological Research Site; http://lter.limnology.wisc.edu), and the California lakes (University of California, Davis, Tahoe Environmental Research Center).

Light

All primary productivity measurements were made during midday on virtually cloudless days. k_d was measured in each lake with a LiCor cosine sensor (LiCor, Lincoln, Nebraska). k_d was measured at least every 2 wk in the Michigan and Wisconsin lakes and at the time of productivity measurements in all lakes. We standardized the effect of depth on light among lakes with very different k_d values by converting depth (z) to % surface light (%*Light*). We calculated an average summer k_d for each lake and transformed each sampling depth:

$$\%Light = 100e^{-k_d z} \quad \text{(Eq. 1)}$$

Phytoplankton

We used phytoplankton data from long-term monitoring programs that were contemporaneous with our sam-

Table 1. Study lake (smallest to largest) characteristics: average depth (z_{avg}), euphotic zone depth ($z_{1\%}$), surface area (Area), water-column total P (TP), and down-welling light attenuation coefficient (k_d>). If $z_{1\%}$> maximum depth (z_{max}) then z_{max} is given (bold; Central Long Lake and Little Rock Lake). Columns for epipelic productivity (PPR) and chlorophyll *a* (Chl) indicate the number of sample days (N), followed by the number of transects (n) in parenthesis. Where the sample depths for PPR and Chl include hyphenated ranges, samples were collected at 1-m depth intervals on each transect. One sample was collected at each depth on each chlorophyll transect. NA = not available.

Lake (Group)	z_{avg} (m)	$z_{1\%}$ (m)	Area (km^2)	TP (μg/L)	k_d (m^{-1})	Epipelon (N [n]) PPR	Epipelon (N [n]) Chl	Sampling depths (m) PPR	Sampling depths (m) Chl
Paul (Michigan)	3.9	13.2	0.017	11	0.35	8 (1)	4 (4)	1.5, 2.5, 4.5	0.5, 1, 1.5, 2–7
Central Long (Michigan)	1.9	**5.0**	0.021	19	0.66	8 (1)	4 (4)	1.5, 2.5, 4	0.5, 1, 1.5, 2–4
East Long (Michigan)	4.9	3.7	0.023	36	1.25	8 (1)	4 (4)	1.5, 2.5	0.5, 1, 1.5, 2–4
Peter (Michigan)	6.0	11.5	0.027	22	0.40	8 (1)	4 (4)	1.5, 2.5, 4.5	0.5, 1, 1.5, 2–8
West Long (Michigan)	4.7	1.2	0.034	22	0.45	8 (1)	4 (4)	1.5, 2.5, 4.5	0.5, 1, 1.5, 2–7
Little Rock (Wisconsin)	3.1	**7.0**	0.080	34	0.33	4 (1)	3 (3)	1, 3, 5	0.5, 1–6
Castle (California)	11.4	19.2	0.20	10	0.24	1 (1)	0	2, 5, 11	NA
Crystal (Wisconsin)	10.4	14.4	0.37	8	0.32	4 (1)	3 (3)	2, 4, 8	0.5, 1–10
Sparkling (Wisconsin)	10.9	13.5	0.64	15	0.34	8 (1)	7 (3)	0.5, 2, 4, 8	0.5, 1–10
Big Muskie (Wisconsin)	7.5	14.4	3.96	18	0.32	4 (5)	2 (3)	0.5, 2, 4, 8	0.5, 1–10
Trout (Wisconsin)	14.6	12.5	16.1	14	0.37	6 (2)	5 (8)	0.5, 2, 4, 8	0.5, 1–10
Tahoe (California)	113	57.6	499	7	0.08	1 (1)	0	2, 5, 11	NA
Tanganyika, Tanzania	572	38.4	32,600	7	0.12	1 (1)	1 (1)	2.5, 5, 10	2.5, 5, 10

pling of epipelon. Phytoplankton chlorophyll was sampled at 100, 50, 25, 10, 5, and 1% of surface light on a biweekly (every 2 wk) basis in the Michigan lakes. Phytoplankton chlorophyll was collected biweekly at 8 or 9 depths from the surface to hypolimnion in the Wisconsin lakes (http://lter.limnology.wisc.edu). Chlorophyll data were collected to depths with <1% incident light in August 2004 in the California lakes. Chlorophyll samples were collected weekly from Lake Tanganyika at 1, 10, 20, 30, 40, 60, 80, and 100 m in 2004 (Corman et al. 2010).

Phytoplankton productivity was measured in all lakes with ^{14}C light-and-dark incubation methods. Biweekly in situ incubations of phytoplankton in the Michigan lakes were conducted at midday at the same depths at which chlorophyll was sampled (Carpenter et al. 1993, Cottingham et al. 1998). For the Wisconsin lakes, photosynthesis–irradiance (P–I) curves were generated from integrated epilimnetic and integrated metalimnetic water samples that were incubated in the laboratory with a ^{14}C tracer for 4 h (http://lter.limnology.wisc.edu). Phytoplankton productivity in Lake Tahoe was measured in situ at 13 depths (from the surface to 0.01% surface light) during the same week that we measured benthic primary productivity using a standard ^{14}C technique (Goldman et al. 1989). We obtained depth-specific (0, 5, 10, 20, and 40 m) phytoplankton P–I parameters from Sarvala et al. (1999) for Lake Tanganyika.

P–I parameters

The in situ incubation methods for the Michigan and California lakes were designed to detect variation in photosynthesis as a function of light by incubating phytoplankton at different depths within the lake. We used variation in chlorophyll-specific productivity with depth to establish the light-limited, photosaturated, and photoinhibited portions of the P–I relationships for phytoplankton. The P–I relationship was measured directly by exposing phytoplankton from the Wisconsin lakes to different light intensities in a laboratory setting (http://lter.limnology.wisc.edu). Sarvala et al. (1999) used a combination of in situ and laboratory incubations to derive P–I curves for Lake Tanganyika phytoplankton. We were primarily interested in whether phytoplankton and periphyton differed in their likelihood of photoinhibition at ambient light intensities. We interpreted an increase in phytoplankton photosynthesis between the surface of the lake and subsequent epilimnetic depths as evidence of photoinhibition for the Michigan lakes, California lakes, and Lake Tanganyika. For the Wisconsin lakes, we estimated the light intensity at which photoinhibition occurred by visually examining the laboratory-generated P–I curves. We estimated the light intensity at the onset of photoinhibition by taking the average of the 2 light intensities where the first downward slope of the P–I curve was observed.

Epipelon

Chlorophyll We used a 20-cc-syringe piston corer to collect sediment plugs >5 cm deep, and we retained the top 0.5 cm of sediment for analysis. We freeze-dried each sediment sample, weighed it, and ground it to a fine powder (Hansson 1988). We removed a 5- to 25-mg subsample for chlorophyll extraction at 4°C for 24 h in the dark in 100% methanol for the Michigan lakes, 95% ethanol for the Wisconsin lakes, or 90% ethanol for Lake Tanganyika. We measured chlorophyll *a* and phaeophyton fluorometrically with an acidification step (Arar and Collins 1997). The freeze-drying (Hansson 1988), homogenizing, and subsampling steps are critical for consistent, repeatable results that are free from quenching effects from extracted sediment organic C.

