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# *Possible Interactions Between Phytoplankton and Semidiurnal Internal Tides<sup>1</sup>*

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## ABSTRACT

Computer programs are used to analyze some possible interactions between phytoplankton and semidiurnal internal tides. The internal tides are modeled in a two-layer ocean using small amplitude wave theory. Wave characteristics representative of southern California coastal waters are used as input for the equations.

Biological sampling problems arising from the horizontal and the vertical water motions are discussed. It is concluded that internal tides can contribute significantly to the biological variability observed at a geographic location.

Three cases of phytoplankton behavior are considered as they are influenced by the internal tide model. Non-motile phytoplankton at the thermocline are treated in Case 1. Motile phytoplankton that undergo diurnal vertical migrations are discussed in Cases 2 and 3. Though small-scale, physically-generated patchiness occurs, non-motile phytoplankton and motile phytoplankton that remain above the thermocline are most affected by the physiological implications of the wave. In addition to physiological effects, motile phytoplankton that cross the thermocline are strongly aggregated due to physical causes. All three cases can result in patchiness of biomass, species and, possibly, organic composition.

Aliasing of surface patterns and food web interactions are discussed.

*Introduction.* In some coastal areas the internal tide is a conspicuous element in the spectrum of thermocline movements. The physical characteristics of this phenomenon are especially well known for the southern California coast (Cairns 1966, 1967, 1968; Cairns et al 1966, 1968). Some observations of biological interest are reported between the vertical oscillation and such factors as plant nutrients (Armstrong and LaFond 1966) and turbidity (Ball and LaFond 1963). Fuks and Meshcheryakova (1959) discuss the effect of internal tides on the observation of the diurnal vertical migration of zooplankton. The interaction between internal tides and biological productivity and patchiness has received much less attention.

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Table I. Definition of Symbols.

$\lambda$	-	wavelength
$c$	-	phase speed
$T$	-	period
$g$	-	acceleration of gravity
$D$	-	mean water layer thickness below interface
$d$	-	mean water layer thickness above interface (mean thermocline depth, <i>MTD</i> )
$\rho$	-	density of layer below thermocline
$\rho'$	-	density of layer above thermocline
$z_{TC}$	-	thermocline depth
$TC$	-	thermocline
$a$	-	amplitude
$t$	-	time variable
$u_d$	-	horizontal component of water velocity above thermocline
$u_D$	-	horizontal component of water velocity below thermocline
$k$	-	wave number ( $k = 2\pi/\lambda$ )
$x$	-	space variable
$\omega$	-	angular frequency ( $\omega = 2\pi/T$ )
$w_d$	-	vertical component of water velocity above thermocline
$w_D$	-	vertical component of water velocity below thermocline
$z$	-	depth variable
$s_d$	-	water motion ellipse diameter above thermocline
$s_D$	-	water motion ellipse diameter below thermocline
$ss$	-	swimming speed

In the present paper a computer simulation of semidiurnal internal tides is constructed. This is achieved by inserting values for the physical characteristics of the wave as observed off southern California into the equations of motion from small amplitude wave theory. Biological sampling problems arising from these water motions are discussed. Various cases of phytoplankton behavior are superimposed on the physical model to investigate possible biological effects derived from the interaction. Some of the results apply to smaller zooplankton.

*Methods.* An IBM 1800 computer is used to perform an iterative calculation on a model simulating the biological effects of a semidiurnal internal tide. The physical aspects of the model are based on the following assumptions:

1. A day-night cycle with 12 hours light : 12 hours dark.
2. A two-layer ocean of uniform undisturbed water depth with a surface layer that is nutrient depleted and a subthermocline layer (the thermocline is the interface between the two layers) that is nutrient rich.
3. Small amplitude wave theory (amplitude  $\ll$  wavelength).
4. Long waves (wavelength  $\gg$  water depth).
5. Neglect earth's rotation.

Assumptions 2, 3, and 4 allow the use of simplified equations (Defant 1961). Assumption 5 reduces a three dimensional ( $x, y, z$ ) problem to two dimensions



$(x, z)$ . The  $x$ -axis (positive toward shore) is perpendicular to shore and the  $z$ -axis (negative below surface) is the water column.

The basic relationship describing the wave (Haurwitz 1950) is given by

$$\lambda = c T \quad (1)$$

where

$$c = \left( \frac{gDd}{D+d} \frac{\rho - \rho'}{\rho} \right)^{1/2}. \quad (2)$$

Symbols are defined in Table I. The interfacial level associated with the passing wave is given by

$$Z_{TC} = -d + a \sin \frac{2\pi t}{T}. \quad (3)$$

This equation denotes a sine wave centered at the thermocline. The approximation is appropriate for deep water but becomes inaccurate near the coast because the wave form assumes increasing asymmetry as the water shoals (Cairns 1967). The horizontal and the vertical components of water particle motion above the interface are given by

$$u_a = -\frac{ac}{d} \sin(kx - \omega t), \quad (4)$$

$$w_a = -\frac{z}{d} a \omega \cos(kx - \omega t). \quad (5)$$

The corresponding components of motion below the interface are given by

$$u_D = \frac{ac}{D} \sin(kx - \omega t), \quad (6)$$

$$w_D = -\frac{d+D+z}{D} a \omega \cos(kx - \omega t). \quad (7)$$

The horizontal components above and below the interface are reversed and are inversely related to the mean layer thicknesses. These currents are uniform vertically from the interface to the respective boundaries. They reach a maximum over the crest and the trough and decrease to zero midway between these extremes. The vertical components decrease linearly from the interface where they are maximum to the respective boundaries where they are zero. These currents are zero at the crest and the trough and are a maximum midway between these extremes.

The path followed by a single water parcel over one period of the wave describes an ellipse perpendicular to shore. The minor diameter ( $Z$  axis) dec-



reases with increasing mean distance from the interface. The major diameters ( $X$  axis) in the layers above and below the thermocline are obtained by inserting the amplitude, the phase speed, the angular frequency, and the mean thermocline depth or the water depth below the thermocline in the following equations

$$s_a = \frac{2ac}{\omega d} \quad (8)$$

$$s_D = \frac{2ac}{\omega D} \quad (9)$$

The values substituted for the variables in equations 1–9 are based on observations made off southern California. A total water depth of 200 meters is representative of the near shore depths; this figure is used in all of the calculations. The density below the interface is held at 1.025 and the density difference across the interface is 0.001. Mean thermocline depth depends on wind velocity, geostrophic conditions, and season. Inshore, it varies from 7 m in July to 50 m in February. The mean thermocline depth deepens with distance from shore at all times of the year. The average amplitude of the semidiurnal internal tide as measured at NUC Tower (about 1.6 km offshore from Mission Beach, California) is about 5 meters. A range of amplitudes extending from 2 meters to 15 meters are used in examining the implications of the model. The larger amplitudes are not really compatible with small amplitude wave theory. These conditions are considered, however, in the belief that the qualitative results can be related to the “natural” situation.

Two biological sampling problems arising from the horizontal and vertical characteristics of the wave are treated. The first concerns the hourly changes in the ecological community that is expected at a station along a coast where the biological characteristics change rapidly in an offshore direction. The second considers the changes in the biological vertical profile due to the vertical fluctuations of the thermocline and to the differences in the vector of the horizontal currents above and below the thermocline.

