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## Possible interactions between plankton and semidiurnal internal tides. II. Deep thermoclines and trophic effects

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### ABSTRACT

Previous results of a computer model suggested a number of possible interactions between semidiurnal internal tides and phytoplankton. One extension considers a phytoplankton grid (swimming speed  $1-2 \text{ m h}^{-1}$ ) that is initially distributed at sunset in the upper layer of a water column characterized by a relatively deep mean thermocline depth (25 m). The organisms undergo a diurnal vertical migration while the water column is simultaneously disturbed by successive semidiurnal internal tides. The deeper members cross the thermocline and consequently form subsurface patches that daily change location, size, shape, and contributing members. This patch variability contrasts with the predictable patches that form when the computer simulation is applied to migrating organisms that cross a relatively shallow mean thermocline (10 m) and that return to the surface during the day.

Secondly, a community of organisms composed of species capable of different swimming speeds undergoes diurnal vertical migrations through a water column with a relatively shallow mean thermocline depth (10 m) that is disturbed by successive semidiurnal internal tides. The phytoplankton ( $1-2 \text{ m h}^{-1}$ ) are at the surface during the day; the zooplankton ( $5-100 \text{ m h}^{-1}$ ) are at the surface at night. Each swimming speed attains a population convergence at a unique rate or geographic location compared to the other swimming speeds. Both phytoplankton and zooplankton form patches through the modeled mechanism and the phytoplankton patches are probably reinforced by reduced grazing pressure.

### 1. Introduction

Kamykowski (1974) suggested a number of possible interactions between the

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physical properties of semidiurnal internal tides and phytoplankton physiology and behavior. One case concerned swimming phytoplankton that crossed the thermocline during diurnal vertical migrations that initiated and terminated at the sea surface. On crossing the thermocline, the phytoplankton moved from the relatively rapid horizontal flows above the thermocline to the slower opposing horizontal flows below the thermocline. The phytoplankton aggregated into patches after successive diurnal vertical migrations through these current regimes.

The applicability of this interaction to the oceans partly rested on whether phytoplankton crossed natural temperature gradients. Kamykowski and Zentara (1976) confirmed this ability from literature data and from original experiments in a 10 m tower tank (Aquatron Facility, Dalhousie University). In the laboratory experiments, *Cachonina niei* crossed a 5°C gradient during its diurnal vertical migration.

Other possible interactions between semidiurnal internal tides and organisms capable of crossing the thermocline during diurnal vertical migrations are considered. The first extension investigates the dynamics of subsurface phytoplankton interacting with a thermocline beyond the reach of surface organisms that descend at speeds of 1-2 m h<sup>-1</sup> for 12 hours. The second extension compares the spatial positions achieved by phytoplankton and zooplankton that simultaneously swim through the same internal wave.

## 2. Methods

A computer model (Fortran IV) that simulates the physical properties of semidiurnal internal tides is described in Kamykowski (1974). An iterative calculation (CDC 6400 computer) is performed on a set of equations that compute the horizontal and vertical currents above and below the thermocline at successive positions along a semidiurnal internal wave. The currents computed for the organisms' coordinates, together with an imposed rate of planktonic diurnal vertical migration, yield a trajectory of an organism's position in the water column over a 24 hour period. The equations applied previously overestimate the horizontal current velocities by about 25%. The general results are not affected, but the specific convergences change in rate of formation and in position.

In the first part of this paper the corrected computer simulation is adapted to study the interaction between the semidiurnal internal tide and the diurnal vertical migration of a phytoplankton grid composed of 52 organisms. The grid is initially distributed between the sea surface and the thermocline at sunset. The wave characteristics in the two-layered ocean are determined by a water depth of 200 m, a mean thermocline of 25 m and a wave amplitude of 5 m. The layer above the thermocline is considered nutrient depleted.

