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Effects of Nitrate on the Diurnal Vertical Migration, Carbon to Nitrogen Ratio, and the Photosynthetic Capacity of the Dinoflagellate *Gymnodinium splendens*

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Abstract

A non-thecate dinoflagellate, *Gymnodinium splendens*, was studied in a 12 d laboratory experiment in 2.0 × 0.25 m containers in which light, temperature, and nutrients could be manipulated. Under a 12 h light:12 h dark cycle, the dinoflagellates exhibited diurnal vertical migrations, swimming downward before the dark period began and upward before the end of the dark period. This vertical migration probably involved geotaxis and a diel rhythm, as well as light-mediated behavior. The vertical distribution of nitrate affected the behavior and physiology of the dinoflagellate. When nitrate was present throughout the container, the organisms resembled those in exponential batch culture both in C:N ratios and photosynthetic capacity (P_{max}); moreover, they migrated to the surface during the day. In contrast, when nitrate was depleted, C:N ratios increased, P_{max} decreased, and the organisms formed a subsurface layer at a depth corresponding to the light level at which photosynthesis saturated. When nitrate was present only at the bottom of the tank, C:N ratios of the population decreased until similar to those of nutrient-saturated cells and P_{max} increased; however, the dinoflagellates behaved the same as nutrient-depleted cells, forming a subsurface layer during the light period. Field measurements revealed a migratory subsurface chlorophyll maximum layer dominated by *G. splendens*. It was just above the nitracline during the day, and in the nitracline during the night, which concurs with our laboratory observations.

Introduction

Dinoflagellates migrate vertically (Hasle, 1950 and references therein), with patterns influenced by environmental conditions (Forward, 1976; Kamykowski and Zentara, 1977; Heaney and Furnass, 1980; Staker and Bruno, 1980; Heaney and Eppley, in press; Kamykowski, 1981). The responses of some dinoflagellates to physical and chemical variables have been well enough characterized to assess the interactions leading to well developed temporal and spatial patterns in phytoplankton abundance. For instance, Tyler and Seliger (1978) have documented the transport of *Prorocentrum mariae-lebouriae* from the mouth of the Chesapeake Bay (USA) to its bloom area in the upper bay, describing how interactions between behavior and water circulation result in the annual cycle in the distribution of this organism. Comparable processes have been invoked to explain blooms of *Gymnodinium breve* off the west Florida coast and *Gonyaulax excavata* off Maine and Massachusetts (Seliger *et al.*, 1979). Laboratory studies (Heaney and Furnass, 1980) and field observations (Harris *et al.*, 1979; Heaney and Talling, 1980) have provided enough information to describe most aspects of the temporal and spatial variation of the dinoflagellate *Ceratium hirundinella* in a small English lake; for this species, light intensity, anoxic conditions, and growth phase of the population are important factors modifying the behavior.

Other examples of well developed dinoflagellate aggregations are reflected by toxic blooms (discussed by Provasoli, 1979) and subsurface chlorophyll maximum layers (Epply *et al.*, 1968; Kiefer and Lasker, 1975; Holligan, 1979). Although phytoplankton behavior may be an important factor in formation or maintenance of these features, sufficient information is not available to identify completely the processes responsible for these phenomena.

In the present paper, we report how different nitrate regimes affect vertical movement of the non-thecate dinoflagellate *Gymnodinium splendens* in an attempt to identify some behavioral mechanisms responsible for subsurface chlorophyll maximum layers in the Southern California Bight (cf. Cullen and Eppley, 1981).

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We studied *Gymnodinium splendens* because it is an ecologically important organism (Lasker, 1975), which may or may not migrate vertically (Kiefer and Lasker, 1975). Kamykowski (1979) simulated the growth response of *G. splendens* in an internal wave field, but recognized that his results were limited by the lack of pertinent information on its behavior and physiology. We made physiological measurements on pure cultures of *G. splendens* under conditions closer to nature than standard batch cultures, in order to determine reasons for different field observations on the vertical migration of this dinoflagellate. In the Southern California Bight, *G. splendens* is a common component of subsurface chlorophyll maximum layers (R. Lasker, personal communication; cf. Kiefer and Lasker, 1975; Cullen and Renger, 1979), which are often in the vicinity of the nitracline (Cullen and Eppley, 1981); therefore, we studied responses of this species to different vertical distributions of nitrate.

Our experiments were designed to examine two hypotheses: (1) that a dinoflagellate in water of adequate nitrate concentration swims up during the early part of the day, and (2) that such upward swimming ceases when nitrate is below a threshold concentration. Dinoflagellates exhibiting this hypothetical behavior should be found in layers near the nitracline; this distribution is often found in field observations (Cullen and Eppley, 1981). Our experiments test the null hypothesis that the behavior of *Gymnodinium splendens* is unaffected by nitrate distribution.