Phytoplankton utilize various adaptations to maintain their position in the euphotic zone (Smayda 1970). Two major classes are flotation and motility. The three cases of phytoplankton-water parcel interaction treated below are: Case 1 – non-swimming phytoplankton; Case 2 – vertically swimming phytoplankton that always stay above the thermocline; and Case 3 – vertically swimming phytoplankton that cross the thermocline.

Organisms that depend on various flotation mechanisms to retard sinking comprise Case 1. Their vertical position relative to the oscillatory temperature structure is determined by their density (i.e. neutral bouyancy). The vertical and horizontal coordinates of their position in the water column are determined by the movements of the water parcel within which they are entrained. Sinking is not considered in the treatment of this case.

Cases 2 and 3 involve motile organisms. There is evidence in the literature that phytoplankton can undergo extensive diurnal vertical migrations. Both laboratory (Eppley et al 1968; Hand et al 1965) and field (Hasle 1950, 1954) data suggest swimming velocities of  $1-2 \text{ m hr}^{-1}$ . It is the interaction between a 24 hr migration cycle and the 12.4 hr internal tide that is of interest.

Case 2 includes weak swimmers that do not reach the thermocline and stronger swimmers ( $1.0 \text{ m hr}^{-1}$ ) that have an aversion to crossing the thermocline. The organism's vertical position relative to the oscillatory temperature structure is determined by its migration behavior. Its vertical position in the water column is determined by a combination of its migration pattern and the vertical component of water motion. The organism's horizontal position is determined solely by the horizontal component of the water velocity above the thermocline.

Case 3 considers stronger swimmers that cross the thermocline. Two different types of behavior are considered. Either the organism maintains a constant velocity throughout its migration despite crossing the thermocline, or the organism decreases its downward velocity on crossing the thermocline because a nutrient pool is reached.<sup>3</sup> The upward migration for both types of behavior is made at the maximum velocity despite vertical location. The organism's vertical position is again determined by the interrelationship between its vertical swimming speed and the vertical component of the water motion. The horizontal position of an organism which swims through the thermocline is affected by passage from one current regime into another. Since the speeds of water parcels above and below the thermocline are inversely related to the layer thicknesses, the flow below the thermocline is usually less than that above. In addition, the direction of particle motion below the thermocline is reversed from that above. Therefore, an organism which passes through the interface on its downward migration will usually enter a different water column when it migrates back up through the thermocline at some later time. This behavior gives the organism the potential to move large distances in space since the major axis of the particle ellipse above the thermocline may extend over kilometers (see below). These consequences are similar to Hardy's conclusions about the interaction of zooplankton and differential currents with depth (Hardy & Gunther 1935). Colebrook (1960) discusses a related hypothesis for Windermere.

All three cases are simulated on a computer. The calculation for Case 1 considers the thermocline phytoplankton population associated with the interface oscillations governed by equation (3). A solar radiation curve and an extinction coefficient for radiation in sea water are assumed. These are combined with the vertical movements of the organisms due to the wave to yield an estimation of the relative radiation field which representatives of the population

3. The latter behavior is distinguished from constant velocity by the notation: maximum velocity (half-maximum velocity), i.e.  $1.0 (0.5) \text{ m hr}^{-1}$ .



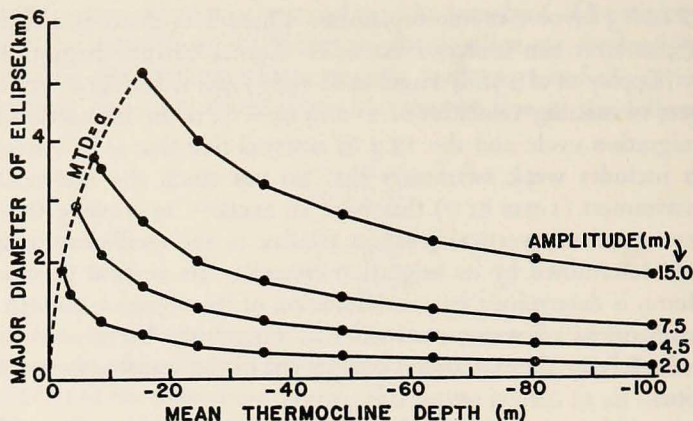


Figure 1. Major diameter of the ellipse ( $x, z$ ) above the thermocline formed by a water particle moving under the influence of water currents associated with the semidiurnal internal tide. Various mean thermocline depths for different amplitudes are given.

occupying different positions along the wavelength experience. Case 2 uses equations (3), (4), and (5) to model the thermocline fluctuations and the above-interface current regime. Since the organism is given only a vertical swimming component, equation (4) determines its horizontal progress while equation (5) added algebraically to the swimming component determines the vertical position. Case 3 requires a description of the motion in both layers. Equations (3), (4), (5), (6), and (7) are combined in one program to define the pattern of water motion upon which the organism's swimming behavior is superimposed. The phytoplankters' horizontal position is determined by equations (4) or (6) while its vertical progress results from the algebraic sum of either equation (5) or (7) and the swimming component.

*Results and Discussion.* The water motions associated with semidiurnal internal tides offer theoretical sampling problems to coastal studies of planktonic organisms. The first problem is due to the extensive onshore-offshore water motion and to the frequent occurrence of a rapid change in biological characteristics seaward. Fig. 1 is a graph derived by entering selected values into equation (8). The boundary to the left is set at the amplitude of the wave equal to the mean thermocline depth. A mean thermocline depth of 100 meters is taken as an arbitrary boundary on the right. As the mean thermocline depth shoals on a seasonal basis, the extent of the onshore-offshore movement of water above the interface increases. For a constant mean thermocline depth, an increase in amplitude increases the ellipse's major diameter. The amplitude shows some relationship to near-spring tidal cycles with greater amplitudes at spring tides (Cairns 1968). If the seasonal density changes are considered, the shallower mean thermocline depths have larger major diameters than Fig. 1 while the



deeper mean thermocline depths become smaller. A graph corresponding to Fig. 1 for equation (9) would show major diameters extending only over hundreds of meters for a water depth of 200 meters.

Biological heterogeneity marked by decreasing biomass seaward is commonly observed in coastal waters (Kamykowski 1973). This patchiness considered together with Fig. 1 suggests that a fixed station can be subject to a changing biological community on a semidiurnal basis. The actual extent of the change varies with the time of the year, the energy of the tide, and the amount of biological variability.

A second problem arising from these water motions is the interpretation of single vertical profile. Observations off La Jolla, California, in a water depth of 23 m have shown that the thermocline can move from 7 m to 22 m in 6 hr. One sample during this time interval gives a false view of the water column and its associated biota. The different current vectors above and below the thermocline also affect the interpretation of vertical profiles. Any sample of the water column is merely a single example of a continuously changing juxtaposition of water masses above and below the thermocline. These factors require either that samples are taken at intervals over the period of the physical phenomenon to determine the average conditions or that the interpretation of the single sample is adjusted to allow for greater variability in the population that could be sampled.

The interaction between the semidiurnal internal tide model and phytoplankton physiology and behavior offers an interesting basis for speculation. The three previously defined cases are considered below.