The initial phytoplankton grid ( $x$ : 13 positions;  $z$ : 4 positions) is followed for 15 days through successive diurnal vertical migrations that are synchronized with

the daylight cycle (12:12 h). The  $x$ -axis represents a transect that is perpendicular to shore; the length of the transect is determined by the wavelength of the semi-diurnal internal tide. The  $z$ -axis represents the water column. The initial vertical position of each organism is derived from the equation,

$$z_w = z_m + \frac{z_m a}{d} \text{SIN} \left( kx - \frac{\pi}{2} \right) \quad (1)$$

where  $z_w$  is the depth of the  $x$ -position organism centered around a mean depth  $z_m$ ,  $a$  is the amplitude of the wave,  $d$  is the mean thermocline depth and  $k$  is the wave number ( $2\pi/\lambda$ ). The four values that are substituted for  $z_m$  are 0, 8, 16, and 24 m. The application of (1) for each  $z_m$  to various  $x$  positions traces the depth that isotherms would occupy along a natural wave form. The grid of phytoplankton are thus initially placed on a series of hypothetical isotherms (8 m intervals) throughout the water column above the thermocline. These isotherms are hypothetical since they do not really exist in the two-layered ocean model.

The phytoplankton swim at a constant swimming speed of 1 or 2 m h<sup>-1</sup>. They begin their descent at sunset and continue downward for 12 hours. The ascent begins at sunrise and continues for 12 hours or until the organisms reach the surface. At the surface, the organisms experience horizontal motion, but display no further vertical displacement until their swimming effort is directed downward. The daily coordinates at sunset are discussed in all of the grid comparisons.

In the second part of this paper, the food web implications of the computer simulation are investigated. The wave characteristics of the semidiurnal internal tide are identical to those modeled in Kamykowski (1974); i.e., a water depth of 200 m, a mean thermocline depth of 10.5 m and a wave amplitude of 4.5 m. Phytoplankton that swim at speeds of 1 or 2 m h<sup>-1</sup> migrate to the surface during the day and to depth at night. Zooplankton that swim at speeds of 5, 10, 15, 20, 25, 50 and 100 m h<sup>-1</sup> (Hardy and Bainbridge, 1954; Cushing, 1959) undergo a diurnal vertical migration that is reversed from the phytoplankton; i.e., the organisms are at depth during the day and at the surface at night (Vinogradov, 1970). The five fastest swimming speeds attributed to zooplankton would carry the organisms through the bottom of the modeled ocean. The greatest depth of downward migration is therefore limited to the 10<sup>-8</sup> isolume (Kampa and Boden, 1954; Clarke and Backus, 1956). A depth of 150 m is representative of coastal waters (Secchi depth ca. 15 m).

The migrations of all swimming speeds occur along approximately the same transect perpendicular to shore, but there is a difference in the absolute geographic starting positions for phytoplankton and zooplankton. The phytoplankton begin their migration from evenly spaced surface positions relative to the crest of the wave at sunset; the zooplankton begin their migration from evenly spaced surface positions relative to the crest of the wave at the following sunrise. Since the wave

has a period of 12.4 h, i.e., 0.4 h longer than the 12 h interval between sunset and sunrise, the  $x$ -coordinates of the initial phytoplankton and zooplankton positions are offset by 450 m. This offset of the starting positions does not affect the following discussion.

### 3. Results and discussion

*Deep thermocline.* Kamykowski (1974) considered the interaction between the currents associated with semidiurnal internal tides and motile phytoplankton that begin the descent of a diurnal vertical migration from the surface at sunset. The organisms cross a shallow mean thermocline (10 m) while swimming away from the surface through the night, begin an upward migration at sunrise, recross the thermocline and return to the surface during the day. A phytoplankter that is capable of swimming at  $1 \text{ m h}^{-1}$  and that returns to the surface each day requires a mean thermocline depth of less than 12 m to show a significant response to the current changes incurred on crossing the thermocline. Mean thermocline depths of less than 12 m, at least off Southern California, ordinarily occur only near the coast during the summer. These constraints prompted an investigation of phytoplankton that were not required to return to the surface.