Productivity We used ^{14}C to measure benthic primary productivity in situ on intact sediment cores in the Michigan lakes (Vadeboncoeur and Lodge 2000, Vadeboncoeur et al. 2001). We used in situ O_2-exchange methods to measure epipelic productivity in the remaining lakes (Vander Zanden et al. 2006, Devlin et al. 2013). We sampled each Wisconsin lake 2 to 7 times during a single summer between 2005 and 2007 (Devlin et al. 2013). In the California lakes (Tahoe and Castle) and Lake Tanganyika, we restricted sampling to 3 depths, and we sampled individual sites only once because of the logistics of diving at high altitudes in remote locations.

The O_2-exchange method entailed collecting 5 to 8 intact sediment cores at each depth (5 cm diameter, ~10 cm of sediment plus 15 cm of overlying water) in clear (n = 3–6) and opaque (n = 2) acrylic tubes. Immediately upon descending to the sampling site, a diver used a 60-cc syringe to collect 3 water samples from just above the sediments. These samples established O_2 concentrations at the beginning of the incubations. Undisturbed sediments were collected by inserting an acrylic tube 10 cm into the sediments and covering the top of the corer with a tight-fitting lid with a small central port. The diver then carefully removed the core from the sediments, sealed the bottom of the core with a nylon plug, adjusted the overlying water to a standard volume, and sealed the sampling port. Zero to 4 layers of neutral density shade cloth were placed over 4 of the light cores in the Wisconsin lakes to create a gradient of light intensities. Cores were incubated in situ at ambient light intensities >200 μmol m^{-2} s^{-1} for epilimnetic samples collected from 0.5 to 5 m, or 20 μmol m^{-2} s^{-1} for metalimnetic cores collected from 8 m. Standard incubations were 2 h, but incubations were terminated immediately if bubbles formed in the chambers.

Immediately upon removal from the lake, we rotated each core gently to mix the overlying water without disrupting the periphyton. We uncapped the sampling port in the lid and attached a 10-cm piece of tubing to the port. We expelled the overlying water through the tubing directly into a 60-mL biological O_2 demand (BOD) bottle without introducing air bubbles and fixed the sample immediately for Winkler titrations (Carignan et al. 1998). We removed and fixed water from each core before terminating the incubation of any subsequent core to minimize errors associated with varying the light exposure at the end of the incubation. We estimated gross primary productivity by adding dark respiration rates to the net primary productivity measured in the light cores. We expressed all primary productivity measurements as midday photosynthetic rate at a specific depth to permit direct comparisons of areal productivity rates that are not confounded by seasonal or latitudinal differences in day length.

P–I relationships We used laboratory experiments to generate P–I curves for epipelon from different depths in the Michigan lakes (Vadeboncoeur and Lodge 2000). We used neutral-density shade cloth to create a gradient of light intensities for the epipelon in the Wisconsin lakes. We fit these data to the hyperbolic tangent function of Jassby and Platt (1976) to estimate maximum photosynthesis rates (P_{max}) for each date. In 2008, we used a diving PAM (pulse amplitude modulated fluorometer; Walz, Effeltrich, Germany) to generate in situ P–I parameters (Uthicke 2006) for epipelon in Sparkling and Trout Lakes (Wisconsin). The PAM measures the relative electron transport rate (*ETR*) of photosystem II at each of the light intensities that the instrument generates. *ETR* units are arbitrary, but are an index of primary productivity. *ETR* values cannot be directly related to C uptake or O_2 evolution unless the methods are cross-calibrated.

We used the PAM to generate P–I parameters at 1-m depth intervals on 2 transects in each lake. We placed the fiber-optic cable of the PAM 5 mm above the sediment and generated rapid light curves (RLC) by exposing the biofilm to light intensities from 0 to 1500 μmol m^{-2} s^{-1} for 20 s. The range of 9 light intensities to which the algae are exposed in any given RLC is adjustable. We reduced the light range used at deeper sites to collect data primarily in the light-limited and light-saturated region of the P–I curve. We constrained the light range so that photoinhibition was evident only at the final (highest) light intensity. This approach generates robust estimates of photosynthetic efficiency (α) and ETR_{max} (an analog of maximum photosynthetic rate [P_{max}]). The light ranges used were not useful for generating photoinhibition (β) coefficients, but we were able to estimate the light intensity at onset of photoinhibition.

We used PROC NLIN (SAS version 9.2; SAS Institute, Cary, North Carolina) to fit PAM data to the hyperbolic tangent function of Jassby and Platt (1976). This analysis yielded ETR_{max} and α for each depth on each transect.

We calculated the intensity of onset of photosynthetic saturation ($I_k = ETR_{max}/\alpha$) for each P–I curve, and regressed average I_k on %*Light* using PROC GLM (SAS). We standardized P–I measurements for within-lake comparisons. The depth at which the highest ETR_{max} occurred was assigned an ETR_{max} value of 1 and ETR_{max} at all other depths was expressed as a fraction of the highest ETR_{max}. We estimated the light intensity at the onset of photoinhibition by taking the average of the 2 light intensities where the first downward slope of the P–I curve was observed.

C and nutrient content We subsampled sediment chlorophyll samples from a subset of lakes to measure epipelic organic matter and C, N, and P content from samples along 1–3 transects collected on multiple dates. We measured organic matter as loss on ignition (LOI) at 500°C for 1 h (APHA 2005). We measured P content by the molybdate method (Stainton et al. 1977) after combusting a 5 to 40-mg homogenized subsample (1 h, 500°C) and digesting it in hot HCl. C and N content was measured on an elemental analyzer at the University of California Davis Stable Isotope Facility on a PDZ Europa ANCA-GSL elemental analyser (Sercon, Cheshire, UK). We had sufficient %C and C : N data to assess depth patterns only for the Michigan lakes. P data were sufficient to test depth effects only in the Wisconsin and California Lakes.

Statistical analyses

We $\log_{10}(x)$-transformed chlorophyll data and $\sqrt{(x)}$-transformed epipelic %P data. We averaged epipelic data across transects for each depth on each date. This step was unnecessary for most phytoplankton data, which, except in Lake Tanganyika, were collected from a single mid-lake station. Both light and disturbance decrease logarithmically with depth, and these 2 gradients are expected to have opposite and interacting effects on periphyton. The maximum horizontal acceleration of a wave at the sediment surface increases with wave period (larger waves exert more force) and declines logarithmically with water-column depth (Denny and Wethey 2001). The maximum wave size in a lake is a function of lake size, but the decline in disturbance is a nonlinear function of e^{-z} (Denny and Wethey 2001). Including both %*Light* and disturbance as individual terms in the statistical model is not meaningful because the 2 variables are autocorrelated in lakes. Therefore, we used general linear models (PROC GLM) to regress chlorophyll, productivity, and nutrient content on %*Light* for each lake. If the residuals of the regression on %*Light* were not randomly distributed with respect to predicted values, we ran a model that included both %*Light* and the interaction term %*Light* × e^{-z}. We calculated Pearson correlation coefficients between epipelic chlorophyll and %P in the Wisconsin lakes.

RESULTS

Phytoplankton

Phytoplankton chlorophyll showed little variation between the surface and 5% light in most lakes, but increased slightly from the surface to 5% light in the California lakes. Phytoplankton chlorophyll was 3 to 5× higher at <5% light than at shallower depths in the North American lakes (Fig. 1A–C), but declined sharply at <5% light in Lake Tanganyika (Fig. 1C). Phytoplankton productivity showed some photoinhibition at 100% of surface light in all lakes, and usually decreased below 20% of surface light (Fig. 1D–F).