Since the organisms in Case 1 depend on flotation to maintain their position in the water column, they follow the vertical and horizontal movements of the water corresponding to their buoyancy (assuming sinking to be slow relative to the movements of the density layer (Smayda 1970)). In the absence of turbulent mixing across the thermocline, the organisms experience no change in temperature or nutrient concentrations. The radiation field available to each organism, however, is significantly affected by the vertical movements. This is especially true for the phytoplankton at the thermocline. Fig. 3 is a result of a computer simulation of the solar radiation experienced by thermocline organisms at various positions along a semidiurnal internal tide wavelength. The mean thermocline depth is  $-10.5$  m and the wave amplitude is 4.5 m. The incident radiation follows a sine function with a peak intensity at  $1.05 \text{ ly min}^{-1}$  at noon, and the extinction coefficient of the water column is set at 0.21. The lines in Fig. 2 represent the relative mean radiation intensities over the within block interval (1 hr). Each block of Fig. 2 represents different starting positions at sunrise spaced at 1-hr intervals of the period (except the last block of 12.4 hr) along the wave form. The first block has an organism at the crest of the wave at sunrise, in the trough near noon, and approaching the crest at sunset. The seventh block represents the light regime experienced by an organ-

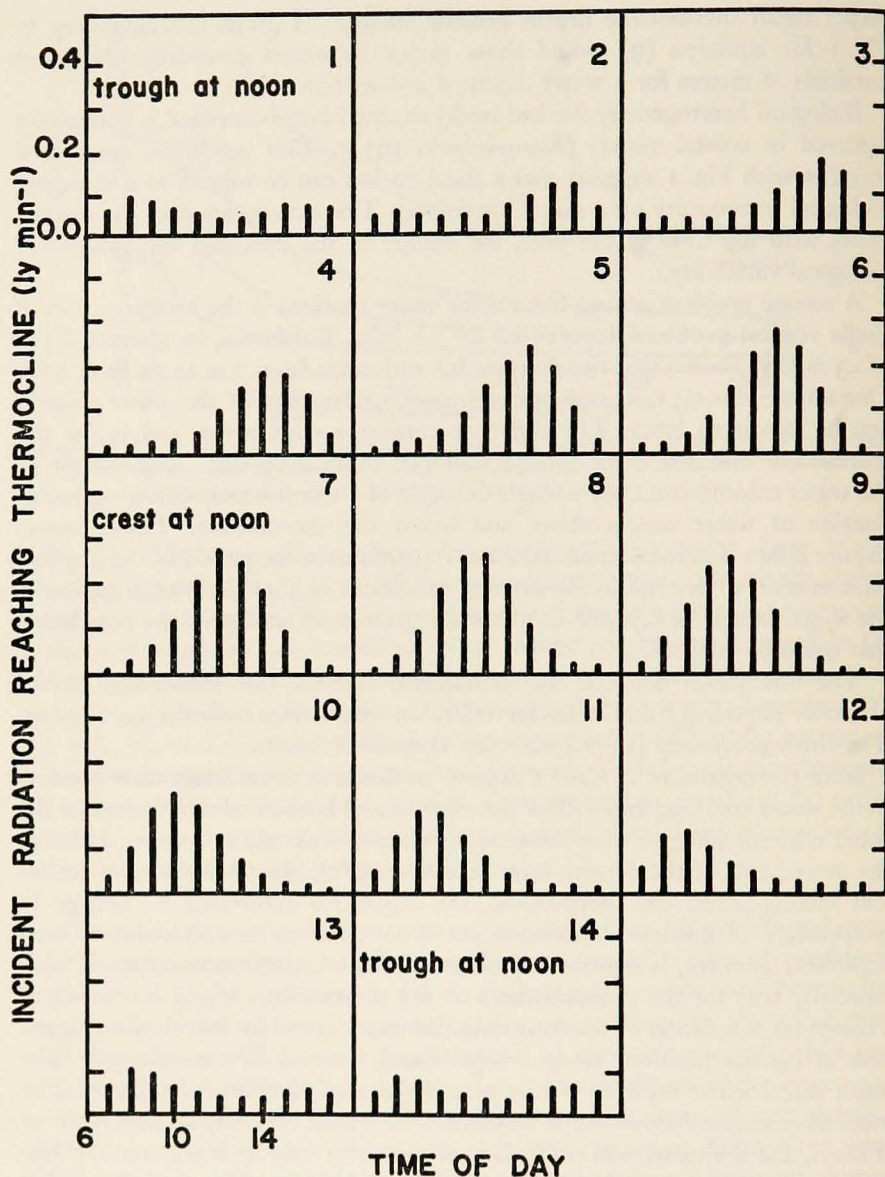


Figure 2. Case 1: Mean hourly radiation intensities for 12 hr. The blocks represent organisms that are on the thermocline at a number of simultaneous starting positions (hourly intervals of the period) along the wavelength of a semidiurnal internal tide.



ism that is in the trough of the wave at sunrise, spends noon near the crest, and returns to the trough shortly after sunset.

Some simplifications in the simulation are the use of a constant mean thermocline depth and a constant extinction coefficient for radiation along the wave form. The usual trends in coastal waters are a deepening mean thermocline depth and a decreasing extinction coefficient seaward. The simulation also neglects cell sinking and the presence of short period waves superimposed on the semidiurnal oscillation (Armstrong & LaFond 1966).

It is apparent from Fig. 2 that the range of radiation intensities to which various thermocline organisms are exposed each day varies with their position along the internal wave at sunrise. For example, those in the first block experience intensities only up to  $0.13/1 \text{ min}^{-1}$  while the range for those in the seventh block is up to  $0.31 \text{ ly min}^{-1}$ . The effect that this may have on the productivity and species composition depends on the ability of the different phytoplankton species to adapt their photosynthesis to different intensities. The interaction between a day-night cycle of 12–12 hr and a semidiurnal tidal period yields a 15.5 day period for an organism to move through all the blocks of Fig. 2. Since some phytoplankton do have extensive and relative rapid adaptations (1–3 days) to solar radiation (Fogg 1966), changes in the photosynthesis-intensity (P-I) relationship of thermocline populations are expected along the wave form. This ability partly determines a species biomass distribution along a wavelength. If the phytoplankton species differ substantially in their ability to adapt, then species changes are expected. The effect in Fig. 3 decreases away from the thermocline due to the linear decrease of vertical water movement to zero as the surface is approached and to the increased importance of sinking above the thermocline.

The decrease of radiation intensity with depth is accompanied by changes in the spectral distribution of the radiation (Jerlov 1968). Marmelstein (1970) finds that the organic composition of marine phytoplankton diatoms changes with light intensity. Wallen and Geen (1971) suggest that qualitative chemical changes occur in phytoplankton grown under different wavelengths of light. Such changes whether due to radiation intensity or to spectrum could be significant in terms of the food value of the phytoplankton. It is, therefore, possible that internal tides may affect not only the quantity and kinds but also the quality of thermocline phytoplankton along a wave form. Since the efficiency of zooplankton grazing is thought to be influenced by all of these factors (Mullin 1963; Shiraishi and Provasoli 1959; Davis and Guillard 1958), phytoplankton changes along a wavelength may influence the other levels of the food web.