Previous experiments on other dinoflagellates have shown that nutrition has an affect on behavior (Eppley *et al.*, 1968), and recent laboratory studies on *Gonyaulax polyedra* and *Ceratium furca* (Heaney and Eppley, in press) have verified the basic features of our model. In this paper we will demonstrate that the behavior of *Gymnodinium splendens* responds to nutrient regimes in a previously undescribed fashion which is, nevertheless, consistent with field observations.

Materials and Methods

Laboratory Studies

Unialgal (but not axenic) cultures of *Gymnodinium splendens* (Haxo strain PY-14) were grown in 20-liter Pyrex carboys containing 15-liters of IMR/2 medium (Eppley *et al.*, 1967) with 2 ml l^{-1} soil extract and only 100 μM nitrate. Starter cultures were grown in smaller flasks with IMR/2. Temperature was 20 °C, and irradiance, on a 16 h light:8 h dark cycle, was approximately 80 $\mu E\ m^{-2}\ s^{-1}$.

Preliminary observations were made on tens to hundreds of *Gymnodinium splendens* cells in cylindrical glass tubes (10 cm × 0.55 cm i.d.), sealed at both ends with silicon stoppers and suspended vertically for several days in a water bath at 17 °C on a 12 h light: 12 h dark cycle at 85 $\mu E\ m^{-2}\ s^{-1}$ of light filtered to approximate the natural submarine light spectrum off the southern California coast. The tubes were periodically removed for inspection under a dissecting microscope while temperature was maintained at 17 °C by a water bath.

The major experiments were conducted in the "cheap tank" (Heaney and Eppley, in press), a 2.02 m high by 0.25 m (i.d.) opaque polyvinyl chloride cylinder containing approximately 78 liters of 0.22 μm-filtered seawater and a 15-liter inoculum from the cultures grown in 20-liter carboys. The tube was enclosed in an outer jacket in which water from a cooling bath could be circulated to produce temperature stratification. Illumination was provided on a 12 h light:12 h dark cycle by one or two 500 W tungsten halogen lamps shining through a running water heat-filter.

Vertical profiles were made by lowering and raising a weighted tube (silicon rubber, 1.6 mm i.d.) through the culture vessel. Sampled water was withdrawn at about 30 ml min^{-1} with a peristaltic pump, passed through a Turner 111 fluorometer with microflow door No. 110-872PLX for *in vivo* fluorescence measurements every 10 cm, and returned to the sampling depth with little disruption of the water column. Motility and control-level photosynthetic capacity of the organisms were retained after passage through the pump system.

Samples for discrete analyses were taken at 3 to 5 depths from a valve in the stream from the pump. Cell counts were performed by the Utermöhl inverted microscope technique (statistical counting accuracy usually better than ± 20%), extracted chlorophyll *a* was determined by fluorescence (Strickland and Parsons, 1972), and particulate carbon and nitrogen were measured according to Sharp (1974). A Technicon autoanalyzer was used to determine nitrate and nitrite; the phenol hypochlorite (Solórzano, 1969) method was used for ammonia. Nutrients in seawater solution were added to the tank by reversing the pump and delivering the solutions to selected depths. Mixing in the tank was minimal: no trace of nitrate added to the bottom was ever detected at 100 cm depth.

Temperature was measured with a thermistor attached near the inlet of the sampling tube. Photosynthetically active quantum scalar irradiance was measured with a submersible 4π collector (Biospherical Instruments, San Diego, California, Model QSL-100).

Photosynthetic carbon fixation was measured in 25 ml screw-cap test tubes containing a 15 ml sample and 3.3 μCi Na $H^{14}CO_3$. Six light levels were obtained by placement of neutral density screens between a 500 W tungsten halogen lamp and the samples, which were in a partitioned water bath. After incubation for 1 h, the samples were filtered onto Whatman GF/C filters, rinsed well, and analyzed for labelled organic carbon on a liquid scintillation counter; the filtrate was also analyzed for labelled organic carbon (Anderson and Zeutschel, 1970). Duplicate blanks of filtered seawater were run with each experiment. Total CO_2 was assumed

to be 24 000 $\mu g\ l^{-1}$ for the first photosynthesis versus light intensity (P versus I) experiment from the tank (Day 3), and decremented to 23 000 $\mu g\ l^{-1}$ on Day 6 to adjust for carbon fixation in the stratified tank. A subsequent determination from another tank experiment confirmed the validity of this approach. Total CO_2 for batch cultures was assumed to be 24 000 $\mu g\ l^{-1}$ minus the particulate carbon. Thus, although P versus I curves are internally consistent, absolute values of carbon fixation are subject to an uncertainty of about 10 to 20% corresponding to the range of probable CO_2 concentrations. Comparisons among the tank profiles are not compromised, however, because photosynthesis affected only a small proportion of the carbon pool between the third and sixth days.