Epipelon

Chlorophyll on soft sediments increased linearly with depth down to 20% surface light in all lakes (Fig. 2A–C, Table 2). A subsequent decline in chlorophyll with depth occurred in 3 of the 10 lakes in eastern North America. The best model for epipelic chlorophyll in Crystal and Trout lakes in Wisconsin included an interaction between light and disturbance (Table 2).

Midday area-specific epipelic primary productivity varied between 5 and 80 mg C m^{-2} h^{-1}. A monotonic decline in productivity occurred with depth in the Michigan lakes, Castle Lake (California), and Lake Tanganyika (Fig. 2D, F). Epipelic productivity had a unimodal distribution with depth in the Wisconsin lakes and peaked between 40 and 60% of surface light (Fig. 2E, Table 3). Productivity on sediments increased with depth in Lake Tahoe (Fig. 2C). In situ chamber incubations in the Wisconsin lakes yielded P–I patterns similar to those in previous experiments in the Michigan lakes (Vadeboncoeur and Lodge 2000). Productivity in the epilimnion plateaued at the highest field light intensities, and photoinhibition was never evident (data not shown). Cores collected from and incubated at 8 m showed a linear response to the imposed light gradient and did not appear to reach photosaturation.

The PAM fluorescence method yielded depth patterns similar to those of the in situ incubations. Maximum biomass-specific ETR_{max} on sediments in Sparkling and Trout Lakes was highest in the mid-epilimnion and declined with depth only at <50% of surface light. Light intensity at onset of photosaturation decreased with depth (Fig. 3A, B, Table 4). The PAM exposed epipelon to light intensities up to 1500 μmol m^{-2} s^{-1} and allowed us to detect photoinhibition. Onset of photoinhibition occurred at substantially higher light intensities than the maximum light intensity that epipelon at a given depth would experience at midday (Fig. 3C).

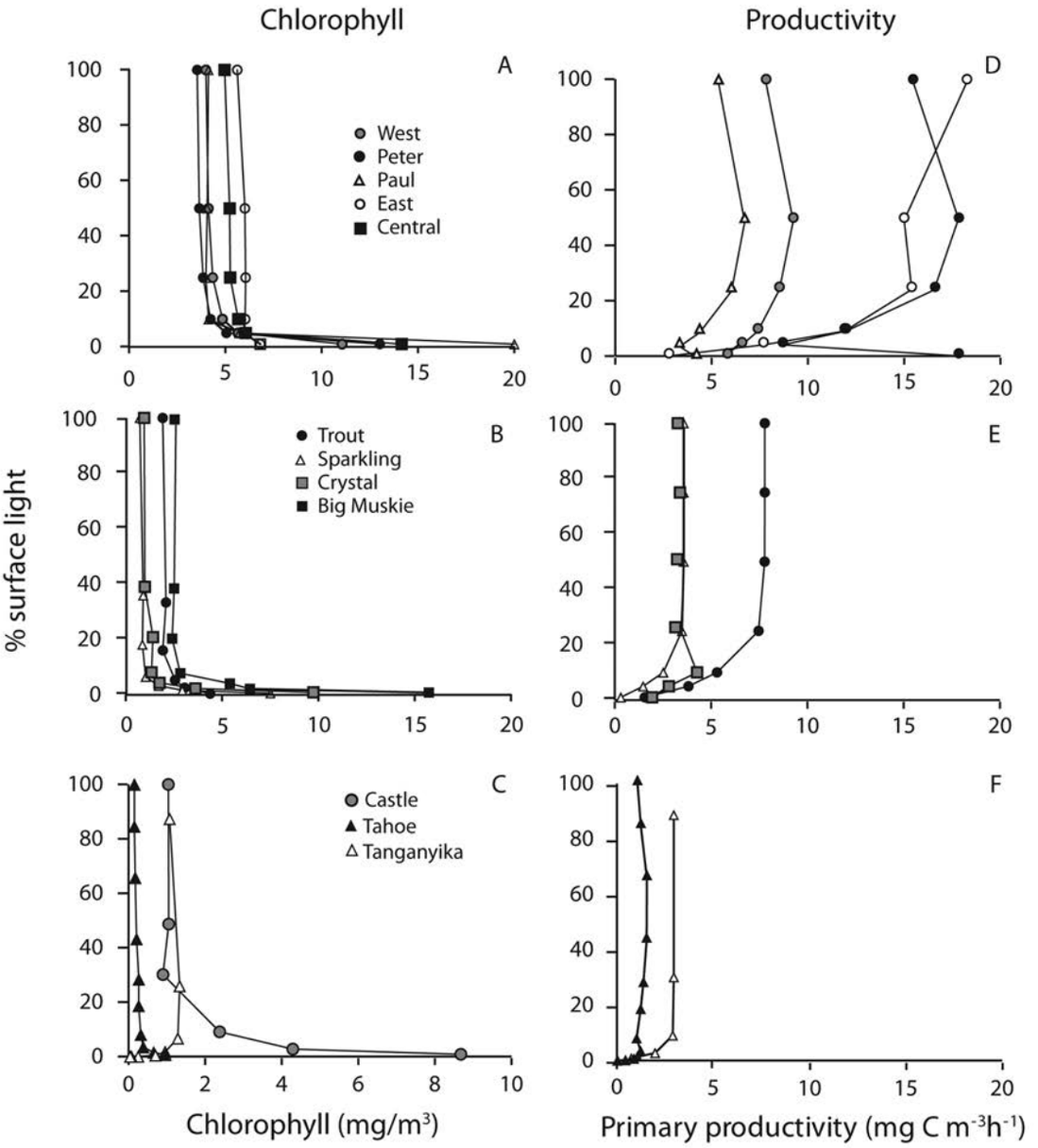

Figure 1. Phytoplankton chlorophyll *a* (A–C) and productivity (D–F) as a function of changing light intensity with depth in Michigan (A, D), Wisconsin (B, E), California, and Lake Tanganyika (C, F). Chlorophyll *a* concentrations are summer means for each lake and % light intensity is based on average light attenuation coefficient (k_d) in each lake during the sampling period. Productivity was measured at midday using ^{14}C incubations.

C content (%C) of littoral surface sediment containing the epipelic mat was highest in the smallest study lakes (Michigan lakes and Little Rock Lake, Wisconsin). Percent C of sediment did not change with depth in the Michigan lakes (data not shown), but molar C : N decreased with depth in the epilimnion (Fig. 4A). C : N ranged between 15 and 25 at 80% of surface light (0.5 m) and reached a minimum C : N of 12 between 15 and 40% of surface light (Fig. 4A). Percent organic matter (%OM measured as LOI) of surficial sediments showed no consistent pattern with depth in the Wisconsin lakes, except that %OM was lowest at 0.5 m in all lakes. In the Wisconsin lakes and the California lakes, %P of surface sediments increased substantially below 10% light, but a smaller secondary increase occurred at ~40% light (Fig. 4B). Chlorophyll *a* and %P in the Wisconsin lakes were not significantly correlated when all depths were included in the analysis. However, chlorophyll *a* and %P were correlated