Cases 2 and 3 consider swimming organisms. Fig. 3 is an example of the computer-generated swimming paths resulting from the interaction of the semidiurnal internal tide and the diurnal vertical migration of phytoplankters. The organisms swim at  $2.0 \text{ m hr}^{-1}$  during all directed swimming except down-



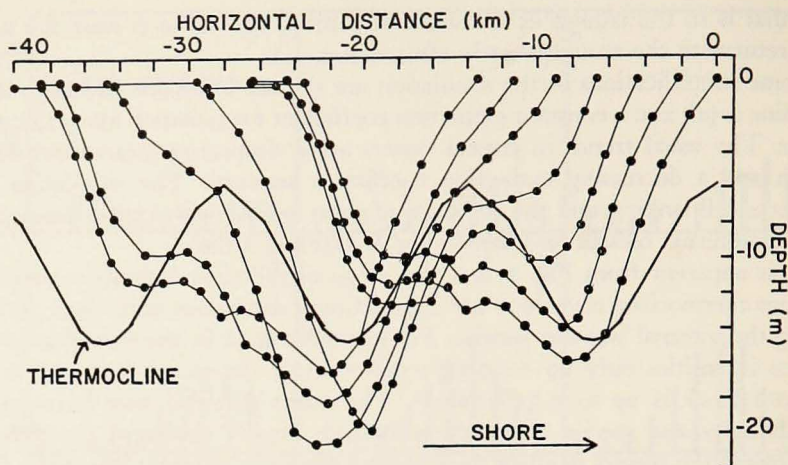


Figure 3. The paths of organisms ( $x, z$  points; hourly intervals) swimming ( $2.0 (1.0) \text{ m hr}^{-1}$ ) vertically in the current systems derived from a semidiurnal internal tide. The horizontal axis is obtained by adding the phase speed of the wave to the horizontal water particle velocity. The seven example organisms are simultaneously released at the surface from positions between 0 and  $-14 \text{ km}$ .

ward below the thermocline when the swimming speed is  $1.0 \text{ m hr}^{-1}$ . The semidiurnal internal tide modeled in this figure has an amplitude of  $4.5 \text{ m}$  with a mean thermocline depth ( $-10.5 \text{ m}$ ) such that the phase speed is  $1.1 \text{ km hr}^{-1}$ . The horizontal distance of an organism is computed by adding the constant phase speed to the variable horizontal component of the orbital motion from equation (4) or (6). This procedure spreads the paths of the seven example organisms that are simultaneously released at the surface from positions between 0 to  $-14 \text{ km}$ . The addition may be interpreted as superimposing a steady uniform current to render the progressive internal wave stationary. The vertical axis is the depth axis and the combination of vertical swimming speed and vertical component of orbital motion controls the vertical position of the organism. The dark wavy line represents the position of the thermocline at time zero as it is influenced by the internal tide. The effect of the internal tide's horizontal component of motion is seen in the bending of the paths. The effect of the internal tide's vertical component of motion is seen in the different gap size along a path between the successive dots representing 1 hr intervals.

Fig. 4 is a plot of the trajectories of the 0 km (right) and 7 km (left) starting positions in Fig. 3 drawn on a real horizontal distance axis. The zero points for the crest and trough graphs mark geographic positions that are occupied simultaneously by anchored platforms 7 km apart along the  $x$  axis. The  $x, z$  positions of a phytoplankter swimming in a current regime generated by a semidiurnal internal tide are presented every hour for 24 hr. Figs. 5 through

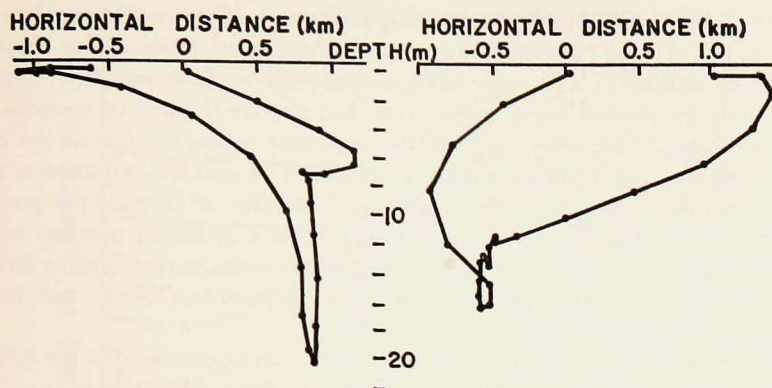


Figure 4. The trajectories of organisms swimming in an internal tide. The real space ( $x, z$ ) positions of the 0 km (right) and the 7 km (left) organism starting positions in Figure 3 are depicted over a 24 hr interval.

13 discussed below consider internal tides with a range of characteristics (amplitude; mean thermocline depth) interacting with organisms with a range of behavioral and physiological characteristics in a way similar to Figs. 3 and 4.

Case 2 includes organisms that do not cross the thermocline either because it is beyond their reach or because of an aversion to shear or to temperature

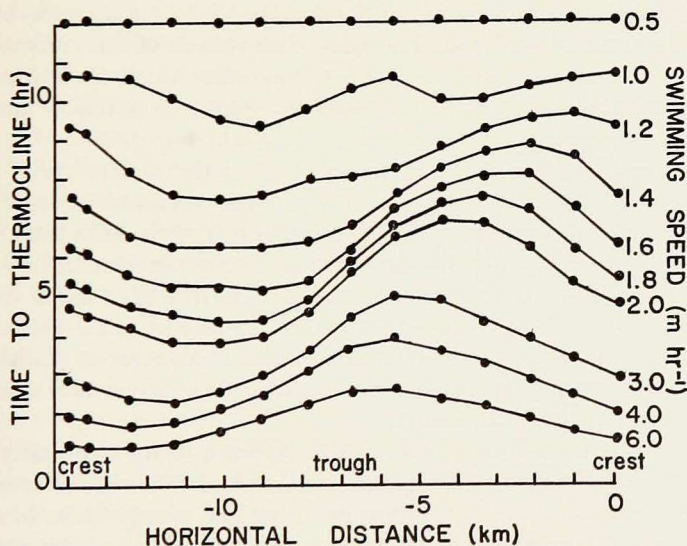


Figure 5. Case 2: Motile ( $0.5-6.0 \text{ m hr}^{-1}$ ) phytoplankton swimming times to the thermocline. The organisms start simultaneously from various positions (hourly intervals of period) along the wavelength of a semidiurnal internal tide. ( $a = 4.5 \text{ m}$ ;  $d = -10.5 \text{ m}$ ).



change. Since the organism's swimming ability is ineffective compared to the physically generated horizontal currents, the horizontal relationships observed are similar to Case 1. The organism's vertical position, however, is determined not merely by vertical water movements, but also by the ability to swim. In the hypothetical migration modeled, the organism swims up toward the light at sunrise and down from the surface at sunset. The upward migration is used to position the organism at some optimum intensity or is merely a positive phototactic response. The downward migration is a geotactic response representing an adaptation to utilize nutrient rich water near the thermocline formed by the regeneration of organic matter or by turbulence (Woods and Wiley 1972).

The behavior modeled in the next two figures can be described in the following way. The organism starts at the surface and swims down at sunset until it reaches the thermocline. Twelve hours are allowed for this migration. If the thermocline is reached before 12 hr have elapsed, the organism follows the thermocline movements exposed to the current regime above the thermocline. At the end of 12 hr (sunrise) all of the organisms begin an upward migration which is again allotted 12 hr time. If the surface is reached before 12 hr have elapsed, the organism is kept at the surface exposed to the same horizontal current regime.

Fig. 5 is a plot of the elapsed time to a thermocline oscillating as in Fig. 3 but with the organism paths stopping at the thermocline. Different organisms exhibiting a range of swimming speeds are represented. The internal tide with a wavelength of 14.15 km is again characterized by an amplitude of 4.5 m centered at a depth of  $-10.5$  m. The rates of movement which apply to phytoplankton are between  $0.0$  and  $2.0$  m  $\text{hr}^{-1}$ . The other speeds are characteristic of small zooplankton. Fig. 6 gives the swimming times required for the return migration to the surface by the organisms shown in Fig. 5.