Fig. 1 displays the positions of a grid of organisms on an  $x$ -axis that represents an offshore transect perpendicular to the coast and on a  $z$ -axis that represents the depth of the water column. The mean thermocline depth is 25 m. The organisms begin their migration by swimming downward at sunset with a constant speed of  $1 \text{ m h}^{-1}$  from the initial positions given at Day 0 of Fig. 1. Their positions at sunset are plotted after 3, 6, 9, 12, and 15 days of diurnal vertical migration through the currents associated with the modeled semidiurnal internal tide.

The general trend of the result is apparent by the third day. Positions 1-26 designate organisms that do not reach the thermocline on their downward migrations. These phytoplankton maintain approximately the same mean geographic position from day to day. The horizontal movement they do show in Fig. 1 is in response to the sinusoidally varying currents above the thermocline that are associated with the semidiurnal internal tide (Kamykowski, 1974). The ellipse ( $x, z$ ) that a water particle describes under the influence of these currents for the modeled wave (period 12.4 h) has a major diameter ( $x$  axis) of 1.0 km.

Positions 27-52 designate organisms that cross the thermocline. These organisms generally change their mean geographic location on succeeding days. By Day 3 subsurface patches have already formed. For example, organisms 27, 28, and 29 cluster at +1 km; organisms 43, 44, and 45 at -7 km; and organisms 34, 35, 36, 37, and 38 at -16 km. As the days pass, the size, the shape, and the location of the clusters change. The organisms contributing to the clusters also change. The densest patches in Fig. 1 occur above the crest of the wave.

