

Internal wave effects on photosynthesis: Experiments, theory, and modeling

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Abstract

Using field experiments and mathematical models, we tested whether internal waves enhance photosynthesis as they move phytoplankton through a nonlinear light field in situations where photosynthesis is light limited. Phytoplankton circulated at depths mimicking isotherm displacement for moderate wind speeds had elevated photosynthetic rates compared to static incubations. Experiments and modeling revealed that surface light variation due to cloud cover interacts strongly with the effects of internal waves and may have positive or negative effects on photosynthesis depending on the relative phase of internal wave displacement and light variation. The combined effects of internal waves and fluctuations in surface irradiance ranged from a 15% reduction up to a 200% enhancement. The distribution (sine wave vs. Gaussian) of the vertical displacement of internal waves is also important in determining the internal wave effect on photosynthesis. Internal waves in a wide variety of aquatic systems and with hourly to weekly periods show a strong potential for internal wave-induced enhancement of photosynthesis. The realization of this enhancement is dependent on characteristics of the internal waves, of algal photosynthetic response, and of variable surface light.

Internal waves are ubiquitous features of lakes and oceans and have the potential to influence biological processes such as phytoplankton productivity in several ways. First, when they break, they transport nutrients into the euphotic zone (MacIntyre and Jellison 2001; Sangra et al. 2001; Gaxiola-Castro et al. 2002); second, upwelling brings nutrient-rich waters to the surface in shallow, nearshore areas (Cooper 1947; Ostrovsky et al. 1996; Pringle and Riser 2003); third, their horizontal current components can aggregate phytoplankton above internal wave troughs and below internal wave crests (Kushnir et al. 1997; Lennert-Cody and Franks 2002); and, fourth, they move phytoplankton through a vertical light gradient and influence their light climate. Here we examine this fourth process, in which internal waves affect light and phytoplankton productivity.

A fundamental requirement of phytoplankton is having sufficient but not inhibiting light, and these conditions vary

with depth in the water column. Studies examining phytoplankton response to varying light exposure have been conducted mostly in the weakly stratified upper mixing layer where light intensities are saturating or inhibiting for phytoplankton production (Ferris and Christian 1991). At these depths, turbulence has been invoked as a mechanism to circulate phytoplankton away from harmful irradiance. For this case, Patterson (1991) showed that turbulent eddies can increase primary productivity by 20% relative to a stationary water column. However, fluctuations in light exposure will have a qualitatively different effect on phytoplankton at subsaturating light intensities because increases in light are noninhibiting and thus enhance photosynthesis. At subsaturating light intensities, vertical movements must increase the average useable light exposure to enhance photosynthesis. In deeper, stratified layers, theoretical modeling has shown that phytoplankton moved by internal waves through the exponential light field increase their average light exposure (Kamykowski 1974; Haury et al. 1983), and if the movement is at depths where the cells are light limited, productivity may be increased (Holloway 1984; Holloway and Denman 1989). However, little if any empirical work has been done to confirm these theoretical predictions of the effects of internal waves on photosynthesis. Here we provide the first empirical test of these effects in stratified waters where low light intensities limit photosynthesis.

Holloway and Denman (1989) showed that internal waves with an average depth below a predictable “crossover depth” have a consistently positive effect on photosynthesis; this enhancement of photosynthesis can also

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deepen the compensation depth for photosynthesis. Specifically, the relationship of light intensity at the average depth of a moving cell, $E(z)$, and the light level at which photosynthesis becomes light saturated (E_k) determines the minimum depth (crossover depth) for vertical movements to cause enhancement of photosynthesis. When $E(z) < E_k$, vertical movements of phytoplankton cells will enhance primary production (Holloway and Denman 1989). The maximum depth where vertical movement can enhance photosynthesis is defined when cells at the top of the internal wave just reach their compensation depth. These maximum and minimum depths vary among and within aquatic ecosystems, and here we further review biological and physical parameters from various geographic locations to illustrate where internal wave enhancement of photosynthesis should be important.

The light climate of phytoplankton is also controlled by irradiance at the water surface (Ferris and Christian 1991) where intermittent cloud cover occurs on time scales similar to those of internal waves. The interaction of surface irradiance and internal waves on photosynthesis has not been addressed in prior modeling research (i.e., Holloway 1984; Lande and Yentsch 1988; Holloway and Denman 1989). In an analogous situation, the co-occurrence of internal tides (internal waves with periods of 12.4 h) and other long (semidiel to diel) period internal waves with diel light cycles has been noted to cause an interactive effect on light exposure at the thermocline (Kamykowski 1974; Haury et al. 1983; Granata et al. 1995). The potential exists for similar interactive effects of internal waves with light variations from intermittent cloud cover. Despite this potential, the theory of internal wave effects on photosynthesis either explicitly assumes constant surface irradiance (Holloway and Denman 1989) or focuses only on wave amplitude, ignoring both period and phase (Holloway 1984; Lande and Yentsch 1988). Here we analyze the interactive effects of intermittent cloud cover and internal waves for both idealized (sine wave) and real (measured) wave forms.

Methods

Study site—Field experiments were conducted in Toolik Lake, Alaska (68°38'N, 149°38'W), a 1.5-km² oligotrophic kettle lake. Its general limnological characteristics are described in Miller et al. (1986) and O'Brien et al. (1997). During the summer, the lake surface receives sunlight 24 h per day, but light intensity varies from ~20 to 1,800 $\mu\text{mol quanta m}^{-2} \text{s}^{-1}$. Attenuation of light is due primarily to humic substances, and the diffuse attenuation coefficient is ~0.5 m^{-1} . Internal waves with amplitudes up to 1.5 m and frequently over 0.5 m have been reported near the base of the euphotic zone in Toolik Lake (MacIntyre et al. 2006). The seasonal progression of temperature stratification and chlorophyll *a* (Chl *a*) distribution are typically characterized by rapid stratification after ice-off and a ~4-m-thick metalimnion descending from ~6 to ~8 m as the season progresses (MacIntyre et al. 2006; Evans 2007). A deep Chl *a* maximum (DCM) develops within the metalimnion early in the summer but is dispersed by midsummer mixing and

storms; in mid- and late summer, Chl *a* is evenly distributed in the upper mixing layer and decreases with depth below this layer (MacIntyre et al. 2006; Evans 2007). The dates of the onset of stratification and the transition from DCM to surface Chl *a* maximum, as well as the rate of descent of the metalimnion, vary from year to year depending on weather conditions (Evans 2007).

Physical measurements—Downwelling photosynthetically available radiation (PAR) was measured as 60-min averages on the shore of Toolik Lake using a Li-Cor Quantum sensor (Model LI-190SB) at 2.5 m height. Surface PAR was interpolated to a 5-min time step using data from a nearby (<500 m distant) downwelling, shortwave irradiance meter (Kipp and Zonen CNR1 net radiometer). Hourly measurements of shortwave irradiance were regressed against hourly measurements of PAR using a linear model ($r^2 = 0.90$), and this regression equation was then used to calculate PAR from the 5-min averaged shortwave irradiance sensor output. Diffuse attenuation coefficients (k_d) were calculated using Beer's law from depth profiles of downwelling light, measured with a LiCor 2π quantum sensor logged by a LiCor 1400 light meter; profiles were measured at least weekly and always within 1 d of reported experiments.

Time-series temperature measurements were obtained using 25 moored Brancker TR 1050 self-contained temperature loggers at depths from 0 to 19 m in both 2003 and 2004. Readings were taken every 10 s, and thermistors had an accuracy of 0.002°C and a time constant of <3 s. Thermistors were calibrated by the manufacturer before and after deployment. Data records for each thermistor were aligned by time, and the rate of change of temperature between two fixed thermistor depths was used to solve for the depth of a desired temperature (isotherm). Temperature inversions were removed during linear interpolation.

In situ experiments—The in situ experimental system compared phytoplankton production in moving and fixed-depth incubations. Moving incubations had amplitudes of 1 or 0.5 m; these amplitudes are typical of internal waves in Toolik Lake (Fig. 1). Moving incubations vertically traversed a smooth sine wave and were powered by a stepper motor; a programmable controller set both speed and direction. Internal waves of different amplitudes but identical phase were generated by hanging samples at different locations on a bar (~2 m long) that was mounted to a fixed point at one end and suspended from the moving line at the other end. For all experiments this bar started in the horizontal position, and sample racks were attached to the bar using ropes that suspended them at the desired average depth of 5 m. The stepper motor then moved the nonfixed end of the bar up 1 m, down 2 m, and up 1 m for each wave period. The entire assembly was mounted on a float designed to minimize water column shading. For the wave periods tested, differential agitation of the contents of moving versus fixed sample bottles is unlikely to contribute to experimental effects; calculations show that the experimental movement was three to six orders of magnitude slower than the movement of bottles due to surface waves.