Since swimming time to the thermocline or to the surface varies along a wavelength, Figs. 5 and 6 suggest a time dependent patchiness at these boundaries. For most of the swimming speeds the thermocline is more patchy before midnight than after midnight. Similarly, the surface is more patchy before noon than after noon. The exact time and spatial patterns in Figs. 5 and 6 vary with the swimming speed. The trends in the graphs are specific to the wave characteristics (amplitude, mean thermocline depth) used. This suggests that the effect on the different swimming speeds varies with the time of the year since wave characteristics vary with the seasons.

In addition to the effects of differential exposure to light intensity and to the nutrient pool along the wavelength, exertion is also considered as a physiological factor in this case. If it is assumed that the energy spent in directed swimming is lost to productivity, each species has positions along the wave form that require less directed swimming to perform the migration aims. This has the potential of producing a patchy distribution along the wavelength. If



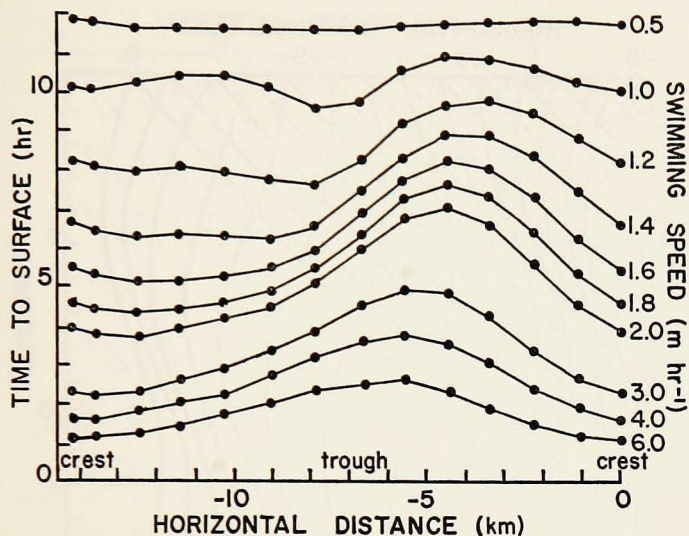


Figure 6. Case 2: Motile ( $0.5 - 6.0 \text{ m hr}^{-1}$ ) phytoplankton swimming times to surface. The organisms start simultaneously from positions reached after 12 hr of combined downward migration (Figure 5) and thermocline riding.

swimming speed is related to the size of the organism (Cushing 1959), a changing size spectrum of organisms is possible along a wavelength. These patterns have significance for other levels of the food web in terms of both the absolute amount of food available at any one place and the size of the "package" in which most if it occurs.

Organisms always above the interface also form physically caused aggregations. If the shape of an equal area plane section of water between the surface and the interface is considered during the passage of an internal tide, it demonstrates changes with the stage of the wave. The shape of the section over the crest has a higher dimensional ratio of  $x/z$  than the same section over the trough (Fig. 7). If a steady state population of organisms is confined to the surface over a period of the wave, a high density occurs over the trough compared to a low density over the

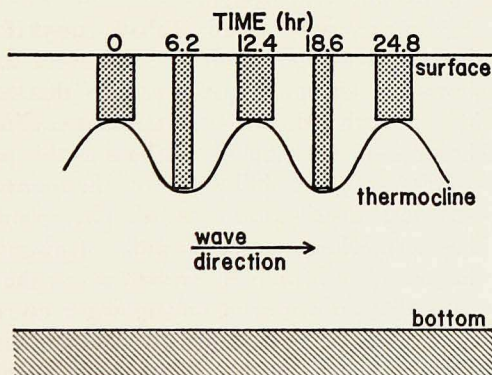


Figure 7. The water column convergence and divergence at a geographic location through time shown by equal area sections above the crest and trough of a semidiurnal internal tide.

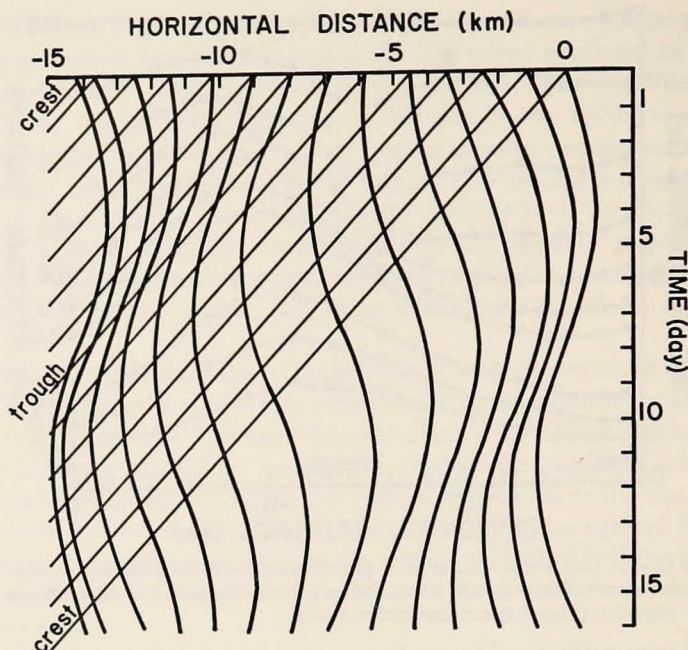


Figure 8. The aliased patterns of surface phytoplankton. The surface patterns perpendicular to shore ( $x$  axis) are sampled at 24 hr intervals for 16 days. The initial organism positions are at hourly intervals of the period. The oblique lines connect the locations of the various initial organism positions along the wavelength of an internal tide ( $a = 4.5$  m;  $d = -10.5$  m) at the time of each successive sample.

crest because of the changing  $x$  dimension in the plane section. The patch reforms for every trough.

This pattern is aliased (Tabata 1965) if samples are taken perpendicular to shore over a wavelength distance every 24 hr for a number of days. Fig. 8 shows the changing spatial pattern that is observed each day over 16 days. Migrators that do not cross the thermocline and that return to the surface at the time of the sample contribute to this pattern.

In Case 3, the ability to cross the thermocline has a profound effect on the horizontal distribution of motile phytoplankton. The current velocities above the thermocline may be an order of magnitude greater than those below and the current direction is reversed across the interface. A high probability thus exists that an organism undergoing a diurnal vertical migration through the thermocline will move spatially at night relative to the water parcel it occupied during the previous day. The overall extent of the movement depends on the swimming speed of the plankter, the mean thermocline depth of the wave, and the amplitude of the wave. Each of these factors is treated separately to determine its relative effect.