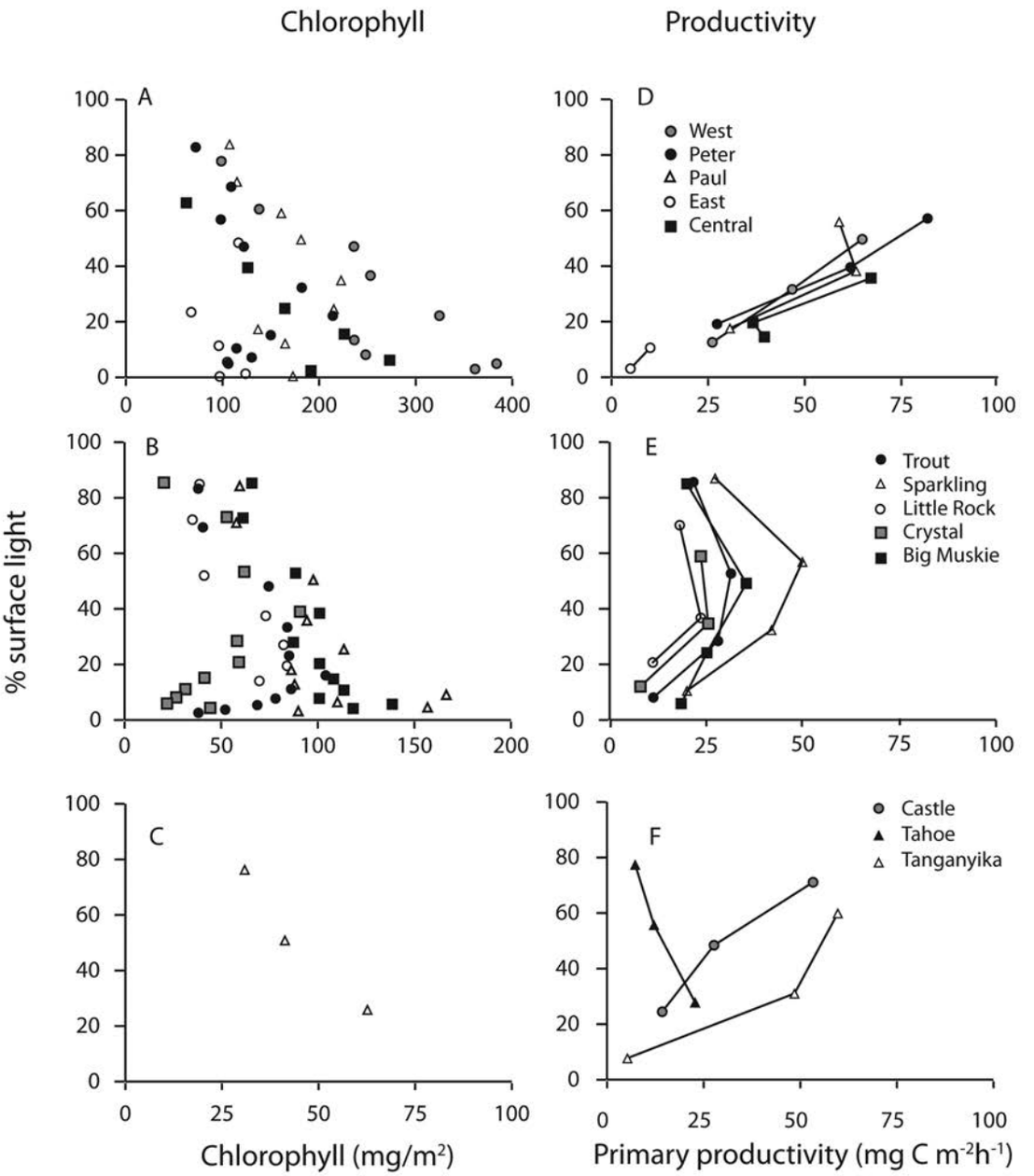

Figure 2. Epipelic chlorophyll *a* (A–C) and productivity (D–F) as a function of changing light intensity with depth in Michigan (A, D), Wisconsin (B, E), California and Lake Tanganyika (C, F). Chlorophyll *a* concentrations are summer means for each lake and % light intensity is based on average light attenuation coefficient (k_d) in each lake during the sampling period. Productivity was measured at midday using ^{14}C (Michigan lakes) or O_2-exchange methods (all other lakes).

in the upper epilimnion (>20% light, ≤5m) in Little Rock Lake (r = 0.47, p = 0.04), Crystal Lake (r = 0.41, p = 0.02), Sparkling Lake (r = 0.37, p = 0.02) and Big Muskie Lake (r = 0.32, p = 0.05).

DISCUSSION

Periphyton and phytoplankton each exhibited consistent patterns among lakes when depth was transformed to % surface light, but the mechanistic drivers of variation in chlorophyll and productivity with depth differed between these 2 key functional groups of primary producers. Epilimnetic phytoplankton chlorophyll was uniform with depth because of mixing, and variation in phytoplankton productivity in the epilimnion was a function of photoinhibition and light attenuation (Fig. 1D–F). Epipelon also was strongly influenced by light. Acclimation of periphyton to ambient light at depth was evidenced by

Table 2. Regression statistics for epipelic chlorophyll. Chlorophyll *a* (Chl) data are $\log_{10}(x)$-transformed for each lake. The original model included %*Light* only. We subsequently tested for an interaction between %*Light* and disturbance (*Dist*), using an index of the change in disturbance with depth ($Dist = e^{-z}$). Average Chl concentrations (mg/m^2) are also presented (mean Chl). Lakes are listed from smallest to largest. ns = not significant.

Lake (Group)	Regression coefficients: Intercept	%*Light*	*Light* × *Dist*	df	*F*	R^2	*p*	Mean Chl (mg/m^2)
Paul (Michigan)	2.2	ns	ns	2,17	2.8	0.25	0.087	160
Central Long (Michigan)	2.43	−0.009	ns	1,16	24.3	0.6	0.0002	155
East Long (Michigan)	2	ns	ns	2,15	2.1	0.22	0.154	99.2
Peter (Michigan)	2.19	−0.003	ns	1,28	4.8	0.15	0.0372	124
West Long (Michigan)	2.4	−0.004	ns	1,16	9.9	0.35	0.0097	198
Little Rock (Wisconsin)	1.99	−0.004	ns	1,16	5.2	0.25	0.0366	63.9
Crystal (Wisconsin)	1.41	0.01	−0.023	2,30	15.3	0.5	0.0001	46.6
Sparkling (Wisconsin)	2.63	−0.004	ns	1,62	17.2	0.22	0.0001	106
Big Muskie (Wisconsin)	2.08	−0.002	ns	1,19	10.5	0.36	0.0043	102
Trout (Wisconsin)	1.8	0.004	−0.013	2,44	9.3	0.3	0.0004	70.2
Tanganyika (Tanzania)	1.97	−0.006	ns	1,6	44.8	0.88	0.0005	43.3

a strong correlation between the onset of photosaturation and light at depth and by a lack of photoinhibition at ambient light intensities. Epipelic productivity showed a unimodal distribution with depth in the lakes for which we included productivity measurements at 0.5 m (Fig. 2D–F). This unimodal response curve is probably caused by limitation of periphyton biomass by the effects of disturbance in the wave zone and light limitation below the zone of disturbance. The patterns in periphyton distribution were remarkably consistent over the broad size gradient of study lakes and showed that light is a robust predictor of changes in periphyton with depth in stratified lakes.

Phytoplankton showed patterns with depth that are typical of unproductive lakes (St Amand and Carpenter 1993, Sawatzky et al. 2006). Chlorophyll concentrations were constant or increased slightly with depth in the epilimnion and increased abruptly in the metalimnion (Fig. 1A–C). This

Table 3. Regression statistics for epipelic productivity. The original model included %*Light* only. We subsequently tested for an interaction between %*Light* and disturbance (*Dist*), using an index of disturbance ($Dist = e^{-z}$). Average midday productivity ($mg\ C\ m^{-2}\ h^{-1}$) is also presented (mean PPR). Lakes are listed from smallest to largest. Ns = not significant.