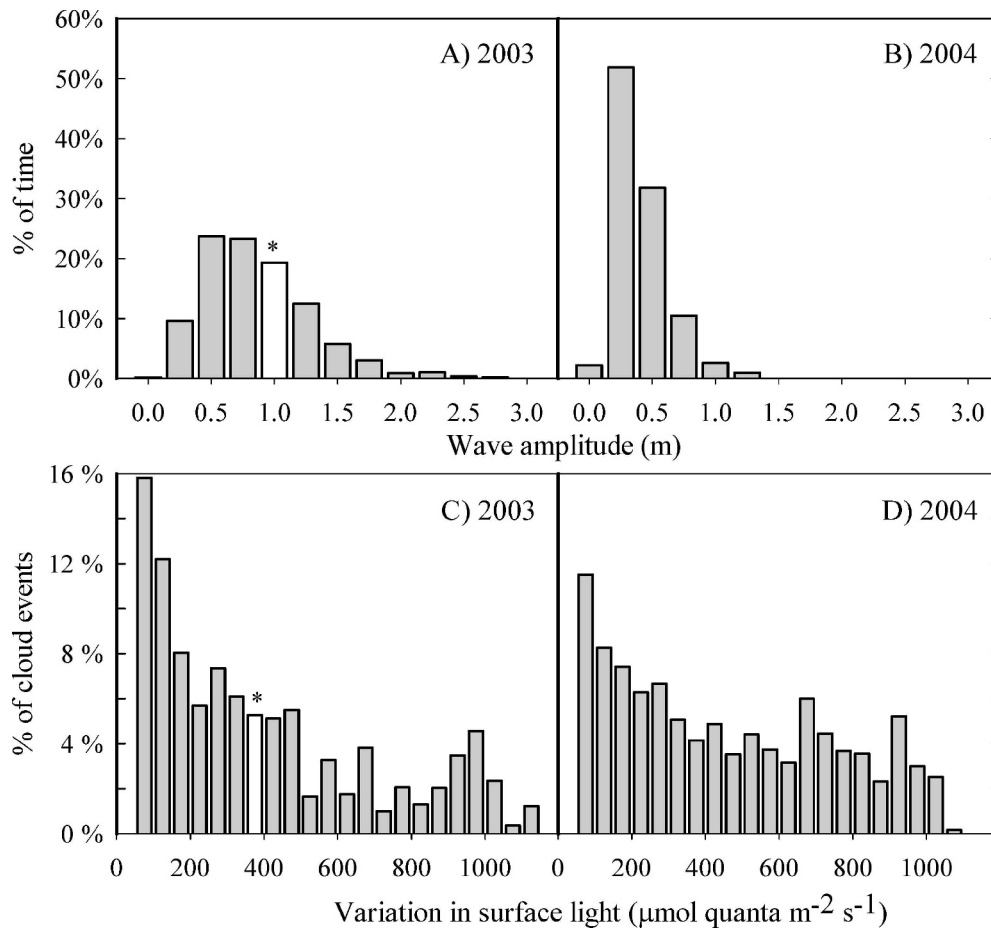


Fig. 1. Histograms of internal wave amplitude for internal waves with period 2–6 h in the metalimnion of Toolik Lake while it was in the euphotic zone during the summer of (A) 2003 and (B) 2004. Histogram of light variation due to clouds (periodicities of 0.2–4 h) at Toolik Lake during the summer of (C) 2003 and (D) 2004. Average internal wave amplitude and light variation due to clouds on days 06–13 July 2003 are indicated by an asterisk (*) and open bar.

Most movement experiments were conducted during mid- to late summer when the upper mixed layer was >6 m. Consequently, experimental movements traversed a small temperature gradient ($\leq 1^\circ\text{C}$), and phytoplankton were not exposed to variations in temperature. The samples incubated on 09 and 30 July 2004 experienced larger temperature variations, 3°C and 2.5°C respectively, during movement from 6 to 4 m depth; however, because temperature does not strongly impact light-limited photosynthesis in this system (see description of model, below), this temperature difference should not affect experimental results. During mid- to late summer, Toolik Lake does not have a strong DCM. However, late summer experiments mimic internal wave conditions in Toolik Lake early in the summer when a DCM and internal waves co-occur at depths of 4–7 m.

Primary production in all experiments was determined by the uptake of ^{14}C -bicarbonate into the particulate fraction and conversion into carbon uptake (Wetzel and Likens 2000). Replicate samples (four per treatment) and dark controls (two per treatment) were inoculated with 18.5×10^4 Bq $\text{NaH}^{14}\text{CO}_3$ and incubated in 72-mL culture flasks

for 24 h. Incubations were ended by placing the samples in the dark and filtering onto $0.45\text{-}\mu\text{m}$ membrane filters within 30 min of terminating the incubation. Twenty-four-hour incubations are routinely used in this system and do not lead to bottle effects (Miller et al. 1986; unpubl. data). Data conformed to assumptions of normality as determined by the Kolmogorov–Smirnov test, and treatments were compared by analysis of variance (ANOVA) within experimental date (significant ANOVAs, $p < 0.05$, were followed by Games–Howell post hoc tests to determine significant groupings).

Determination of algal physiological response—Photosynthesis-versus-irradiance (P vs. E) curves were determined weekly throughout the summer using uptake of ^{14}C -bicarbonate in lab incubations. Subsamples (10 mL) were inoculated with 12.2×10^4 Bq $\text{NaH}^{14}\text{CO}_3$ and incubated at 21 different light levels and in three dark controls for 1.5–2 h. Incubations were terminated by placing samples in the dark and filtering within 10 min. Chl *a* concentration was measured for all P vs. E curves by the fluorometric method (Wetzel and Likens 2000). Incubation temperature was

Table 1. Phytoplankton physiological parameters as determined on the dates of in situ internal wave experiments; units are k_d (m^{-1}), α^* ($\mu g C \mu g Chl a^{-1} d^{-1}$ ($\mu mol quanta m^{-2} s^{-1}$) $^{-1}$), I_k ($\mu mol quanta m^{-2} s^{-1}$), P_{max} ($\mu g C \mu g Chl a^{-1} d^{-1}$), and $Chl a$ ($\mu g L^{-1}$).

Date	k_d	α^*	I_k	P_{max}	$Chl a$
25 Jul 03	0.57	0.26	104	27.0	1.5
01 Aug 03	0.72	0.43	74	31.9	1.0
08 Aug 03	0.73	0.35	83	29.1	1.1
09 Jul 04	0.53	0.22	75	16.5	2.5
30 Jul 04	0.54	0.10	47	4.8	1.4
13 Aug 04	0.54	0.12	50	6.1	1.6
Range given for interpolated values					
06 Jul 03 through 13 Jul 03	0.65 — 0.77	0.12	161	18.8	1.4 — 3.3

matched to in situ temperature by circulating water baths. Incubator light levels were regulated by neutral-density filters and measured with a Biospherical 4π light wand. P vs. E parameters were determined by visual separation of the light-limited and light-saturated portions of the curve followed by linear regression through the light-limited portion (regression slope = α^*) and averaging the production in the light saturated portion (= P_{max}). E_k was determined as (P_{max}/α^*). This regression method produced estimates of α^* with lower errors than did nonlinear curve fitting to Eq. 1. The method was optimized for α^* because this parameter controls primary production in the light range of interest. On the days of experiments, values of α^* ranged from 0.1 to 0.43 ($\mu g C \mu g Chl a^{-1} d^{-1}$) ($\mu mol quanta m^{-2} s^{-1}$) $^{-1}$, $Chl a$ ranged from 1.0 to 2.5 $\mu g L^{-1}$, and P_{max} ranged from 27 to 32 and from 4.8 to 17 $\mu g C \mu g Chl a^{-1} d^{-1}$ in 2003 and 2004, respectively (Table 1). During 2004, pH-induced carbon limitation of primary production occurred in high-light treatments because ^{14}C -bicarbonate solutions of high pH were added to sample waters of low alkalinity. Therefore, the measured P_{max} and E_k used are minimum values; α^* values are not affected by this bias. As a result, conservative (low) estimates of internal wave effects in Toolik Lake were generated when light-saturating conditions were encountered on 30 July and 13 August 2004.

Calculations—Internal wave amplitude and surface light variation were computed using a high-pass filter algorithm to find “local” minima and maxima, where each data point is centered in a window of time equal to the wave period in question and that point is a local minimum if it is the lowest point in that window. A low-pass filter was used to disregard any local minima (maxima) for which there were no other local minima (maxima) within a set time period. The low-pass filter was set to 0.2 h (for light) or 0.5 h (for internal waves) greater than the time cutoff of the high-pass filter. Nearest neighbor interpolation was then used to align adjacent minima and maxima, and internal wave amplitude and surface light variation were calculated. We calculated the percent time that internal waves of different amplitudes were present and the percent of cloud events that resulted in a given drop in light. Because potentially important internal wave amplitudes and surface light variation occur

over a range of periods, this algorithm was repeated for successive bands of periods (e.g., 0.2–0.4 h, 0.4–0.6 h, and so on). The proportion of time that various internal wave amplitudes or cloud events occurred was averaged across period bands. This analysis was done for the 8 d in which isotherm effects were modeled and for the entire season to determine the consistency of effects through time.

Wavelet analyses of surface light and isotherm depth were used to determine the univariate periodicity of these two sources of in situ light variation for days when isotherms were used in the model (Torrence and Compo 1998; Warner 1998; MatLab 7.0, 2004; wavelet software provided by C. Torrence and G. Compo, available at <http://paos.colorado.edu/research/wavelets>). The 8.5°C isotherm was used for this analysis because it persisted in the euphotic portion of the metalimnion throughout the days used in isotherm modeling.