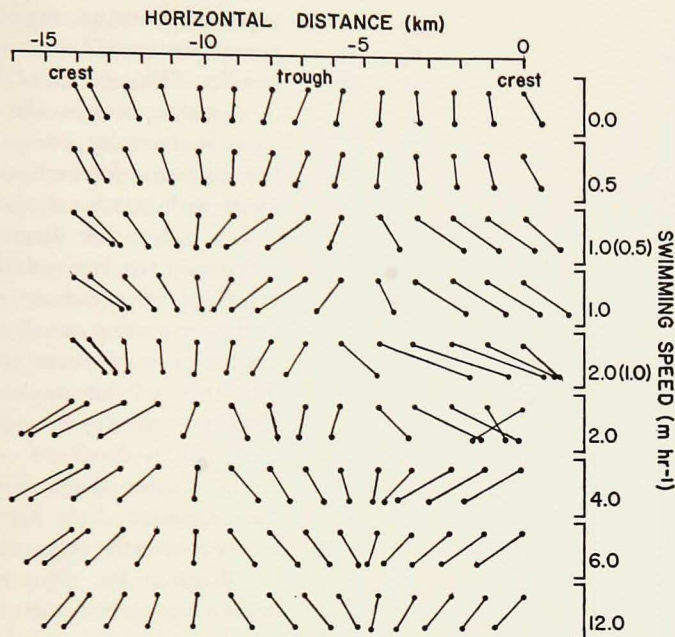


Figure 9. Case 3: A series of bar diagrams showing how the spatial distributions of diurnally vertically migrating organisms swimming at different speeds are affected after 24 hr by the current systems associated with a semidiurnal internal tide ( $a = 4.5$  m;  $d = -10.5$  m). These organisms are capable of crossing the thermocline.

In the following discussion, a temperature effect could be considered. The work of Hand et al. (1965) with *Goniaulax polyedra* and *Gymnodinium* sp. suggests that cells exposed to a  $2^{\circ}\text{C}$  temperature change over a 30 minute period do not lose their motility. Steeper gradients, however, do lead to paralysis. Although the present model considers a two-layer ocean, the temperature gradients in the natural environment are less steep than the modeled situation and are spread through a segment of the vertical column (Woods 1968). Case 3 is treated under the assumption that migrating phytoplankton do cross small temperature gradients. The organisms are thus allowed to cross the interface despite the large temperature gradient in the model.

The next two types of graphs consider a computer simulation that combines the internal tide equations for both layers with the swimming behavior of diurnally vertically migrating phytoplankters (day-night, 12-12 hr). The first is a series of bar diagrams with the top points of each graph representing the starting positions. The points are spaced at hourly intervals along the wavelength except for the last point which represents the next crest. The lower points represent the horizontal position these same organisms occupy 24 hr later. The bar diagram marked 0.0 demonstrates the spatial distribution that is



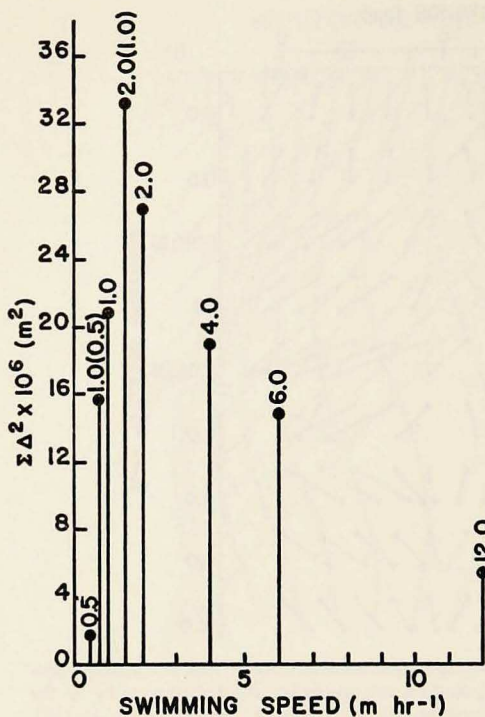


Figure 10. Case 3: The sums of the squared changes in spatial position ( $x$  axis) after 24 hr exhibited by each swimming speed in Fig. 9.

expected from an organism that never ventured below the thermocline. The effect of a migration which crosses the thermocline is seen by comparing the bar diagrams for each swimming speed with 0.0 bar diagram.

At these speeds, however, there is a tendency for a reversal of the pattern in 0.0 for the physical and biological conditions used in Fig. 9. The slower speeds (0.0–2.0 m hr<sup>-1</sup>) are characteristic of phytoplankton (Eppley et al 1968) while the faster speeds (4.0–12.0 m hr<sup>-1</sup>) are representative of small zooplankton (Cushing 1959). Most zooplankton, however, reverse the migration behavior of the phytoplankton and are near the surface at night and at depth in the daytime.

Another way to present the effect of the interaction in Fig. 9 is to compute the square of the distance each organism represented within a bar diagram is from its starting position after 24 hr. The squared distances are summed for each bar diagram. One number then represents a bar diagram and the comparison of these numbers demonstrates the differential effect of a certain wave. Fig. 10 presents this calculation for the information in Fig. 9. Patchiness occurs for all swimming speeds which allow the plankter to reach the thermocline, but the organisms that swim at 2.0 (1.0) m hr<sup>-1</sup> are most affected by the modeled wave.

Fig. 9 is a bar diagram series comparing the horizontal patterns exhibited by organisms with different swimming speeds migrating under the same wave conditions. The internal tide modeled has an amplitude of 4.5 m and a mean thermocline depth of -10.5 m. At the slower speeds (0.5 m hr<sup>-1</sup>) the organism does not or just barely crosses the thermocline. The bar diagram for 0.5 m hr<sup>-1</sup> thus bears a strong resemblance to 0.0. As the swimming speed increases (1.0–4.0 m hr<sup>-1</sup>), the amount of distortion from 0.0 increases and patches apparently form along a wavelength. Finally, the fastest swimming speeds on the graph (6.0–12.0 m hr<sup>-1</sup>) show a decrease in distortion from the 0.0.

As in Case 2, the organisms represented in Figs. 9 and 10 do not all reach the surface at the same time. In fact, the migrations with constant swimming speeds all have positions along the wavelength where the organisms never reach the surface. The initial positions with this tendency for patchiness are between the trough and the following crest. These organisms are not lost to the population, but return to the surface in a few days. All organisms that display migrations with speed reductions after descent through the thermocline eventually return to the surface each day. The 2.0 (1.0) and 1.0 (0.5) m hr<sup>-1</sup> swimming speeds are used in the next two graphs because of the maximum effect on the former in Fig. 10 and because the comparison is limited to the surface.

Fig. 11 shows the effect of changing the mean thermocline depth of an internal tide

with an amplitude of 4.5 m on the spatial distribution achieved by organisms swimming at two different speeds, 2.0 (1.0) m hr<sup>-1</sup> and 1.0 (0.5) m hr<sup>-1</sup>. According to the graph, the effect of the mean thermocline depth depends on the swimming capabilities of the specific plankter under consideration. The organisms with a speed of 1.0 (0.5) m hr<sup>-1</sup> require a relatively shallow thermocline (-10.5 m) in order to demonstrate a horizontal movement relative to 0.0 (compare  $d = -7.5$  m with  $d = -13.5$  m). As the mean thermocline depth deepens, the effect on the spatial distribution decreases. The outcome is similar for faster swimming organisms except that the effective range of mean thermocline depths is increased. This information considered with field measurements off southern California suggests that the mean thermocline depth is within effective range of phytoplankton only from April through November and only within 200 km of shore.

