Impact of inertial period internal waves on fixed-depth primary production estimates[1]

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Abstract. Fixed-depth subthermocline phytoplankton production estimates were compared to variable-depth estimates calculated along the simulated trajectory of an internal wave. The mean of 5000 Monte Carlo simulations, varying wave phase and amplitude, was not significantly different than the fixed-depth estimate for average Lake Michigan internal waves. Differences were significant, however, for wave amplitudes >5 m but only at some depths. Differences between the two estimates were related to differences in irradiance received and the portion of the photosynthesis–irradiance (*P–I*) curve controlling production. Oscillating communities always receive more irradiance than fixed-depth communities and the magnitude of this increase is related to the extinction coefficient and the amplitude of the internal waves. Production was also estimated along an individual isotherm trajectory (isotherm-derived) and compared to fixed-depth production. Larger differences between these isotherm-derived and fixed-depth estimates were noted in some cases and were related to differences in the mean isotherm depth and the sampled (fixed) depth. If one accounts for the trajectory of the sampled community, fixed-depth estimates are reliable; however, if the trajectory is unknown or unaccounted for, any individual fixed-depth production estimate may not adequately measure *in situ* production.

Introduction

Primary production can be difficult to measure because of the coupling of physical, chemical, and biological factors. This coupling is difficult to duplicate with phytoplankton confined in bottles at fixed depths. One consequence of these *in vitro* experiments is that enclosed phytoplankton are held in a relatively constant environment, in contrast to the wide spectrum of *in situ* environmental fluctuations (e.g. widely fluctuating light fields caused by vertical movements). It has been suggested that fixed-depth experiments in the epilimnion of lakes may underestimate actual primary production (Harris and Piccinin, 1977; Marra, 1978). This may also be true in and below the thermocline of large lakes and oceans where internal waves and deep phytoplankton communities exist (Haury *et al.*, 1983). Fixed-depth primary production incubations are routinely used to estimate subthermocline production and to determine the importance of *in situ* growth in the formation of the deep chlorophyll layer (Priscu and Goldman, 1983; Moll *et al.*, 1984; Coon *et al.*, 1987; Fahnenstiel and Scavia, 1987a).

Pronounced subthermocline phytoplankton communities and well defined internal waves make Lake Michigan a good environment to study the impact of internal waves on subthermocline production estimates. In Lake Michigan, the deep chlorophyll layer (DCL) is a persistent feature that develops below the thermocline (Brooks and Torke, 1977; Fahnenstiel and Scavia, 1987a). Environmental fluctuations caused by near inertial period internal waves (13- to 17-h period) are also consistent features in the subthermocline region in Lake Michigan (Mortimer, 1980) that can cause large vertical excursions for DCL phytoplankton (Bowers, 1980) and drastically alter their light climate. If irradiance differences during these excursions are important to the growth of subthermocline communities (Kamykowski, 1979), then fixed-depth, *in vitro* primary production experiments may result in poor estimates of *in situ* primary production.

We investigated the effects of inertial period (17 h) internal waves on primary production measurements by comparing a standard fixed-depth production estimate with ones which consider phytoplankton vertical excursions caused by internal waves.

Methods

Model

To examine effects of internal waves on primary production estimates, we used the incubator and modelling approach of Fee (1973). In this technique, phytoplankton photosynthesis–irradiance (*P–I*) curves are integrated over time by prescribing temporal variation in light. Temporal variations in light can be caused by variations in incident irradiation, water column extinction coefficient and depth of the phytoplankton. We performed integrations based on hourly photosynthetically active radiation (PAR) averages for both 1- and 5-day intervals.

Our fixed-depth production estimate assumes that the phytoplankton are incubated at the depth they were sampled. These estimates were compared to two types of internal wave production estimates, one based on a simulated internal wave (wave-derived) and one based on actual isotherm displacement (isotherm-derived). Simulated wave-derived estimates use an ideal sinusoidal internal wave (Figure 1) whereas isotherm-derived estimates use actual isotherm trajectories (Figure 2). Both estimates simulate the light fluctuations caused by vertical oscillations of internal waves. Light climate at any particular time was determined from incident PAR, the assumed constant extinction coefficient and depth of the community at that time. Extinction coefficient and incident irradiation were identical; only depth was variable.