Description of model—Our modeling strategy uses a deterministic, discrete-time model that calculates phytoplankton production based on surface light availability, attenuation coefficient, phytoplankton depth, and P vs. E curve parameters (Fig. 2). Similar models, though lacking a component to track vertical movement, have been used to calculate depth-integrated primary production (e.g., Fee 1973; Jellison and Melack 1993). Surface light availability was measured in 5-min time steps (Fig. 2B), and the attenuation coefficient was held constant for each day (Fig. 2A). The 5-min time step for the light data sets the model time step. Phytoplankton depth was approximated either by a sine function, for experimental treatments (Fig. 2C), or by isotherm displacements calculated from our time-series temperature measurements, for simulations of natural conditions. P vs. E parameters were determined as described above.

Model results are determined numerically for each time step. The light available (E) at the sample or internal wave depth (z) is determined for each time step as $E(z) = E_0 e^{-kz}$, where $k = k_d$ and $E_0 =$ surface irradiance (Fig. 2E). Light at depth $E(z)$ was then used with the P vs. E curve (Fig. 2D) to predict the volumetric productivity of the sample for each time step (Fig. 2F). P vs. E curves were modeled using Webb et al.’s (1974) formula (Eq. 1) but with the boundary condition of $PP(z)$ set to 0 $\mu g C L^{-1} d^{-1}$ at irradiance

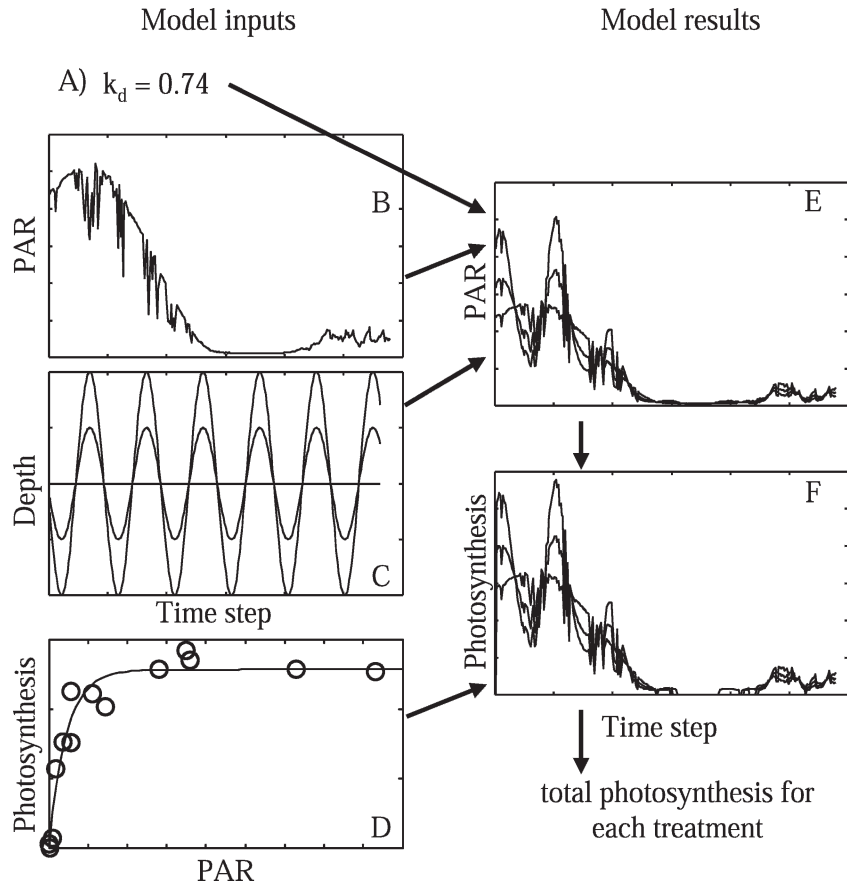


Fig. 2. Graphical representation of model inputs and results. The three lines (C,E,F) are for stationary, 0.5-m wave amplitude, and 1-m wave amplitude treatments. (A) Light attenuation, (B) surface light inputs, (C) depth (isotherm) inputs, (D) biological inputs, (E) sample light exposure, and (F) sample primary production.

$< 1 \mu\text{mol quanta m}^{-2} \text{s}^{-1}$:

$$PP(z) = B \times P_{\max} (1 - e^{-\alpha E(z)/P_{\max}}) \quad (1)$$

when $E(z) \geq 1 \mu\text{mol quanta m}^{-2} \text{s}^{-1}$

where $PP(z)$ = photosynthesis at depth z ; B = biomass represented by concentration of Chl a ; P_{\max} = Chl a -specific, light-saturated photosynthesis; α = Chl a -specific initial slope of the P vs. E curve; and other symbols are as elsewhere. This productivity is summed over the 24-h simulation to give the total daily production for each treatment or isotherm.

Predicted internal wave effects are robust to the formulation of the P vs. E curve. A comparison of our model was made using three formulations of the P vs. E curve: the Webb et al. (1974) formulation, presented above; the Platt et al. (1975) formula as modified in Jassby and Platt (1976) to exclude the effects of photoinhibition ($PP(z) = B \alpha E(z) - (\alpha E(z))^2 / 4P_{\max}$); and a simple linear formula ($PP(z) = B \alpha E(z)$, when $E(z) < E_k$; $PP(z) = P_{\max}$, when $E(z) > E_k$). In a set of 24 model runs for the days of our experiments, the maximum spread among models of predicted internal wave effects for a given parameter combination was $< 8\%$. The maximum difference between the Webb et al. and the Platt et al. models was $< 3\%$.

The effects of photoinhibition and temperature on photosynthesis are not included in this internal wave model. We ignore photoinhibition effects because these generally occur above the point where photosynthesis becomes light saturated (E_k) and internal wave effects diminish. We restricted our sensitivity analysis of internal wave effects to depths where $E(z) < E_k$. Because photoinhibition is rarely observed in our P vs. E measurements at Toolik Lake and not observed for the days modeled here, the nonphotoinhibited P vs. E model is used across light levels in Toolik simulations. Temperature is not included in the model because temperature affects P_{\max} but not α^* in Toolik Lake ($P_{\max} = 34.98 \ln(\text{Temp}, ^\circ\text{C}) - 60.33$, $R^2 = 0.99$, $Q_{10} = 2.2$, and $\alpha^* = 0.0002(\text{Temp}, ^\circ\text{C}) + 0.2327$, $R^2 < 0.01$). This finding is consistent with results from other systems (Raven and Geider 1988; Rae and Vincent 1998). In addition, phytoplankton transported by internal waves do not move through a temperature gradient; thus, any effect of temperature would not form a dynamic component of the model.

The model was tested by comparison to in situ, fixed-depth (no internal waves) photosynthesis measurements in 2003 to validate the light and photosynthesis components of the model. Photosynthesis and Chl a measurements were conducted approximately weekly during the summer of

2003, as described above, at depths of 0.1, 1, 3, 5, and 8 m. On those same dates, k_d and P vs. E curves were measured at two to three depths, one within the surface mixing layer and one or two within the metalimnion. For model simulations, P vs. E parameters for each sample date were interpolated by lake strata (i.e., the mixing layer P vs. E curve was used for all depths above the thermocline, and the metalimnion P vs. E curves were interpolated by nearest neighbor). Model simulations were run corresponding to the deployment depth and times of each in situ measurement, which included light levels both above and below E_k . Model and in situ measurements of photosynthesis were compared by linear regression (total of 34 comparisons). The model provided a good fit to the in situ data, predicting in situ photosynthesis with a regression slope of 0.94, zero intercept, and explaining 89% of in situ variability.

Model behavior for constant (no clouds) and variable (clouds) E_0 —Model analysis was conducted in two steps (1) to explore the general behavior of the model and (2) to determine the effects of variable surface irradiance (E_0) due to cloud cover. In the first step the model was solved analytically for the limits of its validity, following the crossover depth analysis of Holloway and Denman (1989). Numerical solutions of the limit equation were plotted for comparison to parameter value combinations for various aquatic systems.

In order to better understand the role of phytoplankton exposure to varying irradiance, simulations were run assuming that internal wave form can be described by a simple sine function and that E_0 is constant (or varies slowly relative to the period of the internal waves); separate model simulations also used calculated isotherm displacements. Photosynthesis of phytoplankton entrained in isotherms from the metalimnion of Toolik Lake was modeled for 8 d (06–13 July 2003); the isotherms used for modeling varied across days because the lake was warming, and thus a given isotherm became progressively deeper and dropped below the photic zone. Phytoplankton light exposure was below E_k for all points on these isotherms. E_0 was set to the average value for each day, and k , E_k , and α^* were taken from the closest available measurement. The “no wave” treatment used for comparison was photosynthesis at the average depth of each isotherm for each day (greater internal wave effects both positive or negative can be seen if the start depth rather than the average isotherm depth is used; Fahnenstiel et al. 1988).

To determine the effects of internal wave phase relative to that of solar radiation, we ran simulations using a time series of $E_0(t)$ as measured on the days modeled; all other parameters were as before. The effects of phase (the alignment of internal wave crests vs. troughs with variations in $E_0(t)$) were tested by a set of model runs each advancing the isotherm depth time series one time step (5 min) relative to the $E_0(t)$ time series until the complete set of alignments had been simulated. To ensure that the same depths were modeled, the depth time series for one day was looped for this analysis. The variability in internal wave effect due to wave phase was characterized by the

minimum, maximum, and average internal wave effect observed in this set of simulations and by comparing lagged internal wave effect with the lagged cross correlation of internal wave depth and surface light.