Lake (Group)	Regression coefficients: Intercept	%*Light*	*Light* × *Dist*	df	*F*	R^2	*p*	Mean PPR $mg\ C\ m^{-2}\ h^{-1}$
Paul (Michigan)	22.3	0.75	ns	1,7	10.5	0.6	0.0144	50
Central Long (Michigan)	6.7	1.67	ns	1,5	12.9	0.72	0.0157	49
East Long (Michigan)	ns	ns	ns	1,2	2.5	0.55	0.2559	6.4
Peter (Michigan)	4.6	1.37	ns	1,7	14.6	0.68	0.0065	57
West Long (Michigan)	19.1	0.84	ns	1,7	3.7	0.34	0.0964	45
Little Rock (Wisconsin)	15.7	ns	ns	1,8	0.3	0.03	0.61	18
Castle (California)	4.4	1.01	ns	1,7	23.6	0.77	0.0018	38
Crystal (Wisconsin)	−1.3	0.8	−2.81	2,9	11.8	0.72	0.0031	19
Sparkling (Wisconsin)	15.4	0.73	−0.98	2,24	8.8	0.42	0.0014	35
Big Muskie (Wisconsin)	14.0	0.44	ns	1,10	16.4	0.62	0.0023	26
Trout (Wisconsin)	7.8	0.62	−0.76	2,12	10.5	0.64	0.0023	24
Tahoe (California)	38.1	−0.37	ns	1,6	180.7	0.97	<0.0001	13
Tanganyika (Tanzania)	−3.3	0.82	ns	1,3	111.2	0.97	0.018	33

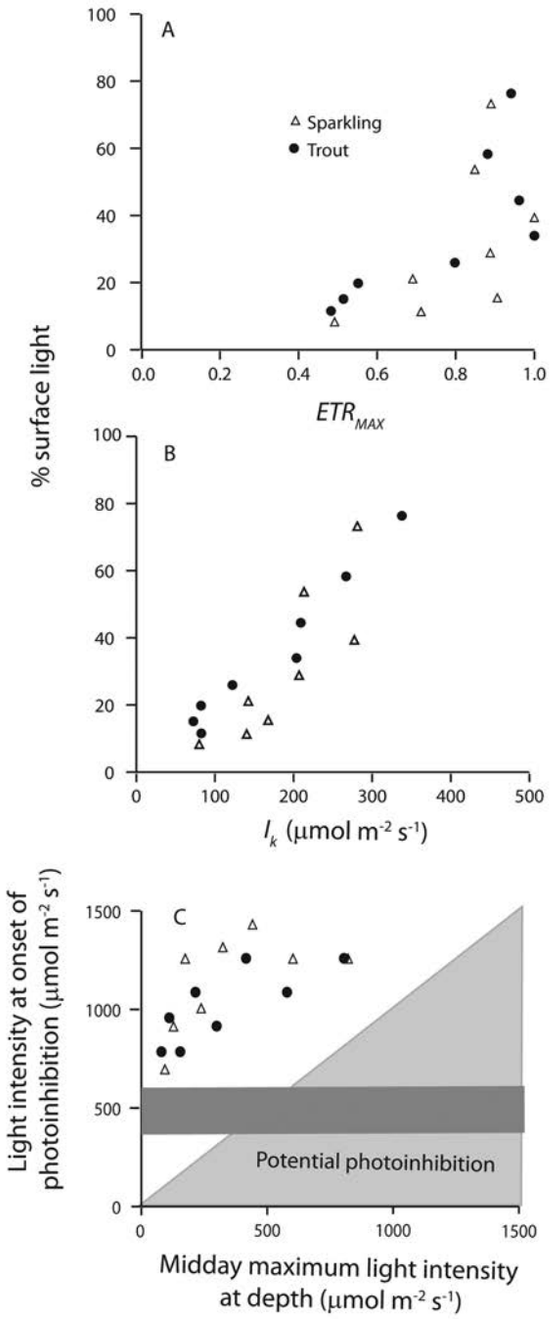

Figure 3. Photosynthesis–Irradiance (P–I) parameters derived from in situ pulse amplitude modulated (PAM) fluorometry on epipelon in Wisconsin (Sparkling and Trout Lakes). A.—Standardized maximum electron transfer rate (ETR_{max}). B.—Light intensity at onset of photosaturation (I_k) as a function of % surface light. C.—Relationship between light intensity at onset of photoinhibition estimated from the PAM P–I curves as a function of the maximum light intensity that periphyton experience at depth they occur. The grey bar denotes the range of light intensities at which phytoplankton from the 2 lakes exhibited photoinhibition. Each point represents epipelon measured at a single depth.

deep chlorophyll maximum emerges because the physical stability of the metalimnion (relative to epilimnetic mixing) subjects metalimnetic phytoplankton to a constant low-light environment that induces phytoplankton to increase cellular chlorophyll content (Falkowski and Raven 2007). Phytoplankton productivity showed strong effects of light availability. In situ incubations in the Michigan lakes, Lake Tahoe, and Lake Tanganyika (Sarvala et al. 1999) all showed evidence of photoinhibition at lake surface (>50% light) followed by light limitation below 25% light (Fig. 1D–F). Phytoplankton data for the Wisconsin lakes were derived from laboratory incubations, and photoinhibition occurred at light intensities >800 μmol m^{-2} s^{-1} (data not shown). Notably, productivity decreased below 5% light in 8 of the 9 lakes for which we have data. Thus, the deep chlorophyll maximum did not translate into elevated productivity. These typical patterns in phytoplankton as a function of light and depth provide a useful model against which to examine the epipelon data: 1) photoinhibition decreases phytoplankton productivity at very shallow depths; 2) below the depth of photoinhibition, productivity and biomass-specific productivity of phytoplankton are inversely related to depth because of light limitation, and 3) physically isolated algal communities in the metalimnion can acclimate to low light by increasing cellular chlorophyll content, but this change does not necessarily result in an increase in productivity.

Are these paradigms of the plankton applicable to epipelic communities, and if so, how are they manifested in a physically stable benthic habitat compared with a miscible water column? Epipelic chlorophyll increased as a function of decreasing light intensity. This increase was either monotonic through the metalimnion or unimodal with a maximum occurring between 20 to 40% light (Fig.2A–C). Unfortunately, chlorophyll is a poor index of algal biomass when comparing assemblages acclimated to different light intensities (Baulch et al. 2009). Stable light ranges at a given depth produce variation in species assemblage (Round 1961, Roberts and Boylen 1988, Cantonati and Lowe 2014) and cellular chlorophyll content (Thompson 1999) that confound the interpretation of chlorophyll data across depth gradients.