For simulated wave-derived estimates, depth at any time (z_t) was simulated with an ideal sinusoidal internal wave:

$$z_t = z_0 + A \cos(\omega t + \phi) \qquad (1)$$

where z_0 = mean depth, A = amplitude of wave, ϕ = phase shift and ω = frequency. Frequency is $\omega = 2\pi/t_i$ and t_i, the inertial period, was 17 h for all simulations. We set the mean depth of the wave community (z_0) equal to the sampled depth (Figure 1). For these wave-derived estimates two sets of calculations were done, one based on a single wave and one based on the

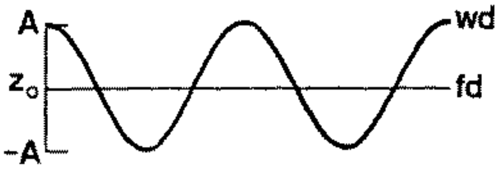

Fig. 1. Production along a simulated sinusoidal wave (wave-derived = wd) was compared to production at a fixed-depth (fd). Note that the mean depth of the oscillating community (z_0) is equal to the depth of the fixed community.

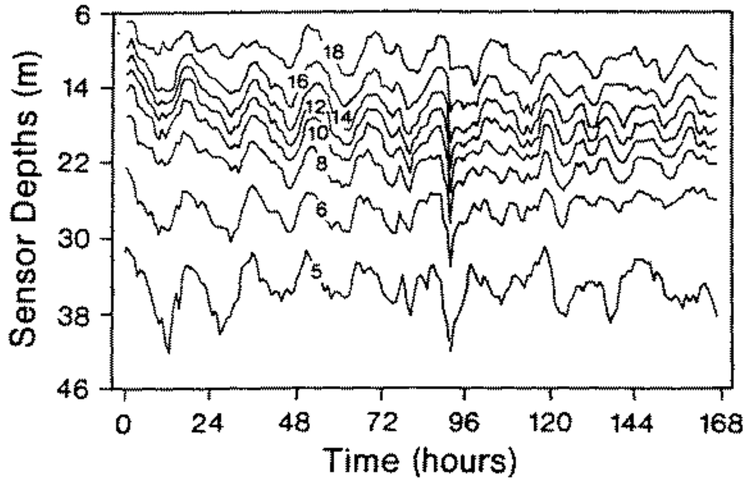

Fig. 2. Temperature contours from fixed thermistor string plotted against depth and time for 28 July–4 August 1984. Plotted results are from thermistors located 8 m apart.

average of many waves with differing amplitudes and phase shifts. For the single wave estimate, amplitude, period and phase shift were held constant. While single wave-derived estimates are influenced by the relationship of phase shift of the wave (ϕ) and the diurnal light–dark cycle, average wave-derived estimates reduce the importance of phase shift and diurnal light–dark cycle and focus on the average effect of vertical excursions. For average wave-derived estimates (i.e. one where amplitude and phase shift are uncertain), Monte Carlo analysis was used. In these simulations, 5000 sets of values for A and ϕ were selected from probability distributions. Amplitude was assumed to be normally distributed with mean and variance calculated from observed isotherm displacements between 7 July and 4 August 1984 (Figure 2). Phase shift was assumed to be distributed uniformly between 0 and 360° to mimic total uncertainty of the relationship between sampling time and wave phase.

Fixed-depth estimates were also compared to isotherm-derived estimates. Isotherm-derived estimates were calculated in the same fashion as single wave estimates, except depth at any time (z_t) was determined from isotherm displacements determined from a moored thermistor string (Figure 2).

Measurements

All samples were collected at an offshore station located 25 km west of Grand Haven, Michigan. Temperature was measured with an electronic bathythermograph and a moored line of thermistors located every 4 m from 6 to 46 m from the surface. The thermistor string recorded observations every hour (Saylor and Miller, 1983). Incident PAR was measured continuously with a Licor LI-190SB sensor and Licor LI-550B printing integrator. Underwater scalar PAR was measured with a Licor LI-193SB sensor and Licor LI-188B integrating meter. Water samples from 24 to 32 m were collected on 23 July 1984 near midday and primary production was measured with 1- to 2-h ^{14}C incubations at a range of light levels (Fahnenstiel and Scavia, 1987b). Chlorophyll concentrations were determined fluorometrically on 90% acetone extracts (Strickland and Parsons, 1972).