The analysis of internal wave phase was continued by simulating the effect of internal wave phase for the six experimental treatments. Internal waves were modeled as 1- or 0.5-m amplitude, 4-h-period sine waves (as above), and $E_0(t)$ was measured on the day of the experiment; other parameters were as above. Because these waves repeat every 4 h, the phase advancement was through 4 h rather than 24 h. For each day, 100 simulations were conducted with phase advanced by 2.4 min in each simulation. The variability in internal wave effect due to wave phase was characterized by the minimum, maximum, and average (mean) internal wave effect.

Phase-induced variability for individual days was calculated for each day as

$$\text{variability}\% = 100 \times (\text{maxPP} - \text{minPP}) / \text{avePP} \quad (2)$$

where maxPP = maximum photosynthesis observed in set of simulations, minPP = minimum photosynthesis observed in set of simulations, and avePP = average of photosynthesis from all simulations in set.

Results

Surface irradiance—Surface light varied from $\sim 1,800$ to $\sim 20 \mu\text{mol quanta m}^{-2} \text{s}^{-1}$ on days with few clouds (Fig. 3B,C) and often was reduced by clouds up to 90% (Fig. 3D,E). Variability in cloud frequency and duration caused large variability among E_0 time series for the various days modeled (Fig. 3). Surface irradiance conditions on these days were representative of those experienced at Toolik Lake during the summers of 2003 and 2004 (Fig. 4). Measured k_d in Toolik Lake ranged from 0.45 to 0.86 m^{-1} (average of 0.65 m^{-1}) during the experiments (Fig. 4).

Internal wave field and variations in surface light—Warming occurred from 06 to 13 July 2003, and isotherms descended in the water column (Fig. 5). Internal waves had larger amplitude during the first 3 d and lower amplitude with occasional excitation events on the following 5 d (Fig. 5). Wavelet analysis showed that internal waves were more energetic on 06–08 July with highest energy in periods of 3–5 h and of ~ 7 –12 h (data not shown). Power was several orders of magnitude lower on the following days, except for a peak from ~ 7 –12 h on 11 July. Peaks in power for surface light variation occurred only at periods of 24 h (data not shown).

During the summer of 2003, 2–6-h-period internal waves in Toolik Lake had amplitudes of >0.5 m for $>75\%$ of the time and >1 m over 30% of the time (Fig. 1A). During the summer of 2004, internal waves were smaller, and amplitudes of >0.5 m occurred $>45\%$ of the time and were always <1.5 m (Fig. 1B). Surface light variations within a 0.2–4-h period were dominated by small light variations but had a fairly even distribution above 400 and

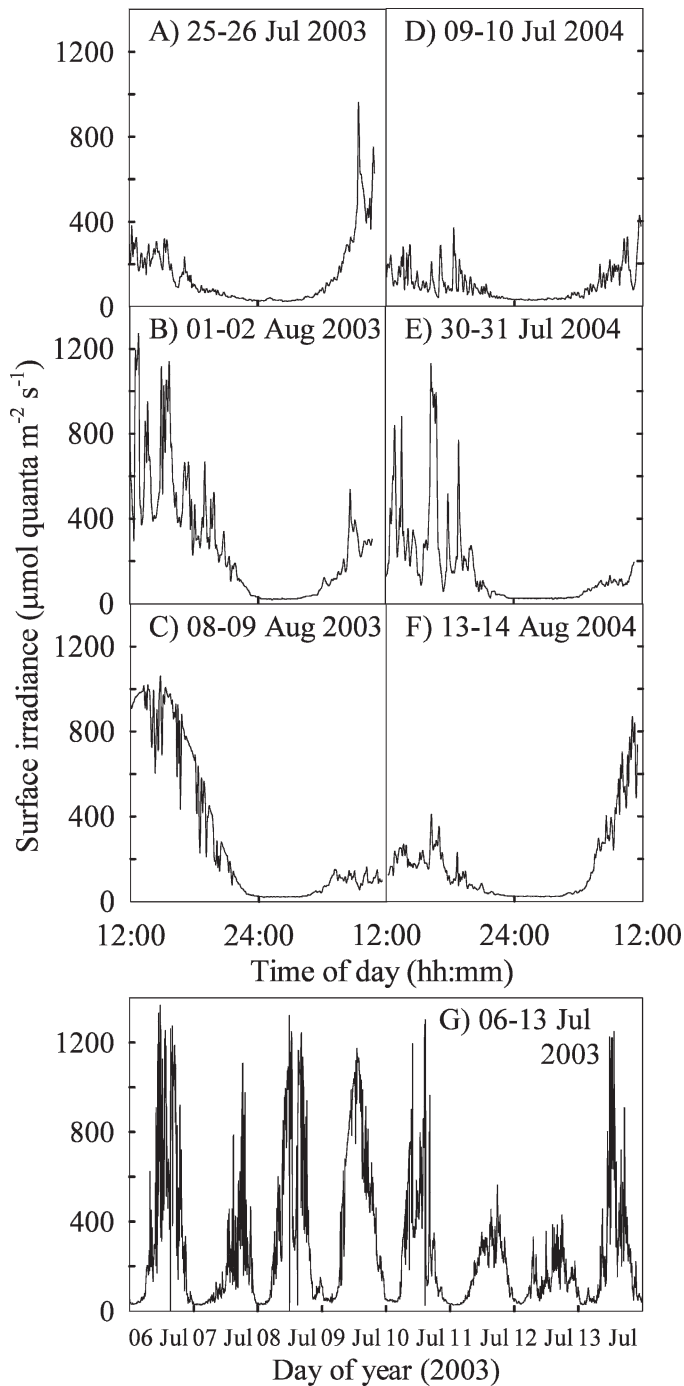


Fig. 3. (A–F) Surface irradiance ($\mu\text{mol quanta m}^{-2} \text{s}^{-1}$) versus time for the experimental incubations and sine-based models and (G) isotherm-based models.

up to $\sim 1,000 \mu\text{mol quanta m}^{-2} \text{s}^{-1}$ during the summers of 2003 and 2004 (Fig. 1C,D); large variations in surface light were more common in 2004 than in 2003. Average internal wave amplitudes were $\sim 0.9 \text{ m}$, and surface light variation was $\sim 392 \mu\text{mol quanta m}^{-2} \text{s}^{-1}$ for the period we modeled, 06–13 July 2003; internal wave amplitudes were larger during the first 3 d of this period than during the final days; thus, a range of natural conditions was included.

Experimental results—The in situ internal wave experiment produced up to a doubling of photosynthesis in moving versus fixed-depth bottles (25 July 2003 and 01 August 2003; Fig. 6), although increases in photosynthesis were generally smaller. All possible combinations of internal wave effects (enhancement, inhibition, and no effect) were observed in the experimental treatments shown in Fig. 6. On two dates (25 July 2003 and 30 July 2004), there was a significant increase in productivity with increasing internal wave amplitude; on another date (08 August 2003), there was increased productivity in the internal wave treatments compared to the no-wave treatment but no difference between the two internal wave treatments. On yet another date (01 Aug 2003), the 0.5-m internal wave treatment shows the highest productivity followed by the 1-m and no-wave treatments; and on the remaining two dates (09 July 2004 and 13 August 2004), there was no significant treatment effect. Combining all dates and treatments, the internal wave effect varied from a $>2\times$ enhancement (ANOVA, $p < 0.0001$; post hoc comparison, $p < 0.0005$, 25 July 2003) to a $\sim 15\%$ reduction (nonsignificant, 13 August 2004) in photosynthesis.

Model results, constant E_0 —Model runs with constant E_0 , actual isotherm displacements (Fig. 5B), and average isotherm depth used as inputs resulted in internal wave enhancement of photosynthesis (Fig. 7, white bars). Internal wave effects for 06–08 July, which generally had larger internal waves, ranged from 1.1 to 1.4. In contrast, internal wave amplitudes were smaller on 09–13 July, and the wave effect, while always positive, was only slightly larger than 1 (Fig. 7).

Model results, variable E_0 (clouds)—When both isotherm depth and E_0 are allowed to vary, internal wave effects differ greatly between the 8 d of the isotherm-based simulation. Maximum internal wave effect increased to 1.8, from 1.4 in the fixed E_0 simulations, and internal wave effects were also observed to reduce photosynthesis (internal wave effect < 1 ; Fig. 7).

Variation in E_0 causes considerable scatter in the depth vs. $E(z)$ relationship (Fig. 8). A regression analysis of the time series of $E(z)$ generated using constant E_0 vs. the time series generated using variable E_0 shows that 28.5% and 92.3% of the variability in $E(z)$ is due to surface light variation on 08 and 09 July 2003, respectively. The other days that were modeled using isotherm records generally had variability within the bounds set by these 2 d. When E_0 is allowed to vary, the maximum light to which the phytoplankton can be exposed increases as $(E_0(\text{max}) - E_0(\text{ave}))$ increases, but whether the phytoplankton can take advantage of this variation in E_0 depends on their location in the water column during high E_0 ; that is, it depends on the phase of the internal wave relative to changes in E_0 .