Fig. 1 displays the shallowest diurnal location (ca. 15 m) of the patches formed

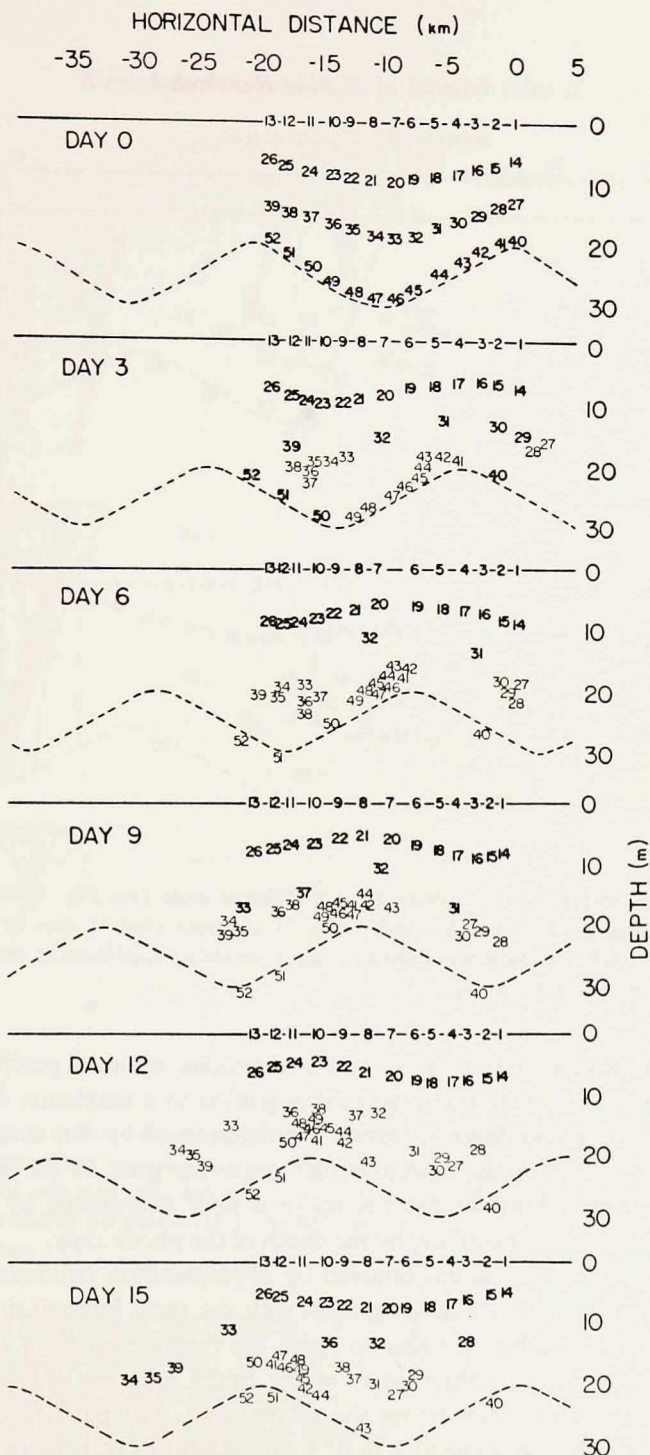


Figure 1. The spatial pattern exhibited by a grid (Day 0) of organisms (swimming speed —  $1 \text{ m h}^{-1}$ ) at sunset after 3, 6, 9, 12, and 15 days of diurnal vertical migration through the currents accompanying a modeled semidiurnal internal tide. The x-axis represents a transect perpendicular to shore; the z-axis represents the water column.

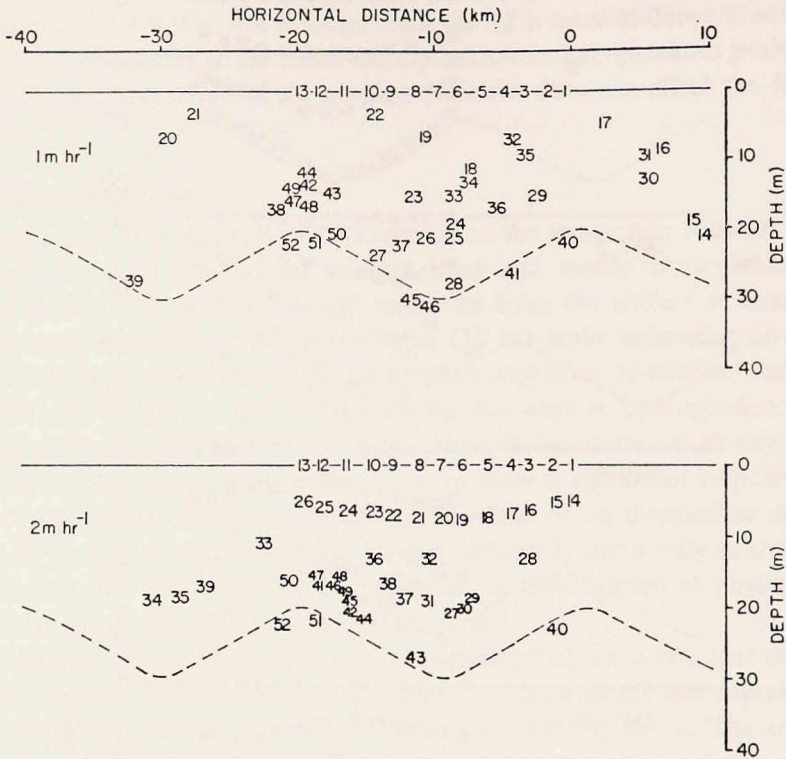


Figure 2. The spatial patterns exhibited by two different grids (see Fig. 1, Day 0) of organisms (swimming speed —  $1 \text{ m h}^{-1}$  and  $2 \text{ m h}^{-1}$ ) at sunset after 15 days of diurnal vertical migration through the currents accompanying a modeled semi-diurnal internal tide. The  $x$  and  $z$  axes are the same as in Fig. 1.

by organisms swimming at  $1 \text{ m h}^{-1}$ . The organisms within a patch migrate as a loosely organized cluster during a vertical migration to a maximum depth of about 30 m at sunrise. These depth extremes are determined by the mean thermocline depth and by the swimming speed of the organism used in the model. Deeper thermoclines form subsurface patches up to a limit determined by the migration behavior of the phytoplankton and by the depth of the photic zone.