Despite the ambiguity of chlorophyll as a biomass index, 2 lines of evidence suggest that epipelic biomass increased from the lake edge to the mid-epilimnion (≥20% light). First, visual observations showed a continuity of biofilm structure with depth in all the lakes. At depth <1 m, epipelic biofilms were poorly developed. In lakes <0.2 km^2, sediments were composed of loose, coarse organic material at depths <1 m, and biofilms did not stabilize the sediment. Sand was the dominant substrate at <1.0 m in the Wisconsin lakes >0.2 km^2, and the periphyton formed a thin, intact crust that consolidated the surface of the sand. In the Michigan and Wisconsin lakes, epipelic biofilms were

Table 4. Regression statistics for pulse amplitude modulated (PAM) fluorometry productivity for epipelon in 2 Wisconsin lakes. The original model included %*Light* only. We subsequently tested for an interaction between %*Light* and disturbance (*Dist*), using an index of the change in disturbance with depth ($Dist = e^{-z}$). The maximum electron transfer rate (ETR_{max}) is analogous to maximum photosynthetic rate. I_k = light intensity at onset of photosaturation, α = photosynthetic efficiency in the light-limited portion of the photosynthesis–irradiance (P–I) curve, ns = not significant.

	Regression coefficients						
Lake	Intercept	%*Light*	*Light* × *Dist*	df	*F*	R^2	*p*
ETR_{max}							
Sparkling (Wisconsin)	22.2	0.13	ns	1,14	3.9	0.22	0.68
Trout (Wisconsin)	10.8	0.46	0.62	1,14	13.6	0.49	0.0009
I_k							
Sparkling (Wisconsin)	107	2.59	ns	1,14	16.8	0.55	0.0011
Trout (Wisconsin)	20.7	4.24	ns	1,14	120.9	0.89	<0.0001
α							
Sparkling (Wisconsin)	0.19	−0.001	ns	1,14	33.4	0.7	<0.0001
Trout (Wisconsin)	0.24	−0.002	ns	1,14	76.3	0.84	<0.0001

thickest (up to 1 cm) in the mid-epilimnion (2–6 m) where the periphyton matrix was integrated with the underlying sediments. Periphyton communities in these lakes transitioned in the metalimnion to 1-mm-thick biofilms superimposed on sediments. Microscopic examination revealed that these deeper periphyton communities were dominated by motile filamentous cyanobacteria and raphid diatoms (YV, unpublished data). In the 2 largest lakes, Lake Tahoe and Tanganyika, sampling extended only to 10 m, which was within the surge zone. Periphyton development on the sand became more apparent with depth in these 2 lakes, but the thick periphyton communities seen in the mid-epilimnion of the smaller lakes were not evident.

The chemical composition of the top 5 mm of littoral sediments also was consistent with low periphyton biomass at the edge of the lakes. The decrease in C:N with depth in the Michigan lakes (Fig. 4A) is consistent with an increasing contribution of periphyton to benthic organic matter relative to terrestrial detritus (Kaushal and Binford 1999) and corroborates our visual observations of surface sediments dominated by coarse terrestrial detritus at the edge of the Michigan lakes. Sediment %OM was lowest at the shallowest depth sampled (0.5 or 1 m) in the Wisconsin lakes. The epilimnetic maximum in sediment %P between 20 and 60% light (Fig. 4B) corresponds to the depths (2–6 m) where the thickest periphyton communities were observed. One interpretation of the correlation between sediment P and chlorophyll *a* in the upper epilimnion (≥20% light) of the Wisconsin lakes is that periphyton determines sediment nutrient content in the epilimnion. Thus, increasing algal biomass with depth in the upper epilimnion leads to higher sediment P. Epipelic chlorophyll, C:N, %P, and our visual observations are all consistent with low periphyton biomass at the shallowest littoral depths and maximum epipelic biomass between 20 and 60% surface light. However, biomarkers other than chlorophyll (e.g., fatty acid profiles, deoxyribonucleic acid [DNA]), or taxonomic data are needed to confirm a unimodal distribution of epipelic algal biomass with depth.

The Michigan lakes, Castle Lake, and Lake Tanganyika showed a continuous decline in epipelic productivity with depth, a pattern that suggests light limitation of epipelic productivity throughout the littoral zone (Fig. 2D–F, Table 3). However, the shallowest depth at which primary productivity was measured in the lakes with this response profile was 1.5 or 2 m (~55% light). We sampled sand habitats at 0.5 m in 4 of the Wisconsin lakes, where maximum productivity occurred between 30 and 75% light. We postulate that the observed patterns in productivity reflect the interaction between light availability and disturbance that has been described for marine microphytobenthos (Forehead and Thompson 2010, Forehead et al. 2012, Mariotti and Fagherazzi 2012). Light and wave action exert opposing effects on biofilm development and productivity. Thus, optimal conditions occur below the zone of wave disturbance (>1 m in all but the 2 largest lakes), and maximum biomass probably is dependent on light intensity after depth.

Epipelic productivity in the surge zone of the 2 largest lakes (Tahoe and Tanganyika) showed opposite patterns with depth. Productivity increased with depth in Lake Tahoe but decreased with depth in Lake Tanganyika. Both lakes were sampled down to 10 m, but the Lake Tanganyika

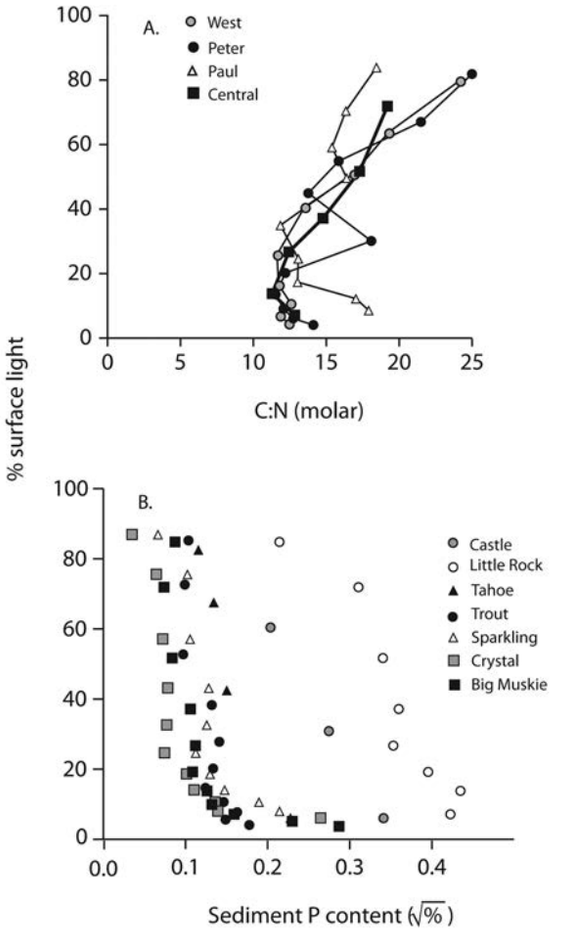

Figure 4. Nutrient content of epipelon in the top 5 mm of sediment. A.—Molar C:N of sediments from 4 Michigan lakes as a function of % light intensity at depth. B.—Sediment %P for the Wisconsin and California lakes.

site was immediately adjacent to a large bedrock outcrop, and the area was protected relative to the exposed sandy habitat typical of Lake Tanganyika's coast. In contrast, the 2 sites in Lake Tahoe were exposed, and ripple marks were a prominent habitat feature at 2 and 5 m, suggesting a stronger influence of wave action on periphyton development than was observed at the same depths at the Lake Tanganyika site. If, as we propose, wave action affects the depth distribution of epipelic biomass, then lake size will partly determine the depth threshold at which waves cease to be a strong structuring force. In addition, the spatial variation in the strength of wind and waves (Weatherhead and James 2001) is expected to cause within-lake horizontal variation in disturbance along the shorelines of lakes, whereas such horizontal variation in phytoplankton has not been reported.