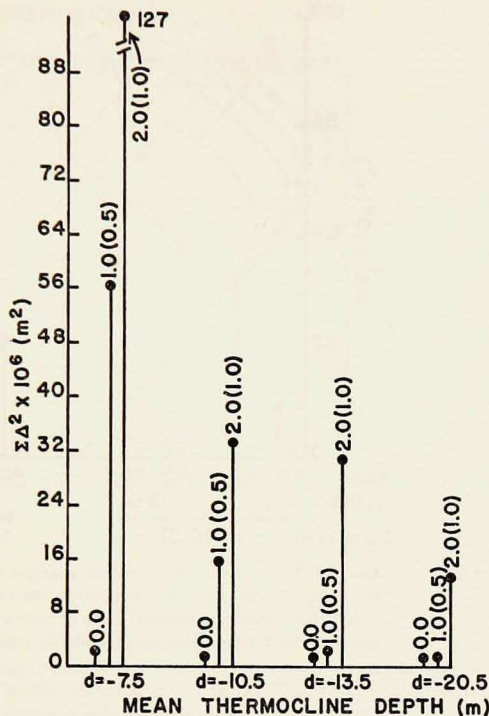


Figure 11. Case 3: The sums of the squared changes in spatial position ( $x$  axis) exhibited along a wavelength after 24 hr for representative swimming speeds (1.0 (0.5) m hr<sup>-1</sup>; 2.0 (1.0) m hr<sup>-1</sup>). The semidiurnal internal tide ( $a = 4.5$  m) is considered at various mean thermocline depths.



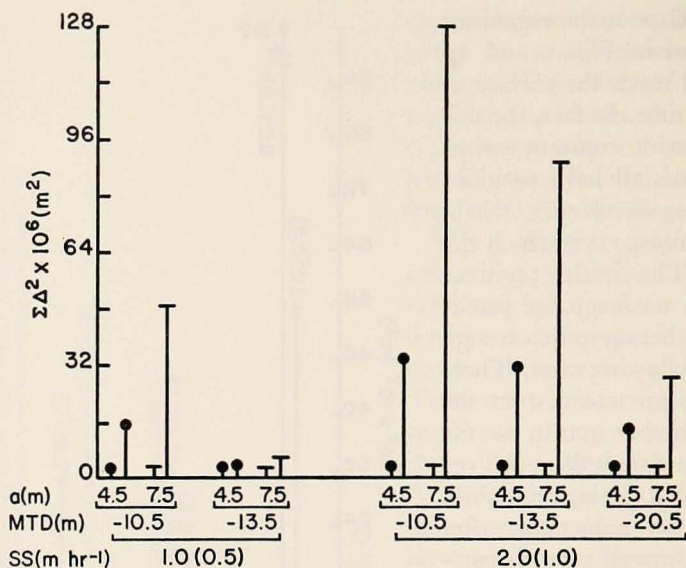


Figure 12. Case 3: The sums of the squared changes in spatial position ( $x$  axis) exhibited along a wavelength after 24 hr for representative swimming speeds ( $1.0$  ( $0.5$ )  $m\ hr^{-1}$ ;  $2.0$  ( $1.0$ )  $m\ hr^{-1}$ ). Semidiurnal internal tides of various amplitudes are considered at different mean thermocline depths. The left line above each amplitude designation is the  $0.0$  standard.

Fig. 12 considers the effects of different amplitude waves at three mean thermocline depths. An increase in amplitude increases the relative horizontal spatial movement for a given thermocline depth. This is expected from the increased ellipse size which accompanies an increase in amplitude (Fig. 2). Larger amplitude waves also increase the range of mean thermocline depths that are effective for a given swimming speed. Since the larger amplitude makes the extreme values of the fluctuation shallower and deeper than the smaller amplitude waves, the thermocline is easier or harder to reach at certain positions along the wavelength.

If one makes the assumption that the semidiurnal internal tide and daylight maintain a constant phase relationship, the implications of the computer model through time are easily studied. The wave characteristics are an amplitude of  $4.5$  m centered at a mean thermocline depth of  $-10.5$  m. The organisms swim at  $1.0$  ( $0.5$ )  $m\ hr^{-1}$  on a 12-hr day: 12-hr night cycle. Fig. 13 is a graph of the positions of the migrating organisms sampled at 24 hr intervals for 16 days. This is accomplished by running the program with the previous day's end position as the starting position for the next day's calculation. A very strong convergence occurs with organisms effectively forming one band per wavelength near the trough by the 9th day. This graph is comparable to Fig. 8, which is a similar presentation for organisms always above the thermocline. A trend sim-

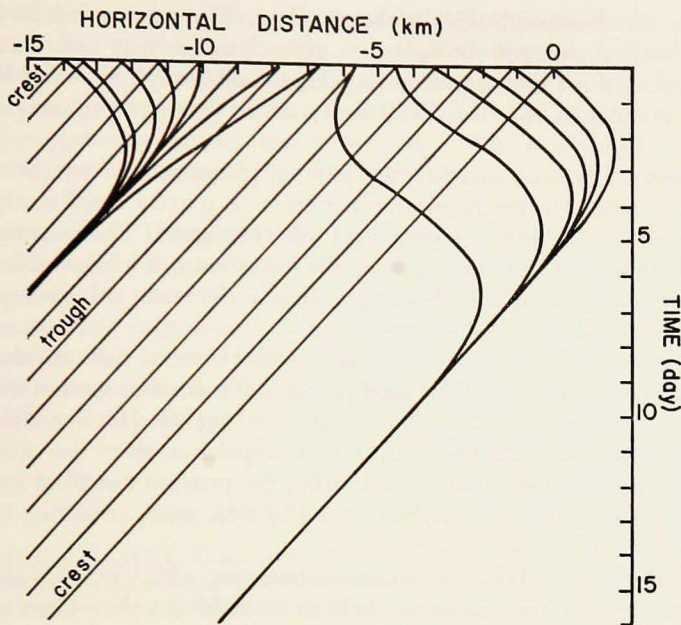


Figure 13. The surface patterns of thermocline crossing phytoplankton undergoing diurnal vertical migrations. The surface patterns perpendicular to shore are sampled at 24 hr intervals for 16 days. The stations are hourly intervals of the period. The oblique lines connect the spatial positions of the various initial sampling points along the wavelength at the time of each successive sample.

ilar to Fig. 13 occurs for the constant velocity organisms with all the original phytoplankton eventually contributing to the surface patterns.

The case of organisms that do cross the thermocline offers a very dynamic method of forming patches. In addition to the physiological effects discussed in the other cases, an actual large scale physical concentration takes place integrating the production of kilometers into hundreds of meters. The food chain implications, especially related to density of prey, may be particularly important in this case.

Despite the many studies on spatial patchiness, field data allowing an unambiguous test of the models are not known to the author. The most direct approach requires the joint use of thermistor chains that monitor thermocline oscillations and phytoplankton sensors that allow repeated measurements along a transect perpendicular to shore. The latter is accomplished by fluorimeters (Lorenzen 1972) or airborne chlorophyll sensors (Arvesen et al<sup>4</sup> 1971). Another approach may utilize the outbreaks of dinoflagellates (red tides) that are

4. Arvesen, J. C., J. P. Millard, and C. C. Weaver. 1971. Remote sensing of chlorophyll and temperature in marine and fresh waters. Ames Res. Center, NASA, Moffet Field, Calif. (Unpublished manuscript).



frequently associated with shallow thermoclines. The relationship between the stage of internal tide and daylight at a given location may contribute to the concentration of red tide organisms. Again, a combined physical and biological sampling program is required. Field tests such as these are planned.

*Conclusions.* The isolation of a single physical phenomenon from the spectrum of motions existing in the physical environment is a gross simplification. This is especially the case when an ecological role is assigned. The present attempt is partially redeemed by the energy and the consistency of internal tides. There are times when the dominant shearing motion in the water column is produced by the internal tide.