Shifting the phase of the internal waves, relative to the time series of E_0 , results in changes in photosynthesis. Thus, because photosynthesis in no-wave treatments is unaffected by this phase shift, shifting the phase when internal waves are present leads to changes in the internal

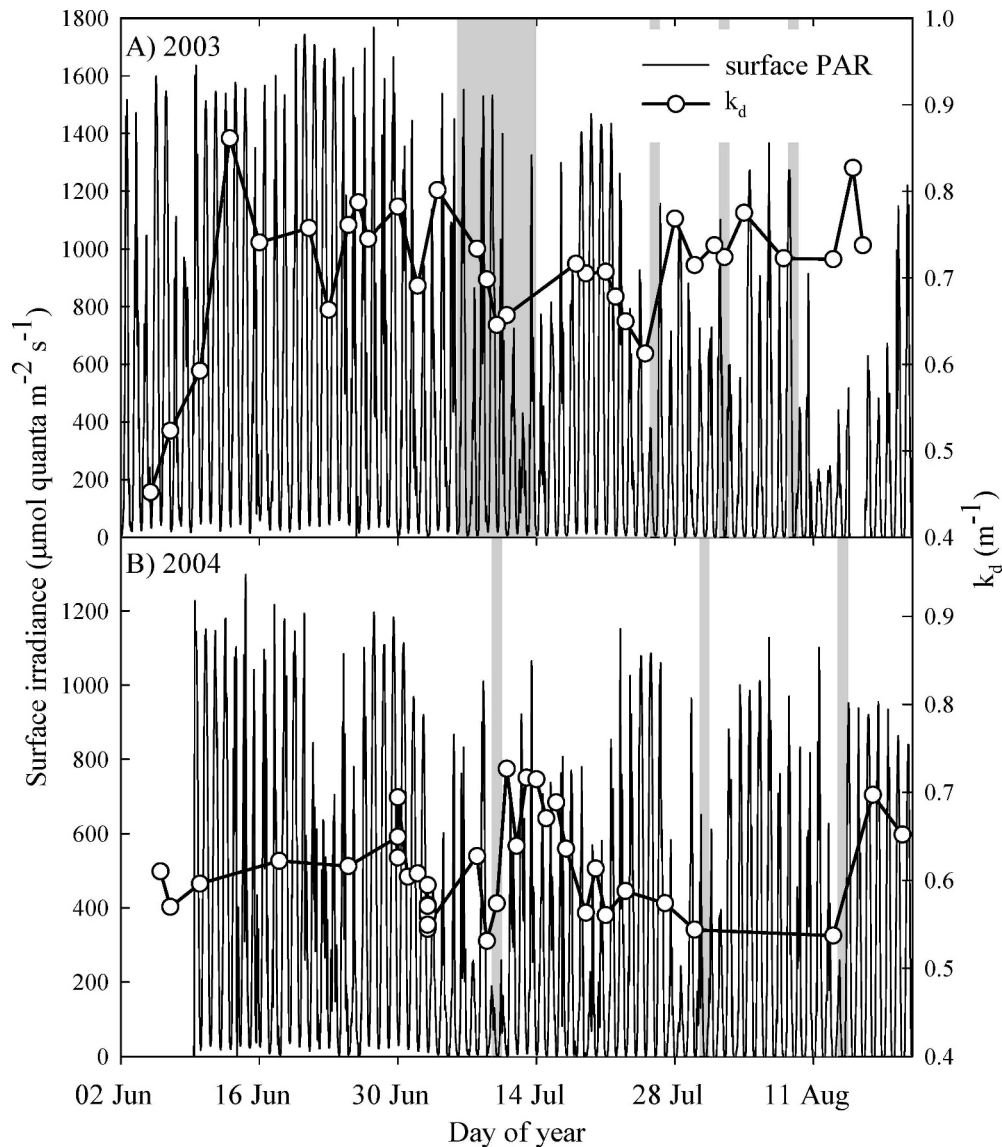


Fig. 4. Surface irradiance and light attenuation coefficient of Toolik Lake for the summers of (A) 2003 and (B) 2004. Days of internal wave experiments and modeling are shaded. PAR was lower in 2004 than in 2003 because of hazy conditions caused by forest fires south of the Brooks Range.

wave effect. Phase shifting resulted in up to a 100% change (variability) in internal wave effects in isotherm-based simulations and a 9% change in internal wave effects in simulations based on sine waves (Fig. 9; note that the range of model-predicted internal wave effects for 1-m internal waves in Toolik Lake on the days of experiments were lower than the in situ sine wave results; see Discussion).

On some days, phase shifting introduced greater variability in internal wave effect. For simulations based on sine waves, phase shifting resulted in higher variability for the 3 d in 2003 (7.3%, 9.0%, and 8.4% for 1-m internal waves) than for the 3 d in 2004 (4.2%, 4.9%, and 2.8% for 1-m internal waves) (Fig. 9A). For isotherm-based simulations, variability was higher than for sine-based simulations and also differed between days (Fig. 9B). Phase shifting resulted in higher variability on the first 3 d of the

isotherm-based simulations when surface light was highly variable (Fig. 3G) and internal wave amplitudes were large (Fig. 5).

The average effects of phase shifting (Fig. 9) were decomposed by plotting the specific changes in internal wave effect on photosynthesis as the internal wave phase and surface light phase were varied (Fig. 10). When the relative phase of the internal wave and surface light time series was shifted within 1 d, the size of the internal wave effect on photosynthesis was negatively correlated with the corresponding lagged cross-correlation coefficient of isotherm depth vs. surface light; in other words, when internal wave crests and cloud breaks are closely aligned by phase shifting, the effect on photosynthesis is greatest. When only one isotherm was modeled or when several isotherms were in phase with one another (i.e., first vertical mode internal

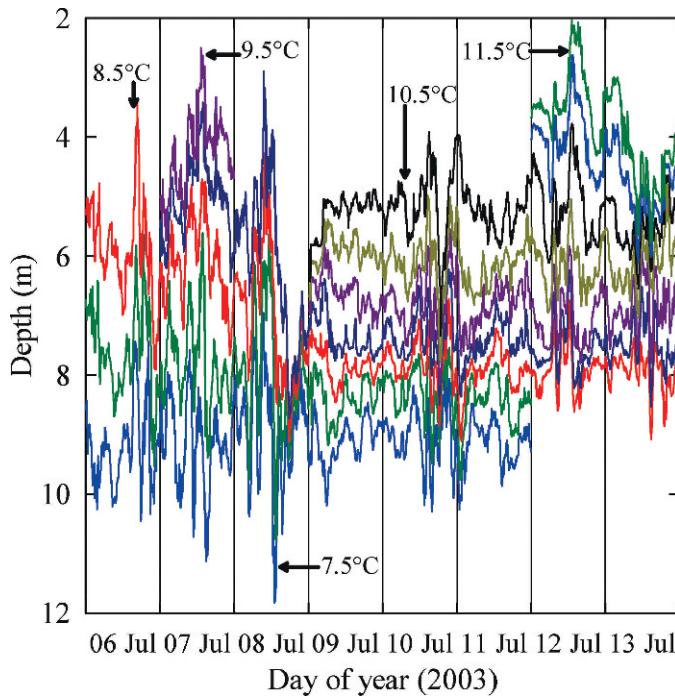


Fig. 5. Isotherms in the metalimnion used for modeling photosynthesis on 06–13 July 2003. The upper most isotherm has temperature 11.5°C (green), and the deepest isotherm has temperature 7.5°C (blue). Temperature increments are 0.5°C.

waves), the cross-correlation coefficient averaged across isotherms was a good predictor of the phase-shifted internal wave effect (Fig. 10). When isotherms at the top and bottom of the metalimnion were out of phase (i.e., second vertical mode internal waves), isotherms higher in the water column exerted greater influence on internal wave effects on photosynthesis. Under these conditions the “average” lagged cross correlation of light and isotherm depth was a poorer predictor of internal wave effects (data not shown). Thus, in order to properly represent the impact of internal waves and their phase alignment with surface light, the contribution of phytoplankton cells riding each isotherm must be determined and then summed.

Our model is in close agreement with Lande and Yentsch’s (1988) prediction of internal wave effects on light, provided that our model is constrained to meet the assumptions of their formulation. Their formulation of internal wave effects (internal wave effect = $\exp(k_d^2 \sigma^2/2)$, where σ = the root mean square isotherm displacement) assumes (1) that internal wave displacements are normally distributed and (2) that surface light is constant and thus internal wave period and phase can be ignored. They also predict the effects of internal waves on total light exposure of phytoplankton rather than on photosynthesis. These effects are approximately the same for very low light exposure ($\ll E_k$), but even below E_k there is some curvature of the P vs. E curve that causes a divergence between internal wave effects on light and on photosynthesis. When our model is run to predict internal wave effects on light given constant surface light with randomly generated, normally distributed, isotherm displacements,

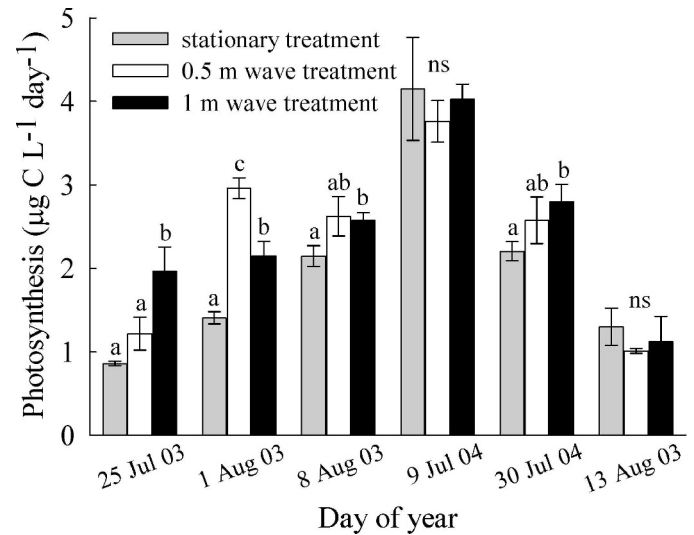


Fig. 6. Phytoplankton primary production ($\mu\text{g C L}^{-1} \text{d}^{-1}$) from a series of in situ internal wave experiments in 2003 and 2004. Stationary treatments (depth = 5 m) had generally lower primary production than treatments in which phytoplankton were moved sinusoidally through the water column with average depth of 5 m, period of 4 h, and amplitude in the vertical of 0.5 or 1 m. Statistically significant differences were determined between treatments within date at the $p = 0.05$ level and indicated by the letters a, b, and c, where treatments with the same letter are not significantly different and where “ns” indicates that there were no significant differences on that date.

the modeled internal wave effects are identical to those predicted by the Lande and Yentsch formulation (always $<0.8\%$ different).