The unimodal distribution of epipelic productivity with depth in some of the lakes may reflect photoinhibition, not wave disturbance. However, we found no evidence of photoinhibition at the highest in situ light intensities in the Wisconsin lakes (this study) or the Michigan lakes (Vadeboncoeur and Lodge 2000). PAM revealed that photoinhibition could be induced only at light intensities far in excess of what the periphyton experienced at depth at midday in full sun (Fig. 3C). Moreover, the correlation between I_k (the light intensity at onset of photosaturation) and depth (Fig. 3B, Table 4) shows strong acclimation to ambient light intensities at a given depth. Despite this acclimation, the PAM data and in situ incubations in the Wisconsin lakes showed a similar unimodal distribution of productivity with depth (Figs 2D–F, 3A). This response profile is consistent with the idea that a mid-epilimnetic peak in epipelic biomass, not photoinhibition, drove the mid-epilimnetic productivity maximum in the Wisconsin lakes.

The lack of photoinhibition in our periphyton surveys contrasts with well recognized patterns of phytoplankton productivity near the surface waters of lakes and oceans (Falkowski and Raven 2007). The benthic growth form alters the relationship between light and photosynthesis at saturating light intensities. Epipelic biomass and productivity per cm^3 of biofilm is orders of magnitude higher than that of phytoplankton in a comparable water volume because benthic communities are composed of densely packed layers of cells (Krause-Jensen and Sand-Jensen 1998). This layering reduces the probability of photoinhibition of the epipelic community as a whole. High light intensities may inhibit cells at the surface of the periphyton, but a compensatory increase in photosynthesis occurs as cells deeper in the biofilm become illuminated under high-light conditions (Hill and Boston 1991, Dodds et al. 1999). Thus, the depressed productivity of phytoplankton and epipelon at shallowest depths (Figs 1D–F, 2D–F) reflect fundamentally different processes. Phytoplankton biomass is relatively evenly distributed with depth in the epilimnion, but cells near the lake surface experience photoinhibition. In contrast, epipelic biomass development appears to be depressed by disturbance at shallow depths, but photoinhibition is not evident.

The dominance of a pelagic perspective in limnology has dictated how ecologists perceive, analyze, and interpret littoral production dynamics. Stream ecologists have enthusiastically studied periphyton dynamics for decades, but synthetic assessments of the determinants of spatial variation in periphyton in lakes have largely eluded limnologists. The emergence of consistent patterns in epipelic chlorophyll and productivity among these lakes, which span the global range in depth of stratified lakes, sets the stage for improving predictive models of littoral production dynamics. Such models have existed for decades for phytoplankton, and should now be developed for periphyton.

Our results indicate that light is the primary structuring mechanism for epipelon in lakes of all sizes. The effects of light on chlorophyll content make it challenging to assess depth-related patterns in biomass, but the productivity patterns point to an additional role of wave disturbance in limiting epipelic biomass. We caution that this role of disturbance does not appear to be as important for epilithon as for epipelon (YV, unpublished data) and should not be extrapolated to periphyton on rocks. The interactive effects of light and disturbance on epipelon in lakes need to be tested explicitly, ideally by incorporating wave height and fetch into analytical models. Understanding the contrasts and parallels between periphyton and phytoplankton responses to light, water movement, and nutrient availability are critical to developing comprehensive models of energy flow in lakes.

ACKNOWLEDGEMENTS

We thank the many students from Wright State University and the University of Wisconsin-Madison who helped collect and analyze the data. We also thank the staff of Trout Lake Station and the North Temperate Lakes Long Term Ecological Research (NTL-LTER) program (National Science Foundation grant DEB-0217533). We are grateful to Brant Allen and Charles Goldman of the University of California Davis Tahoe Environmental Research Center and Sudeep Chandra, University of Nevada Reno, for logistic support and phytoplankton data for the California lakes. The Tanzanian Fisheries Research Institute provided logistic support for the Lake Tanganyika research. Funding was provided by National Science Foundation grants DEB-0448682 and DEB 08-42253 (YV), DEB 10-30242 (PBM), and DEB-0449076 (MJVZ). We thank Marie Sullivan, who first queried "Is there light after depth?" on the shores of Hungry Horse Reservoir in Andy Sheldon's limnology class in the 1980s.

LITERATURE CITED

APHA (American Public Health Association). 2005. Standard methods for the examination of water and wastewater. 21st edition. American Public Health Association, American Waterworks Association, and Water Environment Federation, Washington, DC.

Arar, E. J., and G. B. Collins. 1997. In vitro determination of chlorophyll *a* and pheophyton in marine and freshwater algae by fluorescence. US EPA Method 445.0. US Environmental Protection Agency, Washington, DC.

Baulch, H. M., M. A. Turner, D. L. Findlay, R. D. Vinebrooke, and W. F. Donahue. 2009. Benthic algal biomass—measurement and errors. Canadian Journal of Fisheries and Aquatic Sciences 66:1989–2001.

Cantonati, M., and R. L. Lowe. 2014. Lake benthic algae: toward an understanding of their ecology. Freshwater Science 33:475–486.

Carignan, R., A. Blais, and C. Vis. 1998. Measurement of primary production and community respiration in oligotrophic lakes using the Winkler method. Canadian Journal of Fisheries and Aquatic Sciences 55:1078–1084.

Carlton, R. G., and R. G. Wetzel. 1988. Phosphorus flux from lake sediments: effect of epipelic algal oxygen production. Limnology and Oceanography 33:562–570.

Carpenter, S. R., J. J. Cole, J. R. Hodgson, J. F. Kitchell, M. L. Pace, D. Bade, K. L. Cottingham, T. E. Essington, J. N. Houser, and D. E. Schindler. 2001. Trophic cascades, nutrients, and lake productivity: whole-lake experiments. Ecological Monographs 71:163–186.

Carpenter, S. R., J. Morrice, P. A. Soranno, J. J. Elser, N. A. MacKay, and A. St Amand. 1993. Primary production and its interactions with nutrients and light transmission. Pages 225–251 *in* S. R. Carpenter and J. F. Kitchell (editors). The trophic cascade in lakes. Cambridge University Press, Cambridge, UK.

Corman, J. R., P. B. McIntyre, B. Kuboja, W. Mbemba, D. Fink, C. W. Wheeler, C. Gans, E. Michel, and A. S. Flecker. 2010. Upwelling couples chemical and biological dynamics across the littoral and pelagic zones of Lake Tanganyika, East Africa. Limnology and Oceanography 55:214–224.

Cottingham, K. L., S. R. Carpenter, and A. L. St Amand. 1998. Responses of epilimnetic phytoplankton to experimental nutrient enrichment in three small seepage lakes. Journal of Plankton Research 20:1889–1914.

Denny, M., and D. Wethey. 2001. Physical processes that generate patterns in marine communities. Pages 3–38 *in* M. D. Bertness, S. D. Gaines, and M. E. Hay (editors). Marine community ecology. Sinauer, Sunderland, Massachusetts.

Devlin, S. P., M. J. Vander Zanden, and Y. Vadeboncoeur. 2013. Depth-specific variation in carbon isotopes demonstrates resource partitioning among the littoral zoobenthos. Freshwater Biology 58:2389–2400.

Dodds, W. K., B. J. F. Biggs, and R. L. Lowe. 1999. Photosynthesis-irradiance patterns in benthic microalgae: variations as a function of assemblage thickness and community structure. Journal of Phycology 35:42–53.