Fig. 2 compares the positions attained by phytoplankton swimming at  $1 \text{ m h}^{-1}$  and at  $2 \text{ m h}^{-1}$  after 8 days of interaction with the same internal tide. The organisms that swim at  $2 \text{ m h}^{-1}$  are able to reach the thermocline from shallower starting positions. The bottom three rows of the initial grid are redistributed by the opposing horizontal currents across the thermocline. The patches are not as well developed at  $2 \text{ m h}^{-1}$  as those at  $1 \text{ m h}^{-1}$ , but organisms of both swimming speeds aggregate near the crest of the wave.

*Trophic effects.* Diurnal vertical migration is a common though not universal be-

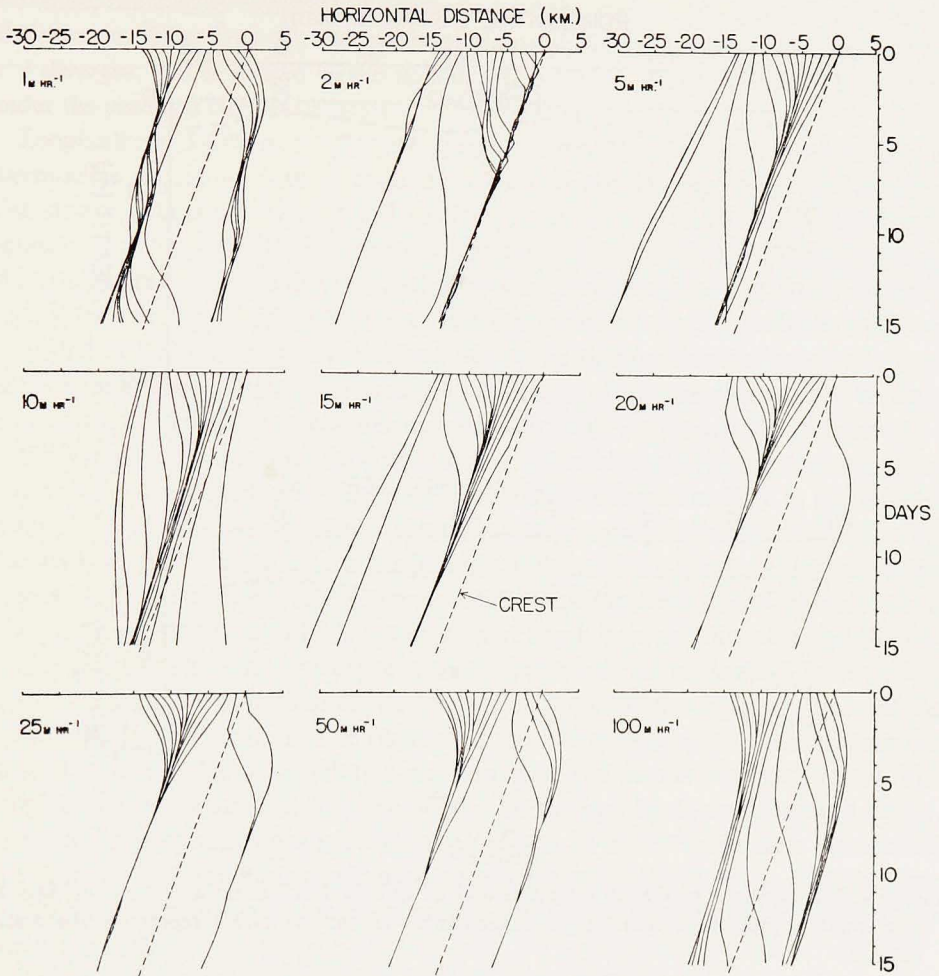


Figure 3. The convergence patterns at sunset achieved by organisms with different swimming speeds (phytoplankton — 1-2 m h<sup>-1</sup>; zooplankton — 5-100 m h<sup>-1</sup>) during 15 days of diurnal vertical migration through the same modeled semidiurnal internal tide. The x-axis represents a transect perpendicular to shore. The y-axis marks time as successive days of interaction occur.