Our modeled internal wave effects on light exposure for sine wave and actual isotherm displacements differed from the Lande and Yentsch model prediction for two reasons. First, sine waves and the isotherm displacements measured

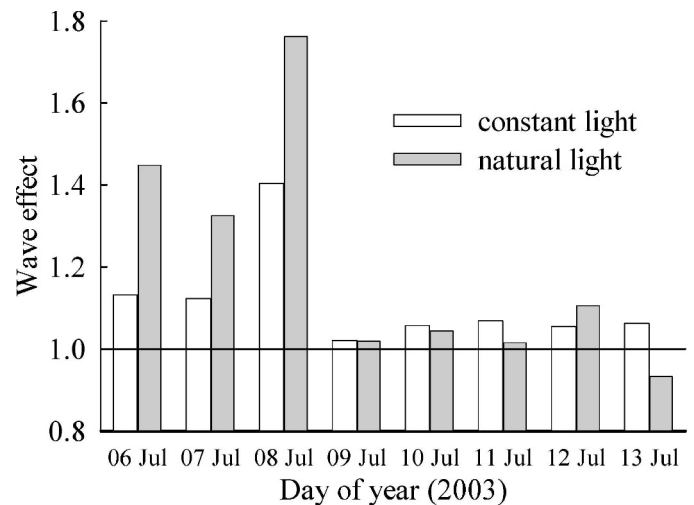


Fig. 7. Internal wave effect (proportional photosynthesis in internal wave versus no-wave treatments) for simulations based on isotherms and using constant and natural light (see text). Internal wave effects >1 (<1) indicate an enhancement (reduction) in photosynthesis relative to the no-wave treatment.

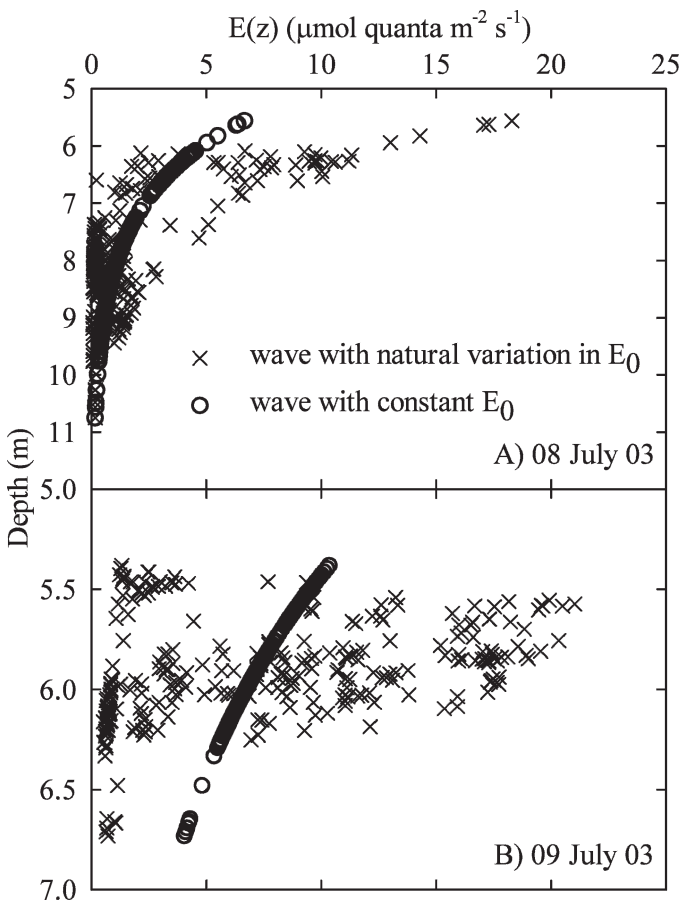


Fig. 8. Light exposure of phytoplankton transported by internal waves. (A) Irradiance at depths of the 8.0°C isotherm on 08 July 2003 and (B) the 9.5°C isotherm on 09 July 2003 assuming constant (average) surface irradiance and measured surface irradiance. Symbols represent 5-min time steps plotted for 24 h. Light at depth is much more variable in the time series in which surface light is allowed to vary (from 28.5% to 92.3% of the total variation in $E(z)$ is due to surface light variation rather than internal wave movements; see text).

in Toolik Lake are not normally distributed. Sine wave displacements are symmetrically distributed around zero but have long, thin tails compared to a normal distribution. Thus, phytoplankton circulating on a sine wave spend more time near the average depth than do those following a normal distribution, and the internal wave effect is consequently slightly smaller than that predicted by Lande and Yentsch's formulation (<1% different in simulations with constant surface light). The isotherm displacements in Toolik Lake on the days modeled were positively skewed (isotherms were often slightly deeper than their average depth). This nonsymmetrical distribution of the isotherm displacements caused a large difference in the modeled internal wave effect compared to the Lande and Yentsch formulation (modeled internal wave effect on light was on average 25% less than the Lande and Yentsch prediction); thus, skew may have a larger effect than kurtosis on the predicted light exposure. Second, we found that the interaction of variable surface light with internal wave phases introduces large variation in internal wave effect on

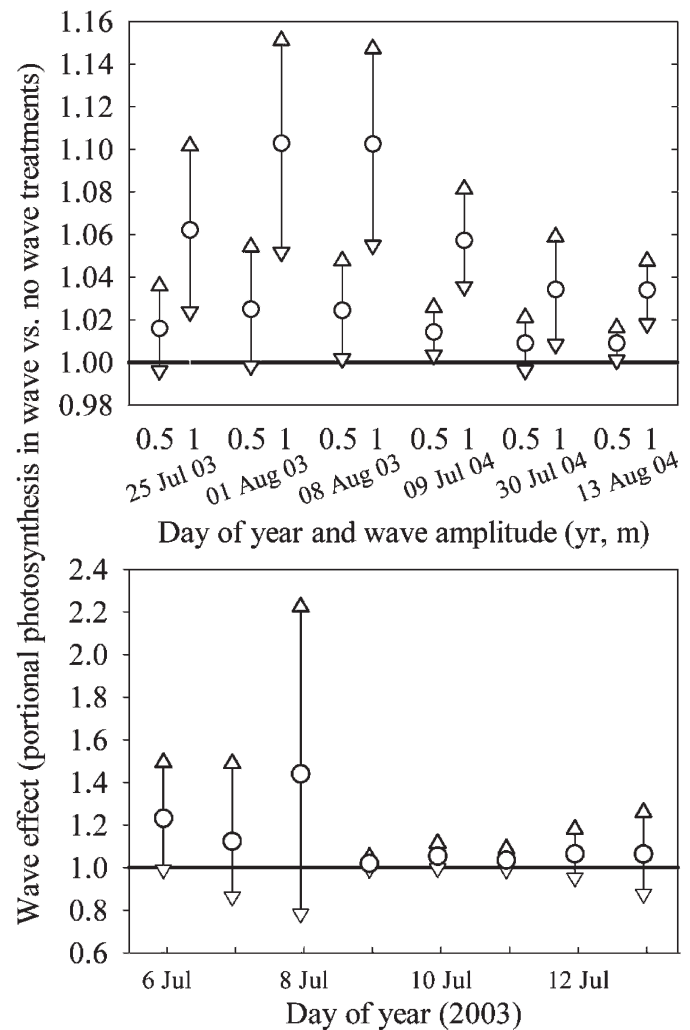


Fig. 9. (A) Internal wave effect obtained by varying the phase of the internal wave relative to variations in E_0 for the six experimental treatments in Fig. 6. Average (O), maximum and minimum (arrows) internal wave effects observed out of 100 equally spaced phase alignments (note: average, maximum, and minimum internal wave effects were robust to number of tested alignments above 50). (B) As in A for the eight days when isotherms were modeled. All possible alignments of 5-min time steps were used (see text). Shifting internal wave phase relative to surface light causes large variations in the modeled internal wave effect.

light and photosynthesis. Because this variability is missing in the Lande and Yentsch model, our reported internal wave effects differ from their formula's predictions. These differences highlight the need to incorporate actual isotherm displacements and surface light variations when predicting the effects of internal waves.