Falkowski, P. G., and J. A. Raven. 2007. Aquatic photosynthesis. Princeton University Press, Princeton, New Jersey.

Forehead, H. I., G. A. Kendrick, and P. A. Thompson. 2012. Effects of shelter and enrichment on the ecology and nutrient cycling of microbial communities of subtidal carbonate sediments. FEMS Microbiology Ecology 80:64–76.

Forehead, H. I., and P. A. Thompson. 2010. Microbial communities of subtidal shallow sandy sediments change with depth and wave disturbance, but nutrient exchanges remain similar. Marine Ecology Progress Series 414:11–26.

Genkai-Kato, M., Y. Vadeboncoeur, L. Liboriussen, and E. Jeppesen. 2012. Benthic–planktonic coupling, regime shifts, and whole-lake primary production in shallow lakes. Ecology 93: 619–631.

Goldman, C. R., A. Jassby, and T. Powell. 1989. Interannual fluctuations in primary production: meteorological forcing at two subalpine lakes. Limnology and Oceanography 34: 310–323.

Hansson, L. A. 1988. Chlorophyll *a* determination of periphyton on sediments: identification of problems and recommendation of method. Freshwater Biology 20:347–352.

Hill, W. R., and H. L. Boston. 1991. Community development alters photosynthesis–irradiance relations in stream periphyton. Limnology and Oceanography 36:1375–1389.

Jassby, A. D., and T. Platt. 1976. Mathematical formulation of relationship between photosynthesis and light for phytoplankton. Limnology and Oceanography 21:540–547.

Kahlert, M., A. T. Hasselrot, H. Hillebrand, and K. Pettersson. 2002. Spatial and temporal variation in the biomass and nutrient status of epilithic algae in Lake Erken, Sweden. Freshwater Biology 47:1191–1215.

Karlsson, J., P. Byström, J. Ask, P. Ask, L. Persson, and M. Jansson. 2009. Light limitation of nutrient-poor lake ecosystems. Nature 460:506–509.

Kaushal, S., and M. W. Binford. 1999. Relationship between C:N ratios of lake sediments, organic matter sources, and historical deforestation in Lake Pleasant, Massachusetts, USA. Journal of Paleolimnology 22:439–442.

Kirk, J. T. O. 1994. Light and photosynthesis in aquatic ecosystems. 2nd edition. Cambridge University Press, Cambridge, UK.

Krause-Jensen, D., and K. Sand-Jensen. 1998. Light attenuation and photosynthesis of aquatic plant communities. Limnology and Oceanography 43:396–407.

Lowe, R. L. 1996. Periphyton patterns in lakes. Pages 57–76 *in* R. J. Stevenson, M. L. Bothwell, and R. L. Lowe (editors). Algal ecology: freshwater benthic ecosystems. Academic Press, San Diego, California.

MacIntyre, H. L., R. J. Geider, and D. C. Miller. 1996. Microphytobenthos: the ecological role of the "secret garden" of unvegetated, shallow-water marine habitats. 1. Distribution, abundance and primary production. Estuaries 19:186–201.

Mariotti, G., and S. Fagherazzi. 2012. Modeling the effect of tides and waves on benthic biofilms. Journal of Geophysical Research: Biogeosciences G04010. doi:10.1029/2012JG002064

Reynolds, C. S. 2006. Ecology of phytoplankton. Cambridge University Press, Cambridge, UK.

Roberts, D. A., and C. W. Boylen. 1988. Patterns of epipelic algal distribution in an acid Adirondack lake. Journal of Phycology 24:146–152.

Round, F. E. 1961. Studies on bottom-living algae in some lakes of the English Lake District. Part VI. The effect of depth on the epipelic algal community. Journal of Ecology 49:245–254.

Sarvala, J., K. Salonen, M. Järvinen, E. Aro, T. Huttula, P. Kotilainen, H. Kurki, V. Langenberg, P. Mannini, A. Peltonen, P. D. Plisnier, I. Vuorinen, H. Mölsä, and O. V. Lindqvist. 1999. Trophic structure of Lake Tanganyika: carbon flows in the pelagic food web. Hydrobiologia 407:149–173.

Sawatzky, C. A., W. A. Wurtsbaugh, and C. Luecke. 2006. The spatial and temporal dynamics of deep chlorophyll layers in high-mountain lakes: effects of nutrients, grazing and herbivore nutrient recycling as growth determinant. Journal of Plankton Research 28:65–86.

Stainton, M., M. Capel, and A. Faj. 1977. The chemical analysis of fresh water. Miscellaneous Special Publication 25. Freshwater Institute, Winnipeg, Manitoba.

St Amand, A., and S. R. Carpenter. 1993. Metalimnetic phytoplankton dynamics. Pages 210–224 *in* S. R. Carpenter and J. F. Kitchell (editors). The trophic cascade in lakes. Cambridge University Press, Cambridge, UK.

Sundback, K., F. Linares, F. Larson, A. Wulff, and A. Engelsen. 2004. Benthic nitrogen fluxes along a depth gradient in a microtidal fjord: the role of denitrification and microphytobenthos. Limnology and Oceanography 49:1095–1107.

Thompson, P. 1999. Response of growth and biochemical composition to variations in daylength, temperature, and irradiance in the marine diatom *Thalassiosira pseudonana* (Bacillariophyceae). Journal of Phycology 35:1215–1223.

Uthicke, S. 2006. Photosynthetic efficiency and rapid light curves of sediment-biofilms along a water quality gradient in the Great Barrier Reef, Australia. Marine Ecology Progress Series 322:61–73.

Vadeboncoeur, Y., E. Jeppesen, M. J. Vander Zanden, H.-H. Schierup, K. Christoffersen, and D. M. Lodge. 2003. From Greenland to green lakes: cultural eutrophication and the loss of benthic energy pathways in lakes. Limnology and Oceanography 48:1408–1418.

Vadeboncoeur, Y., and D. M. Lodge. 2000. Periphyton production on wood and sediment: substratum-specific response to laboratory and whole-lake manipulations. Journal of the North American Benthological Society 19:68–81.

Vadeboncoeur, Y., D. M. Lodge, and S. R. Carpenter. 2001. Whole-lake fertilization effects on distribution of primary production between benthic and pelagic habitats. Ecology 82: 1065–1077.

Vadeboncoeur, Y., M. J. Vander Zanden, and D. M. Lodge. 2002. Putting the lake back together: reintegrating benthic pathways into lake food web models. BioScience 52:44–55.

Vander Zanden, M. J., S. Chandra, S. Park, Y. Vadeboncoeur, and C. R. Goldman. 2006. Efficiencies of benthic and pelagic trophic pathways in a subalpine lake. Canadian Journal of Fisheries and Aquatic Sciences 63:2608–2620.

Vander Zanden, M. J., Y. Vadeboncoeur, and S. Chandra. 2011. Fish reliance on littoral–benthic resources and the distribution of primary production in lakes. Ecosystems 14:894–903.

Weatherhead, M. A., and M. R. James. 2001. Distribution of macroinvertebrates in relation to physical and biological variables in the littoral zone of nine New Zealand lakes. Hydrobiologia 462:115–129.

Wetzel, R. G. 1964. A comparative study of the primary productivity of higher aquatic plants, periphyton, and phytoplankton in a large shallow lake. Internationale Revue der gesamten Hydrobiologie 49:1–64.

Wetzel, R. G. 2001. Limnology: lake and river ecosystems. 3rd edition. Academic Press, San Diego, California.