havior pattern (Bainbridge, 1961; Banse, 1964) among zooplankton species. In this extension of Kamykowski (1974), the animals migrate through the thermocline en-route to distributing themselves at the surface at night and at depth during the day (Vinogradov, 1970). The phytoplankton follow a reversed migration.

Fig. 3 is a 15 day (y-axis) comparison of the surface positions (x-axis, transect perpendicular to shore) occupied at sunrise (5-100 m h<sup>-1</sup>) or at sunset (1-2 m h<sup>-1</sup>) by organisms that swim at different speeds. The five fastest swimming speeds (15,



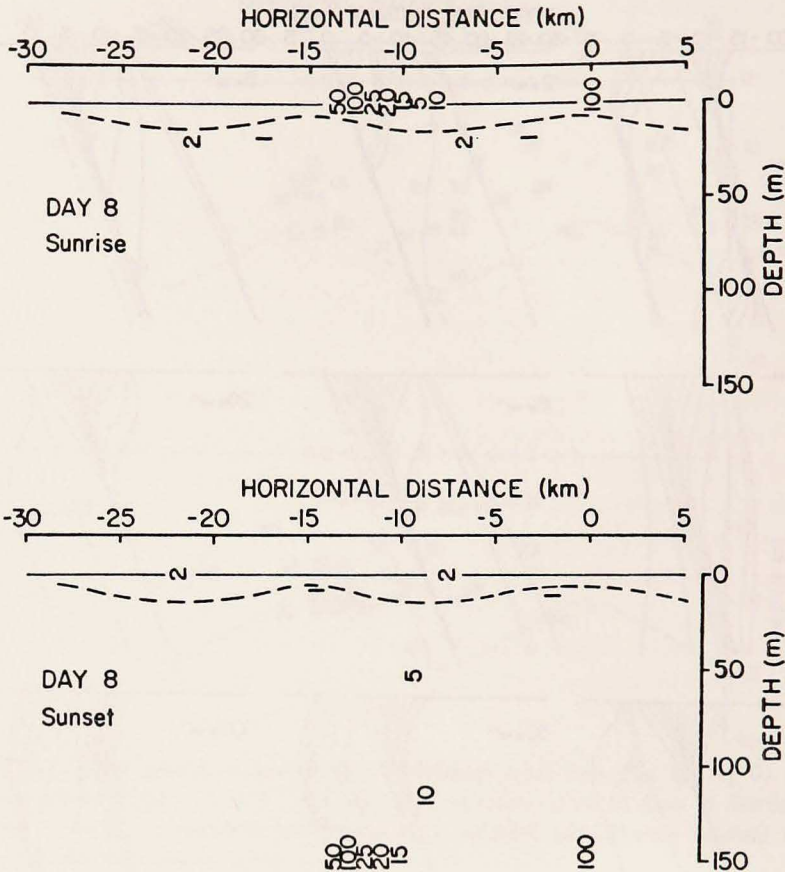


Figure 4. The positions of the convergences derived in Fig. 3 at sunrise and sunset of Day 8. The x-axis represents a transect perpendicular to shore; the z-axis represents the water column.

20, 25, 50, 100 m h) limit their descent depth to the  $10^{-8}$  isolume (150 m). All of the swimming speeds converge to specific locations along the wave form. The convergences move offshore due to the interaction between a wave period of 12.4 h and a day-night cycle of 12:12 h.