Results

Internal waves were common in the region of the DCL (Figure 2). Mean and standard deviation of subthermocline wave amplitudes varied between 2.0 ± 1.0 m at 50 m and 2.8 ± 1.2 m at 30 m for 7 July–4 August 1984. *P–I* data for the 24- to 32-m community, fitted to the following equation (Platt *et al.*, 1980):

$$P = P_{\max}\,[1 - \exp(-\alpha I/P_{\max})]\exp(-\beta I/P_{\max}) \qquad (2)$$

with non-linear regression yielded $P_{\max}$ of 1.0 mg C mg Chl^{-1} h^{-1}, α (initial linear slope) of 5.72 mg C m^2 mg Chl^{-1} Einst^{-1} and β (linear slope at high irradiance) of 0.083 with same units as α (regression $R^2 = 0.978$).

Fixed-depth versus average wave-derived estimates

Using the mean and standard deviation wave amplitude and constant *P–I* parameters, we compared fixed-depth and average wave-derived estimates determined from 5000 Monte Carlo simulations run for 5 days (Table I). Because the actual trajectory of a phytoplankton sample is usually unknown, we

Table I. Five-day Monte Carlo simulations of primary production (mg C mg Chl^{-1}) for various depths and wave amplitudes. Mean and standard deviation are listed for all wave-derived estimates

Depth	Fixed-depth estimate (wave amplitude = 0 m)	Wave-derived estimate (wave amplitude and standard deviation in parentheses)	Wave-derived estimate (constant wave amplitude = 7 m)
15	39.78	39.56 ± 0.49 (2.1 ± 1.0)	37.84 ± 0.36
17	34.36	34.20 ± 0.47 (2.3 ± 1.1)	33.49 ± 0.22
20	25.78	25.83 ± 0.57 (2.4 ± 1.2)	26.67 ± 0.83
22	20.45	20.63 ± 0.65 (2.5 + 1.2)	22.18 ± 1.08
25	13.78	14.04 ± 0.66 (2.6 ± 1.2)	16.02 ± 1.16
28	8.90	9.18 ± 0.62 (2.7 ± 1.2)	10.96 ± 1.01
30	6.54	6.80 ± 0.58 (2.8 ± 1.2)	8.30 ± 0.84
35	2.93	3.05 ± 0.40 (2.6 ± 1.2)	3.90 ± 0.46
40	1.28	1.33 ± 0.26 (2.5 ± 1.2)	1.74 ± 0.22
50	0.23	0.24 ± 0.10 (2.0 ± 1.0)	0.32 ± 0.03

let the phase shift vary randomly in this first set of comparisons. Five days were chosen for the simulations based on our minimum estimate of subthermocline phytoplankton generation time; it was assumed that any short-term change in production would be averaged over the generation time of the phytoplankton. For all comparisons, Monte Carlo mean depth [z_0 in equation (1)] was set equal to that of the fixed-depth model estimate (Figure 1).

Average wave-derived estimates were slightly less than fixed-depth estimates at 15 and 17 m and slightly greater than fixed-depth estimates between 20 and 50 m (Table I) when measured amplitude means and standard deviations were used. None of the differences were significant (two-tailed t-test, $\alpha = 0.05$). Monte Carlo simulations using the maximum observed amplitude (7 m) with zero variance (Table I), resulted in greater differences from the fixed-depth estimates; however, the pattern was similar. In the upper region of the DCL (15–17 m), wave-derived estimates were lower than fixed-depth estimates but in the 20- to 50-m region wave-derived estimates were higher. Comparisons at several depths (15, 17, 30, 35, 40 and 50 m) yielded significant differences (two-tailed t-test, $\alpha = 0.05$); however, these differences were not large (<40%) considering that the assumed vertical displacement was 14 m.

Fixed-depth versus single wave-derived estimates

We compared fixed-depth estimates with those for a community following a single internal wave (i.e. wave amplitude variance = 0, phase shift = 0) to illustrate the effect of varying irradiance. Comparisons of irradiance and production clearly demonstrate the effect of vertical oscillations on average irradiance received by the community and on photosynthesis per unit irradiance (P:I) (Tables II–IV). Oscillating communities always receive more irradiance than a community fixed at the mean depth of the oscillating community (z_0).

The impact of increased irradiance on production is determined by the photosynthesis per unit irradiance (P:I) characteristics of the community. In our examples, the largest difference between P:I for wave-derived and fixed-depth communities was at 15 m (Table II). The difference betwen fixed-depth and wave-derived P:I decreased with depth (Tables III and IV) and at 40 m (Table IV) there was no difference. Differences in P:I with depth are related to the portion of the P–I curve controlling production at that depth.