Discussion

Our in situ experiments show that internal waves can increase photosynthesis within the metalimnion of Toolik Lake (Fig. 6). Furthermore, a review of light, internal wave, and biological data indicates that enhancement of

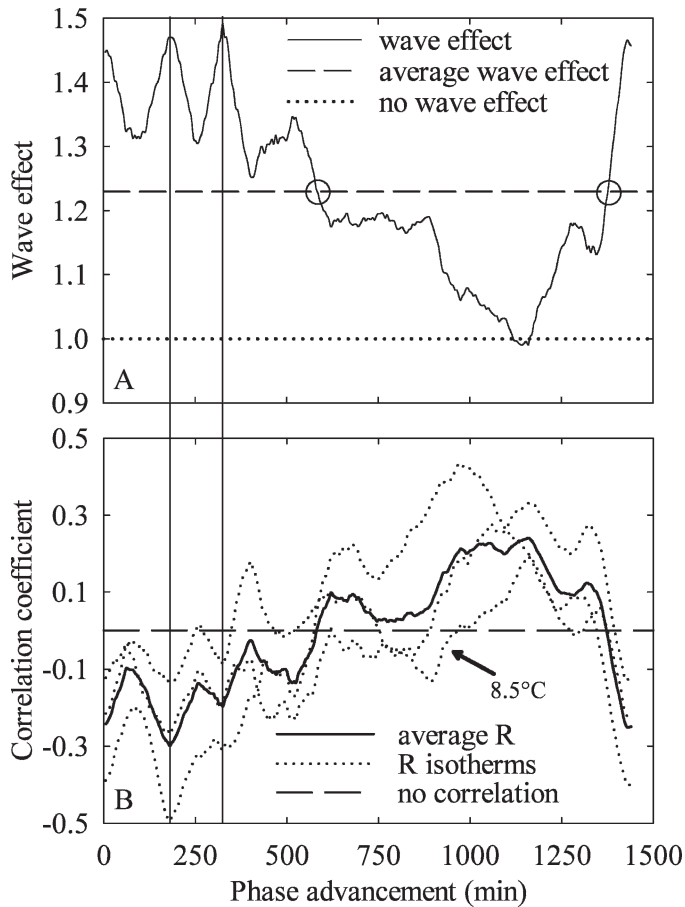


Fig. 10. (A) Relationship between internal wave effect on photosynthesis and phase of internal waves relative to surface light for 06 July 2003. The total wave effect was modeled using three metalimnion isotherms. Dashed horizontal line shows the internal wave effect for constant E_0 ; dotted line at internal wave effect = 1 indicates the switch from internal wave enhancement to internal wave-induced reductions in photosynthesis. (B) Correlation of phase-shifted internal wave depth and surface light for three isotherms (dotted lines, representing 7.5°C, 8.0°C, and 8.5°C) and the average correlation coefficient (solid line). When internal waves crest in the water column at times of full sun (most negative correlation coefficient), internal wave effects are greatest as highlighted by vertical lines in first half of figure. Transitions from above to below average internal wave effect (negative to positive correlation coefficient) and vice versa are circled in both panels.

photosynthesis by internal waves could be important in a wide variety of oceanic and limnological systems (Fig. 11). We have shown, through mechanistic models using field data, that stochastic variation in E_0 due to variable cloud cover interacts with internal waves to modify the effect of internal waves on phytoplankton production. Variable cloud cover and its interaction with internal waves results in the high day-to-day variability of photosynthesis that we observed in experiments mimicking natural internal waves.

Variations in underwater light climate are induced by internal waves, turbulent motions, cloud cover, and their interactions. A strong interaction occurs at diel time scales

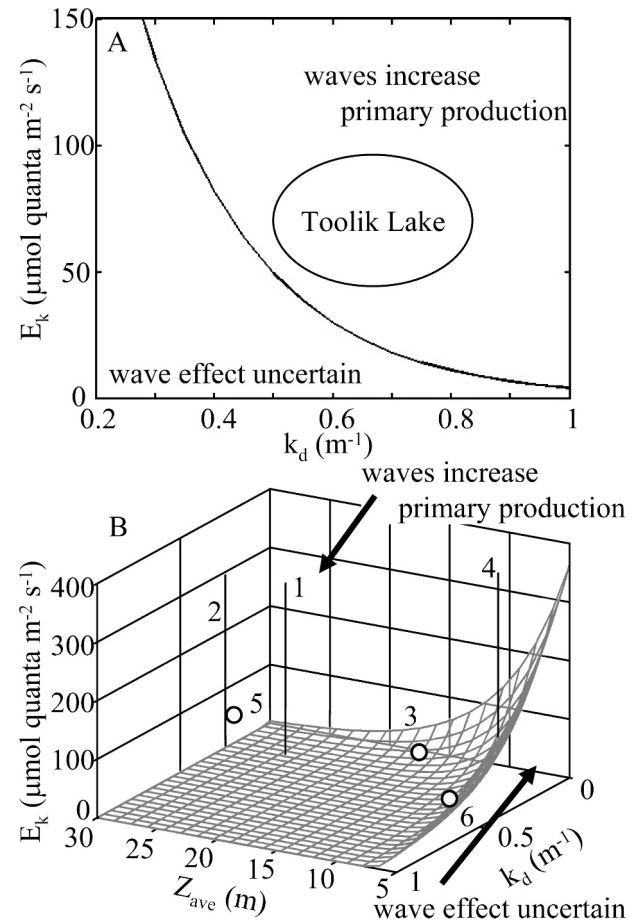


Fig. 11. (A) Phase space indicating effect of internal waves on photosynthesis for a range of k_d and E_k for $E_0 = 600 \mu\text{mol quanta m}^{-2} \text{s}^{-1}$ and average depth of 5 m for internal waves. Parameter values for Toolik Lake are circled. (B) As in A but with third dimension including averaged depth of internal waves, Z_{ave} . Photosynthesis will be enhanced in region above the plotted surface. Parameters are plotted using data from the open ocean (Lande and Yentsch 1988 (1)), the ocean on or near the continental shelf (Kahru 1983 (2); Vandeveld et al. 1987 (3); Kamykowski 1974 (4)), large lakes (Fahnenstiel et al. 1988 (5)), and this study (6). If one parameter is missing, a range of values are used and data graph as a line rather than a point.

because of diel light cycles and the prevalence of internal tides in the ocean (Kamykowski 1974; Haury et al. 1983; Granata et al. 1995) and diel wind forcing of internal waves in lakes. Interactions also occur at shorter time scales. This second situation had not been investigated previously, and prior studies on internal wave effects assumed that surface light variation is of lower frequency than internal waves and thus safely ignored (Lande and Yentsch 1988; Holloway and Denman, 1989). We observed that fluctuations in surface light and internal waves occurred on time scales of less than 6 h (Fig. 1). The amplitudes of both significantly modified the light climate of phytoplankton (Figs. 1, 8). Furthermore, our model shows that coincidence of cloud breaks and internal wave crests can greatly increase internal wave enhancement of photosynthesis. Conversely, coincidence of cloud cover and internal wave crests may reduce

the enhancement. These interactions are observed despite a lack of consistent coherence between internal wave and light spectra, and thus high coherency is apparently not a requirement for noticeable interactive effects. The reversal of internal wave effects when variable E_0 was added to simulations based on real isotherms (13 July; Fig. 7) can be explained only by the internal wave phase coincidence with surface light variation. This conclusion is further supported by the high variability in internal wave effects, including the switch from positive to negative effects, which results when internal wave and E_0 time series are deliberately phase shifted with respect to one another in the model (Fig. 9). A final test of this conclusion is given by the strong relationship between internal wave effects and the specific phase alignment of internal waves and surface light as shown in Fig. 10. Thus, interpretation of results from internal wave models or experiments must consider variations in cloud distributions.

Prediction and interpretation of internal wave effects must also consider the distribution of isotherm displacements. Our model predicts similar results to the Lande and Yentch (1988) formulation of internal wave effects on light exposure to phytoplankton only when surface light was held constant and isotherm displacements were normally distributed. However, substantial differences were found between model results based on the measured (skewed) versus normally distributed isotherm displacements (average of 25% different) for internal waves with the same root mean square displacement. Surface light variability also contributed to the differences between models. Overall, we suggest that in many situations surface light will vary and that isotherm displacements may be nonnormally distributed and conclude that these deviations must be accounted for in predicting the effects of internal waves on photosynthesis.

Results of in situ experiments support our model predictions. Continually moving phytoplankton samples through a depth and light gradient comparable to that produced by internal waves resulted in a significant enhancement of photosynthesis relative to treatments held at constant depth in 8 of 12 trials (Fig. 6). Experimental results also had high between-experiment variability in internal wave effect, as predicted by the model simulations in which E_0 varied. These results provide the first experimental confirmation of internal wave effects on photosynthesis.

Larger internal wave effects were observed in experimental treatments than were predicted by our model. The primary factor that could contribute to this difference is the light acclimatization of phytoplankton. If acclimatization to low light in internal wave troughs increases α^* and this adjustment is sustained through part of the internal wave cycle, then the internal wave effect would increase. Photo-acclimatization of α^* , on the time scales reported in the literature, will enhance rather than diminish the effects of internal waves. This acclimatization occurs on time scales of tens of minutes to hours (Harding et al. 1985; Cullen and Lewis 1988; Cullen 1990), similar to the time scales of light variation caused by internal waves and cloud cover. Harding et al. (1985) found that photo-acclimatization at

these time scales caused the values of α^* and P_{\max} to change in synchrony and that E_k remained constant; thus, the acclimatization of cells at the bottom of the internal wave will not cause photosynthesis to be light saturated at the top of the internal wave, and photosynthesis will be enhanced.