The water motions accompanying the modeled internal tides are also simplified. Field current measurements rarely show uniform water motion with depth following a sinusoidal velocity change over tidal periods (Defant 1961). The theoretical approximation, however, is an extrapolation from the equations of motion descriptive of internal tides. Ideally, the patterns described are a pure signal upon which the other motions caused by tide, wind, or surface waves are imposed as variable noise.

The phytoplankton behavior patterns interacting with internal tides suggest possible sources for the patchiness evident in field samples. Cases are constructed for both non-motile and motile forms based on the physiology of the organisms responding to differential incident radiation, nutrients, or exertion along the wavelength. Actual physical concentration is also described. On a small scale the fluxes above the thermocline act on organisms in that layer. On a larger scale the water motions above and below the thermocline act on motile organisms that traverse the interface. The patchiness refers not only to quantitative changes in phytoplankton abundance but also to species changes resulting from differing adaptation capabilities or from physical segregation of organisms based on their different swimming speeds. Chemical changes may also occur in the composition of a given species depending on light intensity or spectrum.

Though phytoplankton dominate the present discussion, other levels of the food web are also affected. The role of phytoplankton as food for herbivores leads to speculations on the impact of spatial segregation of the quantity, kinds, and quality of food on the distribution of zooplankton and other herbivores. It is certain that patchiness in prey will yield a corresponding patchiness in predators. The effect is amplified by the selectivity of predators for prey size and shape and by the dietary requirements of a predator for a successful life cycle.

The direct interaction between zooplankton and internal tides is only briefly mentioned. Faster swimming speeds of larger zooplankton minimize most of the vertical effects of the internal tides found near the coast. Even these relatively shallow waves, however, have a significant effect on the horizontal position of migrating zooplankton which cross the thermocline. Open ocean ap-

plications of the model require a new set of physical values involving deeper mean thermocline depths and, possibly, larger amplitude waves. This situation offers less interest for direct phytoplankton dynamics since physiological mechanisms mainly apply. However, fertile speculation is initiated on the possibility of extensive zooplankton-internal tide interaction. These relationships may have an effect on phytoplankton patterns through grazing.

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## REFERENCES

- ARMSTRONG, F. A. J., and E. C. LAFOND  
1966. Chemical nutrient concentrations and their relationship to internal waves and turbidity off southern California. *Limnol. Oceanogr.* 11: 538-547.
- BALL, T. F., and E. C. LAFOND  
1961. Turbidity of water off Mission Beach, p. 37-44. *In* J. Tyler (ed.), *Physical aspects of light in the sea*. Univ. of Hawaii Press, Honolulu.
- CAIRNS, J. L.  
1966. Depth and strength of the seasonal thermocline in shallow water off southern California. *U.S.N. Symp. Military Oceanogr.* 3rd. v. 2: 27-28.
- CAIRNS, J. L.  
1967. Asymmetry of internal tidal waves in shallow coastal waters. *J. Geophys. Res.* 72: 3563-3565.
- CAIRNS, J. L.  
1968. Thermocline strength fluctuations in coastal waters. *J. Geophys. Res.* 73: 2591-2595.
- CAIRNS, J. L., and E. C. LAFOND  
1966. Periodic motions of the seasonal thermocline along the southern California coast. *J. Geophys. Res.* 71: 3903-3915.
- CAIRNS, J. L., and K. W. NELSON  
1968. Seasonal characteristics of the seasonal thermocline in shallow coastal water. *U.S.N. Symp. Military Oceanogr.* 5th v. 1: 38-55.
- COLEBROOK, J. M.  
1960. Plankton and water movements in Windermere. *J. Anim. Ecol.* 29: 217-240.
- CUSHING, E. H.  
1959. On the nature of production in the sea. *G.B. Min. Agr., Fish. Food. Fish. Invest. Ser. 2* 22: 23-40.



- DAVIS, K. C., and R. R. L. GUILLARD  
1958. Relative value of ten genera of micro-organisms as food for oysters and clam larvae. Fish. Bull. 58: 293-304.
- DEFANT, ALBERT  
1961. Physical oceanography. v. 2. Pergammon, 589 p.
- EPPLEY, R. W., OSMUND HOLM-HANSEN, and J. D. H. STRICKLAND  
1968. Some observations on the vertical migration of dinoflagellates. J. Phycol. 4: 333-340.
- FOGG, G. E.  
1966. Algal cultures and phytoplankton ecology. Univ. Wis. 126 p.
- FUKS, V. R., and I. M. MESHCHERYAKOVA  
1959. Effect of internal tidal waves on the diurnal vertical migration of plankton. Izv. Tikhookeanskogo Navchno-Issledovatel' Skogo Inst. Rhybnogo Khozyaistra: Okeanogr. 47: 3-35.
- HAND, W. G., P. A. COLLARD, and D. DAVENPORT  
1965. The effects of temperature and salinity change on the swimming rate in dinoflagellates, *Goniaulax* and *Gymnodinium*. Biol. Bull. 128: 90-101.
- HARDY, A. C., and E. R. GUNTHER  
1935. The plankton of South Georgia whaling grounds and adjacent waters 1926-27. Discovery Rep. 11: 1-146.
- HASLE, G. R.  
1950. Phototactic vertical migration in marine dinoflagellates. Oikos 2: 162-175.
- HASLE, G. R.  
1954. More on phototactic diurnal migration in marine dinoflagellates. Nytt. Mag. Biol. 2: 139-147.
- HAURWITZ, BERNARD  
1950. Internal waves of tidal character. Trans. Amer. Geophys. Union. 31: 47-52.
- JERLOV, N. G.  
1968. Optical oceanography. Elsevier. 194 p.
- KAMYKOWSKI, DANIEL  
1973. Some physical and chemical aspects of the phytoplankton ecology of La Jolla Bay. Ph. D. thesis. Univ. of Calif., San Diego, 269 p.
- LAFOND, E. C.  
1963. Internal waves - Pt. 1. p. 731-751. In M.N. Hill (ed.), The sea, v. 1. Interscience.
- LORENZEN, C. J.  
1972. Continuity in the chlorophyll distribution of surface chlorophyll. Jour. du Conseil 34: 18-23.
- MARMELSTEIN, A. D.  
1970. The effect of light intensity on the organic composition of marine phytoplankton diatoms. Ph.D. thesis, Oregon State Univ. 51 p.
- MULLIN, M. M.  
1963. Some factors affecting the feeding of marine copepods of the genus *Calanus*. Limnol. Oceanogr. 8: 239-250.

SHIRAISHI, K., and LUIGI PROVASOLI

1959. Growth factors as supplements to inadequate algal foods for *Tigriopus japonicus*.  
Tohoku J. Agr. Res. 10: 89-96.

SMAYDA, T. J.

1970. The suspension and sinking of phytoplankton in the sea. *Oceanogr. Mar. Biol. Ann. Rev.* 8: 353-414.

TABATA, S.

1965. Variability of oceanographic conditions of Ocean Station P in the Northeast Pacific Ocean. *Trans. Roy. Soc. Can.* 3: 367-418.

WALLEN, D. G., and G. H. GEEN

1971. The nature of the photosynthate in natural populations in relation to light quality. *Mar. Biol.* 10: 157-168.

WOODS, J. D.

1968. CAT under water. *Weather* 23: 224-236.

WOODS, J. D., and R. L. WILEY

1972. Billow turbulence and ocean microstructure. *Deep-Sea Res.* 19: 87-122.