The  $1 \text{ m h}^{-1}$  and  $2 \text{ m h}^{-1}$  swimming speeds represent phytoplankton. Their diurnal vertical migration brings them to the surface during the day and to depth during the night. The rate and direction of convergence which characterize a specific starting position depend on the swimming speed and on the internal wave characteristics. Under the modeled conditions, the  $1 \text{ m h}^{-1}$  swimming speed converges more quickly (4 days) than the  $2 \text{ m h}^{-1}$  swimming speed (7 days). The  $1 \text{ m h}^{-1}$  organisms occur an average of 4 m below the surface at sunset over the trough of

the wave; the  $2 \text{ m h}^{-1}$  organisms converge near the surface at sunset over the crest of the wave. After Day 10, the patch structure of the organisms swimming at  $1 \text{ m h}^{-1}$  diverges; this is related to the inability of these organisms to reach the surface under the modeled current velocities.

Zooplankton ( $5\text{-}100 \text{ m h}^{-1}$ ) that undergo a diurnal vertical migration through a thermocline oscillating with a semidiurnal internal tide also converge into patches. The slower swimming speeds ( $5\text{-}25 \text{ m h}^{-1}$ ) are distinguished by their rate of convergence and by their relative convergence positions. The faster swimming speeds ( $50\text{-}100 \text{ m h}^{-1}$ ) differ in the rate and direction of convergence but attain approximately the same geographic location. The few positions (i.e., 4 positions at  $10 \text{ m h}^{-1}$ ) that do not converge are confined below the thermocline during certain days of their migrations. These organisms do not return above the thermocline because the vertical currents they encounter oppose their progress toward the surface.

Fig. 4 presents the two dimensional ( $x, z$ ) relationship between the phytoplankton and zooplankton depicted in Fig. 3 at sunrise and at sunset of Day 8, the interval required for all speeds to generally complete convergence. In the sunrise section the zooplankton ( $5\text{-}100 \text{ m h}^{-1}$ ) are positioned at the surface. Most of the swimming speeds aggregate between the trough and the following crest of the internal wave. The phytoplankton ( $1\text{-}2 \text{ m h}^{-1}$ ) are located at depth between the crest and the following trough. The  $1 \text{ m h}^{-1}$  organisms are located at 18 m depth. The  $2 \text{ m h}^{-1}$  organisms are located at 20 m depth. In the sunset section the depth positions of the trophic levels are reversed. The phytoplankton convergences are located near the surface at about the same relative position observed in the sunrise section. The zooplankton are located at daytime depths determined by their swimming ability. The  $5 \text{ m h}^{-1}$  organisms are located at 60 m; the  $10 \text{ m h}^{-1}$  organisms are located at 120 m; and the remaining swimming speeds are at the depth of the  $10^{-8}$  isolume at 150 m. The positions of the zooplankton are located beneath the trough and the following crest.

Figs. 3 and 4 show that all of the swimming speeds can converge into separate patches. This analysis, however, neglects directed swimming in the horizontal plane. The larger organisms probably deviate from the restricted vertical migration patterns presented in their search for food. Secondly, under the present conditions, most of the intermediate zooplankton swimming speeds converge at a location quite distant from the phytoplankton swimming speeds. If one assumes that some herbivores swim at these speeds, some members of the primary and secondary trophic levels become spatially separated.

The deep thermocline effects presented in the first section of this discussion significantly affect only the slower swimming speeds in Figs. 3 and 4. The currents associated with the internal tide still cause a geographic separation of the various swimming speeds. Though deep mean thermoclines (deeper than 25 m) decrease the concentration and the temporal stability of the phytoplankton convergences,

the stability of zooplankton convergences may be enhanced by a more uniform food distribution.

#### 4. Conclusions

A consideration of deeper mean thermocline depths (25 m) expands the temporal application of the computer models to include any relationships between the depth of the thermocline and the depth of the photic zone. Surface organisms exposed to shallow thermoclines form predictable patches. Thermoclines that are deep compared to a surface organism's swimming ability result in labile, subsurface patches among migrating organisms that cross the thermocline. The difference in patch predictability between surface and nonsurface organisms is related to the phase realignment between daylight and the semidiurnal internal tide that surface organisms experience. After convergence, surface organisms migrate through a repeating pattern of vertical and horizontal currents. They thus maintain a fixed relationship to the internal wave. In contrast, nonsurface organisms diurnally migrate through a more variable vertical column and experience a changing pattern of vertical and horizontal currents each day.