Fixed-depth versus isotherm-derived estimates

The effect of phase shift or actual trajectory of the community was not considered in the above examples because the mean depth of the wave community was set equal to the depth of the fixed community. For the final comparisons, we used measured isotherm displacements to simulate actual community trajectories. Sample collection time, depth and temperature were matched to observations from the fixed thermistor string to determine at what point along the internal wave the community was sampled. Fixed-depth estimates were then determined assuming the sample was incubated at the collection depth. Isotherm-derived estimates were determined assuming the

Table II. Average 1-h production and irradiance for 15-m sample with different wave amplitudes. Single wave-derived estimates with 0 phase shift, 17-h period and 2.5-, 5- or 10-m amplitude are compared to the fixed-depth production estimate

Amplitude (m)	Production (mg C mg Chl^{-1} h^{-1})	Irradiance (E m^{-2} h^{-1})	Production/Irradiance (mg C m^{2} mg Chl^{-1} E^{-1})
0 (fixed-depth)	0.50	0.20	2.50
2.5	0.50	0.22	2.27
5.0	0.49	0.25	1.96
10.0	0.46	0.40	1.15
r = ratio of 10 m/0 m	0.92	2.00	0.46

Table III. Average 1-h production and irradiance for 30-m sample with different wave amplitudes. Single wave-derived estimates with 0 phase shift, 17-h period and 2.5-, 5- or 10-m amplitude are compared to the fixed-depth estimate

Amplitude (m)	Production (mg C mg Chl^{-1} h^{-1})	Irradiance (E m^{-2} h^{-1})	Production/Irradiance (mg C m^{2} mg Chl^{-1} E^{-1})
0 (fixed-depth)	0.083	0.016	5.19
2.5	0.088	0.017	5.18
5.0	0.100	0.020	5.00
10.0	0.130	0.032	4.06
r = ratio of 10 m/0 m	1.57	2.0	0.78

Table IV. Average 1-h production and irradiance for 40-m sample with different wave amplitudes. Single wave-derived estimates with 0 phase shift, 17-h period and 2.5-, 5- or 10-m amplitude are compared to the fixed-depth estimate

Amplitude (m)	Production (mg C mg Chl^{-1} h^{-1})	Irradiance (E m^{-2} h^{-1})	Production/Irradiance (mg C m^{2} mg Chl^{-1} E^{-1})
0 (fixed-depth)	0.016	0.0029	5.52
2.5	0.017	0.0031	5.48
5.0	0.020	0.0036	5.55
10.0	0.032	0.0058	5.52
r = ratio of 10 m/0 m	2.0	2.0	1.0

Table V. Comparison of isotherm-derived and fixed-depth production (mg C mg Chl^{-1}) for 1- and 5-day experiments starting at 09.00 h on 23 July 1984. The depth of sample collection which is equal to the depth of the community for the fixed-depth estimate is also compared to the mean depth of the community for the isotherm-derived estimate

Experiment duration (days)	Sample depth (m)	Fixed-depth estimate (mg C mg Chl^{-1})	Mean depth of isotherm (m)	Isotherm-derived estimate (mg C mg Chl^{-1})
1	15	6.9	13.9	7.3
5	15	39.8	14.5	40.9
1	20	4.4	20.2	4.1
5	20	25.8	21.1	22.8
1	30	1.1	33.6	0.6
5	30	6.5	35.9	2.7

sample followed the particular trace of the isotherm representing it. Fixed-depth and isotherm-derived production estimates exhibited depth-specific differences (Table V). For the 15-m community, isotherm-derived estimates were greater than fixed-depth estimates; whereas at 20 and 30 m, the opposite was true. These differences were related to the difference between the depth of the fixed sample and the mean depth of the oscillating sample; small differences in these depths resulted in similar production estimates and large depth differences resulted in larger production differences. Thus, the actual community trajectory can be the largest source of variation between fixed-depth and wave-derived or isotherm-derived production estimates.

Discussion

If a subthermocline community is sampled and incubated at the mean depth of its oscillating trajectory (average wave-derived estimate) then conventional fixed-depth primary production estimates are satisfactory for estimating subthermocline production in Lake Michigan. Relatively small (<5%) differences were found between fixed-depth production estimates and average wave-derived estimates for typical amplitude internal waves (Table I). There is no need to simulate the vertical fluctuations in light caused by internal waves. This conclusion is in contrast to suggestions for estimating production in the epilimnion of lakes where vertical movements must be simulated if accurate production estimates are desired (Harris and Piccinin, 1977).