In addition, when time scales of changing light are slow compared to photo-acclimatization, phytoplankton physiology will reflect current light conditions; conversely, when light changes faster than photo-acclimatization, phytoplankton physiology is determined by average light conditions (Dusenberry 1999; Brunet et al. 2003). At subsaturating light intensities, as experienced by phytoplankton entrained in internal waves, Cullen and Lewis (1988) observed a slow increase in α^* (time to reach half of change = 14 h) in response to decreasing light (from 100 to 10 $\mu\text{mol quanta m}^{-2} \text{s}^{-1}$) and little change in α^* with the opposite light transition. Conversely, Flameling and Kromkamp (1997) found that when phytoplankton were held at fixed, medium to high light for a 10-h incubation or were exposed to slowly changing light with a sine wave period of 24 h, α^* decreased over time. However, when phytoplankton were exposed to rapidly varying (2-h period), higher light intensities, there was no change in α^* . Thus, the phytoplankton exposed to rapidly changing light had a higher α^* than those kept at slowly changing light (Flameling and Kromkamp 1997). Because of the acclimatization of α^* in the treatment with slowly varying light, treatments with quickly varying light experienced higher total photosynthesis despite all treatments receiving the same total light over the course of the incubation. Similar photosynthesis results were found by Marra (1978), although α^* was not measured in his study. Thus, both the internal wave enhancement of photosynthesis predicted by our model and the acclimatization enhancement of photosynthesis observed by Marra (1978), Cullen and Lewis (1988), and Flameling and Kromkamp (1997) will contribute to the internal wave effect observed in our in situ experiments and in natural systems.

Another potential cause for the underprediction of internal wave effects by our current model would result from variations in the subsurface light field. If k_d increases within a subsurface Chl *a* maximum or if an intrusion of stream water that is high in particulates occurs in the depth range of internal waves, then the internal wave effect would increase. Although we did not observe such variations during our experiments, deep Chl *a* maxima are common in Toolik (MacIntyre et al. 2006), and in some situations deep Chl *a* maxima (Wurtsbaugh et al. 2001) or particulate layers (Kling 1988) can affect light attenuation. Altering the model to account for a variation of k_d with depth in a subsurface water layer resulted in greater predicted photosynthesis (data not shown). Our results indicate that model-predicted enhancement of photosynthesis may represent a minimum effect, and additional work is needed to develop a model fully specified to account for light acclimatization or dynamic k_d .

The isotherm-based model simulations (for 06–13 July 2003) are generally representative of internal wave and surface light conditions at Toolik Lake. Average internal

wave amplitude on these days was near the median observed during the summer of 2003 (Fig. 1A). Wind forcing caused energetic displacements of isotherms on the first 3 d (Fig. 5; LTER wind data: <http://ecosystems.mbl.edu/arc>). Strong wind on 08 July led to thermocline compression followed by expansion on 09 July as the wind relaxed. The subsequent isotherm displacements were smaller in amplitude and energized at higher frequencies by short windy periods during 10–13 July. Thus, the days studied capture a range of internal wave amplitudes and isotherm dynamics (Fig. 5). Similarly, over the summer, variations in surface light due to clouds during time intervals ≤ 4 h were approximately evenly distributed between 400 and 1,000 $\mu\text{mol quanta m}^{-2} \text{s}^{-1}$, with a higher frequency of small variations in light. Surface light variation on the days modeled was near the median of the distribution (Fig. 1C). Overall, during the summer of 2003 internal waves with amplitudes equal to or in excess of those modeled occurred 40% of the time, and cloud events with light variation equal to or in excess of that modeled occurred 43% of the time. Thus, the conditions modeled were near the median conditions within Toolik Lake.

Given that even larger internal waves occur with some frequency in Toolik Lake and that metalimnetic DCMs are common, the enhancement of photosynthesis by internal waves could contribute substantively to metalimnetic primary production during the ice-free season. The period after ice off in Toolik Lake is often the time with the highest recorded primary productivities (Miller et al. 1986), and the metalimnetic DCM begins to develop shortly afterward when the water column is weakly stratified and internal wave amplitudes are large (MacIntyre et al. 2006). Internal waves also occur in other systems where a DCM has formed by in situ phytoplankton growth (Vandevelde et al. 1987). Our data indicate that because internal waves increase light exposure and photosynthesis of metalimnetic phytoplankton, the internal waves may promote the development or maintenance of the DCM.

Both internal waves and surface light variations occur on a broad range of time scales (from minutes to weeks for internal waves and up to seasonal for surface light variations). We ran additional simulations using a range of these time scales: wave periods from 4 to 60 h and surface light variation including intermittent cloud cover, day–night cycles, and combinations of cloudy and sunny days. These simulations show that the effects of internal waves and surface light variation interact most strongly when they have similar periods (data not shown); for example, the 12- or 24-h wave periods do not interact with shorter-period light variation due to the passage of clouds and do not interact with the sequence of cloudy versus sunny days (2 cloudy days and then 3 sunny days or vice versa). However, in simulations with wave periods of several days, the sequence of cloudy and sunny days did impact the wave effect on photosynthesis.

We evaluated the potential for internal wave effects across 10 sites representing a broad range of oceanic and limnological systems. Sites were selected on the basis of the availability of data (Fig. 11), and the potential for internal

wave effects on photosynthesis was tested by comparing the internal wave depth, light attenuation, and surface light levels to the range of values that produced significant internal wave enhancements in our model. This analysis separates the parameter “light at depth,” which was lumped in the Holloway and Denman (1989) analysis, into its component parameters. A 4-D surface describes the boundary between systems in which internal waves are predicted to increase primary production and those for which other factors, such as photoinhibition, must be considered to determine internal wave effects; the 3-D boundary surface is shown in Fig. 11B for one representative value of E_0 ($600 \mu\text{mol quanta m}^{-2} \text{s}^{-1}$), and a 2-D slice through this surface is presented in Fig. 11A to demonstrate the effects of k_d . The boundary surface is linearly determined by E_0 such that E_k required for enhancement increases with increasing E_0 (data not shown). To include the maximum number of systems, sites were used regardless of internal wave period and even if the biological parameter E_k was not available (in which case a categorization was made on the basis of a range of E_k values). There are three potential categories of internal waves and internal wave effects based on internal wave depth, light attenuation, and surface light levels: (1) those in which internal waves pass through light intensities that saturate or inhibit photosynthesis and in which internal waves may reduce photoinhibition when cells are moved away from damaging light (as can be the case with near-surface turbulence or circulation; Ferris and Christian 1991; Patterson 1991), (2) those in which internal waves occur below the zone of photosynthesis, and (3) those in which internal waves and light-limited photosynthesis co-occur and the potential for internal wave effects is high. Internal waves occur within the diel thermocline of Toolik Lake at depths where light is saturating or inhibiting for photosynthesis (category 1). However, such near-surface internal waves were not reported in the other systems. Three of the examined systems fell into category 2, where the internal waves occur at depths far below the euphotic zone and thus little or no photosynthesis or internal wave effect is expected. Systems fell into this category for one of two reasons: the internal waves occur at great depth, such as deep internal waves in the ocean (parameter values from Holligan et al. 1985; Lande and Yentsch 1988), or the system had very high k_d values, such as turbid estuaries (St. Lawrence Estuary, Frechette and Legendre 1982). The remaining six systems fell into the third category, where there is a strong potential for internal wave enhancement of photosynthesis. This category included systems as diverse as the open ocean (“typical values” for shallow internal waves reported in Lande and Yentsch 1988; line 1 in Fig. 11B), the ocean on or near the continental shelf (Baltic Sea, Kahru 1983, line 2 in Fig. 11B; Gulf of St. Lawrence, Canada, Vandevelde et al. 1987, point 3 in Fig. 11B; and southern California, Kamykowski 1974, line 4 in Fig. 11B), large lakes (Lake Michigan, Fahnenstiel et al. 1988 point 5 in Fig. 11B), and small lakes (Toolik Lake, this study, point 6 in Fig. 11B).

The light gradient traversed by internal waves in these systems, determined by the percent change in light over the

internal wave's displacement, is larger than in Toolik Lake (63%) in all cases (up to a gradient of 95% in the open ocean) except in Lake Michigan (56%). Thus, internal wave effects would be predicted to be larger in these systems than the effects observed in Toolik Lake. However, as we have shown for short-period internal waves at Toolik Lake, the internal wave effect will be modified (positively or negatively) by sporadic surface light variations. This sporadic surface light variation will vary by geographic region; overall, Toolik Lake falls in a region that has on average 50–60% cloud cover (annual average; International Satellite Cloud Climatology Project, <http://isccp.giss.nasa.gov>). However, cloudiness at scales matching internal wave periods must be known in order to predict the internal wave effects in any particular system. For internal waves with longer periods (semidiel to several days), internal wave effects will be modified by interactions with the daily light cycle and with cloudy-to-sunny transitions associated with meteorological fronts. The amplitude of internal waves has been observed to be positively correlated with lake size in a series of northern Ontario lakes (0.89–347 km²; Kratz et al. 2005), indicating the potential for stronger internal wave effects on photosynthesis in moderate-sized to larger lakes. Thus, current assessments of primary production using infrequent or fixed-depth incubations or models are likely biased low in many aquatic environments; these assessments may improve by consideration of the effects from internal waves.

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