The interactions between primary producers and herbivores reacting to the same internal wave suggest another possible cause of the frequently reported negative correlation between phytoplankton and zooplankton biomass (Bainbridge, 1953). Swimming speeds characteristic of each trophic level converge at different geographic locations along a transect perpendicular to shore. In addition to a physical convergence of phytoplankton, trophic level separation based on swimming speed allows the growth of phytoplankton under reduced grazing pressure. The phytoplankton patch formation is thus reinforced. When the thermocline is deep in the water column ( $> 25$  m) the differential grazing pressure caused by zooplankton convergence may dominate the phytoplankton spatial patterns.

The developed phytoplankton concentration may be utilized by various components of the herbivore trophic level. Some fortunate representatives of the non-migrating zooplankton will be present within the phytoplankton patch; highly motile herbivores may actively search for phytoplankton concentrations; the zooplankton exhibiting intermediate activity may change the migration behavior that brought them into low phytoplankton areas and thus utilize the currents to move into the areas richer in phytoplankton (Isaacs, *et al.*, 1974). The dynamic phytoplankton patch structure hypothesized can contribute to the growth and reproductive success of herbivores by presenting a more concentrated food source than that of the ambient environment.

The spatial and temporal patch structures presented are unique to the specific wave conditions modeled. The prediction of patch structure in a given field situation requires detailed knowledge of the local characteristics of the semidiurnal internal tide.

Kamykowski (1974) stressed the limitations of these computer simulations. A single physical phenomenon, semidiurnal internal tides, is isolated from the spectrum of motions existing in the ocean. The extreme developments presented rarely occur in nature. The tendencies, however, appear probable and offer a point of view for field sampling and for the study of trophic dynamics.

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#### REFERENCES

- Bainbridge, R. 1953. Studies on the interrelationships of zooplankton and phytoplankton. *Jour. Mar. Biol. Ass. U.K.*, 32, 385-447.
- 1961. Migrations, in *The Physiology of Crustacea. II Sense organs, integration and behavior.* T. H. Waterman, ed. New York, Academic Press, 431-463.
- Banse, K. 1964. On the vertical distribution of zooplankton in the sea, in *Progress in Oceanography*, M. Sears, ed., New York, Pergamon, 2, 55-125.
- Clarke, G. L. and R. H. Backus. 1956. Measurements of light penetration in relation to vertical migration and records of luminescence of deep-sea animals. *Deep Sea. Res.*, 4, 1-14.
- Cushing, D. H. 1959. On the nature of production in the sea. Great Britain Min. of Agric. Fish and Food, Fish Inv. Series 2, 22, 23-40.
- Hardy, A. C. and R. Bainbridge. 1954. Experimental observations on the vertical migrations of plankton animals. *Jour. Mar. Biol. Ass. U.K.*, 33, 409-448.
- Isaacs, J. O., S. A. Tont, and G. L. Wick. 1974. Deep scattering layers: vertical migration as a tactic for finding food. *Deep Sea. Res.*, 21, 651-656.
- Kampa, E. M. and B. P. Boden. 1954. Submarine illumination and the twilight movements of a sonic scattering layer. *Nature*, 174, 869-871.
- Kamykowski, D. 1974. Possible interactions between phytoplankton and semidiurnal internal tides. *J. Mar. Res.*, 32, 67-89.
- Kamykowski, D. and S.-J. Zentara. 1976. The diurnal vertical migration of motile phytoplankton through temperature gradients. *Limnol. Oceanogr.* In press.
- Vinogradov, M. E. 1970. Vertical distribution of oceanic zooplankton. National Science Foundation, Washington, D.C. TT 69-59015.