The effect of internal waves on primary production estimates is related both to changes in irradiance caused by waves and to the P–I curve. In our examples, the average irradiance received by oscillating communities was always greater than for fixed-depth communities. The increase in irradiance received by oscillating communities increased with wave amplitude and is related to the logarithmic decrease in irradiance with depth. The magnitude of this increase is related to the amplitude of the wave and the extinction of light with depth and can be determined analytically. The average irradiance (I_z) received by an oscillating community can be calculated from:

$$I_z = \frac{1}{T}\int_0^T I_0 \exp[-k\,(z_0 + A\cos\omega t)]\mathrm{d}t \tag{3}$$

where T = time of integration, I_0 = incident irradiation and k = the extinction coefficient. The average irradiance (I_z) received by a fixed-depth community can be determined by:

$$I_z = I_0 \exp(-kz) \tag{4}$$

where I_0 and k are the same as in equation (3). From these two equations, the ratio of irradiance received by an oscillating community relative to a fixed community was determined by numerically integrating equation (3) and comparing the results to equation (4). A long integration time (1000 days) was used to average out the effect of wave period. Incident irradiation was taken from 23 July and repeated 1000 times. For any environment with a known wave amplitude and light extinction coefficient the ratio of oscillating irradiance to fixed irradiance can be estimated from Figure 3. For Lake Michigan with an average July extinction coefficient of 0.14–0.17 m^{-1} and wave amplitude of 2.5 m, an increase of ~5% is predicted. Small effects can also be predicted for other environments where wave amplitude and extinction coefficient are known. For example, Kamykowski (1974) reported semi-diurnal tidal internal waves with an average wave amplitude of 4.5 m and extinction coefficient of 0.21 m^{-1}. In this case, an oscillating community receives on average 20% more irradiance than a fixed community.

The effect of these irradiance differences on production estimates is related to the *P–I* curve. As we demonstrated, increased irradiance received by oscillating communities does not always result in increased production (Tables II–IV). This is due to the non-linearity of the *P–I* curve. The only portion of the curve where increased light is translated linearly into increased production is the initial linear slope at low irradiances. Thus, the effect of increased irradiance received by an oscillating community is maximized in this region. At higher irradiances the *P–I* curve saturates and increased irradiance does not increase production. The effect is to produce a decreased *P*:*I* and minimize any increase in irradiance.

Examples from two environments demonstrate the interaction between increased irradiance received by an oscillating community and production, and the general minimal effect of internal waves. In Lake Michigan, the relatively small differences between fixed-depth and wave-derived estimates were primarily due to the small amplitude of internal waves. The average wave

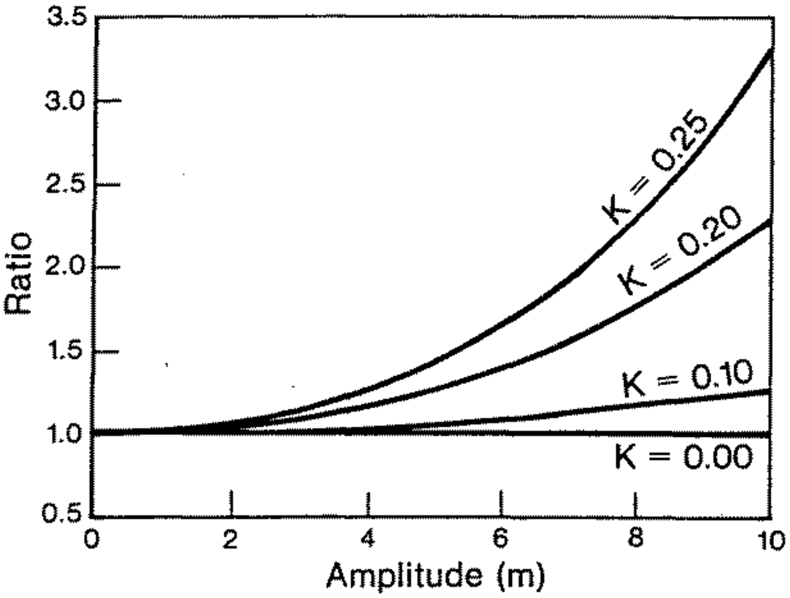

Fig. 3. Plot of ratio (r) of average irradiance for oscillating community relative to fixed-depth community. The ratio was calculated from equations (3) and (4) for different amplitudes and extinction coefficients.

amplitude of 2.8 produced only small irradiance differences and consequently small production differences. Increasing wave amplitude to 7 or 10 m results in 35–75% more irradiance for an oscillating community but production differences of this magnitude were only found deep in the water column where 0.60–0.02% of surface irradiance was received. These deep communities are light limited and therefore exhibit a linear relationship betwen irradiance and production. Above 28 m differences between wave-derived and fixed-depth estimates were much smaller (<17%) than irradiance differences. Communities from 15 to 28 m receive 1–10% of surface irradiance and exhibited decreased *P*:*I* for oscillating cases, indicating that these communities operate along the non-linear part of the *P*–*I* curve. This is supported by the fact that I_k [threshold of light saturation parameter, Talling (1957)] for the sampled community was ~60 μE m^{-2} s^{-1} which is ~5% of mean daily irradiance.

For the example presented by Kamykowski (1974), we estimated that an oscillating community would receive 20% more irradiance than a fixed-depth community. With an extinction coefficient of 0.21 m^{-1} and a thermocline depth of 10.5 m, an oscillating thermocline community would receive ~11% of surface irradiance and probably operate along the non-linear part of the *P*–*I* curve. Thus the 20% increase in irradiance would result in less production increase relative to the fixed depth example, or it may actually decrease. In this case the differences between conventional production estimates and production estimates that include the effects of internal waves would be much less than 20%.

The foregoing discussion of internal wave effects on primary production estimates assumed that the oscillating community is sampled at its mean depth (Figure 1). This does not have to be the case. The mean community depth can in fact be very different from the sampled depth. If this is the case then large differences in production between fixed and oscillating communities are possible. For example, the 30-m fixed-depth production estimates were 1.7–2.4 times greater than isotherm-derived estimates for the 1- and 5-day experiments (Table V). This difference was larger than those found by comparing fixed-depth and average wave-derived estimates for typical Lake Michigan internal waves (Table I). In this example, the fixed depth (30 m) was very different to the depth of the sampled isotherm averaged over 1 (33.6 m) and 5 (35.9 m) days because the community was sampled at the highest point in its trajectory (Figure 4). This error represents the single extreme case, a community sampled at the highest or lowest part of its trajectory. Unlike the 30-m example, only small differences (<10%) were found between production and mean depth for fixed and oscillating communities from 15 and 20 m. Errors caused by community trajectory are difficult to predict without knowledge of sampled community trajectory. However, if very small differences in irradiance are predicted (<5%) from Figure 3, it is reasonable to assume that fixed-depth production estimates are accurate.

Two conclusions can be drawn from this analysis of the impact of internal waves on conventional primary production estimates. First, when the average amplitude of Lake Michigan internal waves (≤2.8 m) was used and the phytoplankton were incubated at their mean depth, significant differences were

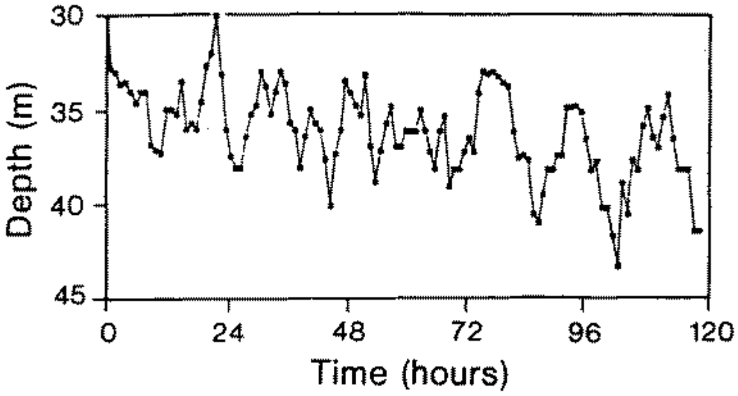

Fig. 4. Trajectory of the 4.75°C isotherm sampled on 24 July 1984 at 09.00 h. The mean depth of the isotherm (33.6 m for first 24 h) was different from the sampled depth (30 m).

not found between standard, fixed-depth production estimates and wave-derived estimates. Only for wave amplitudes >5 m did significant differences occur and only then at depths where phytoplankton communities are primarily light limited. Second, for any given experiment fixed-depth production estimates can be different from actual production of a community moved by internal waves. This difference is a sampling problem caused by the assumption that the sampled depth is the same as the average depth of the community over its generation time. This error can be minimized only by knowledge of the trajectory of the sampled community. While this error may be important in certain environments where vertical excursions cause major changes in the light climate of the phytoplankton, in the majority of cases it appears that fixed-depth estimates of subthermocline production are reasonably accurate.

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