Average carbon-to-nitrogen ratios (C:N) for profiles were determined by adding the concentrations of particulate carbon for the 3 to 5 depths sampled and dividing by the sum of nitrogen concentrations for the same depths; this is the numerical equivalent of pooling equal volumes of water from each depth prior to chemicals analysis. Mean values for such measurements as cell concentration could be calculated by multiplying the mean fluorescence from the profile by the average ratio of cells ml^{-1} to fluorescence.

Most of our laboratory results derive from an experiment during which three nutrient regimes were experienced by *Gymnodinium splendens* over 12 d. The temperature ranged from 18 °C at the bottom to 28 °C at the surface, and incident irradiance was approximately 900 $\mu E\ m^{-2}\ s^{-1}$, decreasing to 33 $\mu E\ m^{-2}\ s^{-1}$ at 190 cm. Despite the appearance of some algal contaminants, *G. splendens* dominated the phytoplankton throughout the experiment, and vertical patterns in fluorescence were clearly indicative of *G. splendens* cell concentration. Two additional laboratory experiments will be considered in less detail. In one, temperature was 11 °C at the bottom and 18 °C near the surface. A cooling system failure terminated the experiment before nitrate was depleted. Another experiment had a surface light intensity higher than our other experiments (1 100 $\mu E\ m^{-2}\ s^{-1}$). Colorless phagotrophic flagellates increased in numbers several days into that study, coincident with the disappearance of *G. splendens*.

Field Observations

In May, 1980, during Southern California Bight Study Cruise 16 of the Food Chain Research Group, a subsurface layer of *Gymnodinium splendens* (R. Lasker, personal communication) was encountered at Station 203, 5.6 km off the coast in the Southern California Bight. Vertical profiles were performed using a rosette sampler with quantum scalar irradiance meter, Sea Mar Tech *in situ* fluorometer, a CTD, and 5-liter Niskin bottles. Station position and analytical methods are described in Cullen and Eppley (1981).

Results

Diurnal Vertical Migration

Gymnodinium splendens displayed a diurnal vertical migration (DVM) in the experimental water column (Fig. 1). Not all aspects of vertical movement could be explained by positive phototaxis, because ascent began in total darkness, and descent commenced well before the lights were extinguished.

The importance of non-phototactic mechanisms was demonstrated by other observations. In a culture vessel exposed to light from below, *Gymnodinium splendens* repeatedly formed a layer at the surface. To establish independence from possible chemical gradients, we observed behavior in small sealed tubes (see "Materials and Methods"). The organisms aggregated near the top of the vertically suspended tubes even though the light source was from the side. When the tube was placed horizontally in a tray for observation, the *G. splendens* cells quickly changed orientation and swam upwards, perpendicular to the long axis of the tube, at about 0.3 mm s^{-1}. This response was observed under diffuse light and light from the bottom, side, or top. Upward movement was independent of chemical gradients because the tube could be rolled to bring cells back to the bottom and they would again swim up.

The DVM of *Gymnodinium splendens* traversed a temperature range of 7 C° in 1 m on Day 4 and similar gradients on other days (Fig. 1). In the low-temperature experiment, with nitrate throughout the tank, *G. splendens* swam into 20 °C surface water during the light period and descended into 11.5 °C water at 100 cm by 21.00 hrs, a change of 8.5 C° in 1 m.

Behavior and Physiological Patterns under Different Nutrient Conditions

Dinoflagellates experienced three nutrient regimes during the 12 d of the experiment. Phosphate was added in eightfold excess of the P:N ratio of phytoplankton (Redfield *et al.*, 1963), so for convenience, we will classify the vertical profiles according to nitrate distribution (Figs. 1, 2). Nitrate was depleted until 16.45 hrs on Day 2, when nitrate was added near the bottom of the tank, and remained $> 1.0\ \mu M$ until 24.00 hrs on Day 4. Nitrate concentration was low for the subsequent 24 h, until nitrate and phosphate were added throughout the water column at 22.00 hrs on Day 5. Nitrate concentrations were high at least through Day 7, and were depleted on Days 9 through 12. We will show that the nitrate regimes correspond to distinct and characteristic behavioral and physiological patterns in the dinoflagellates.

The concentrations of other nitrogenous nutrients were also determined. Ammonia was measured several times during the experiment, but some of the samples were contaminated. Careful analysis in the other experi-

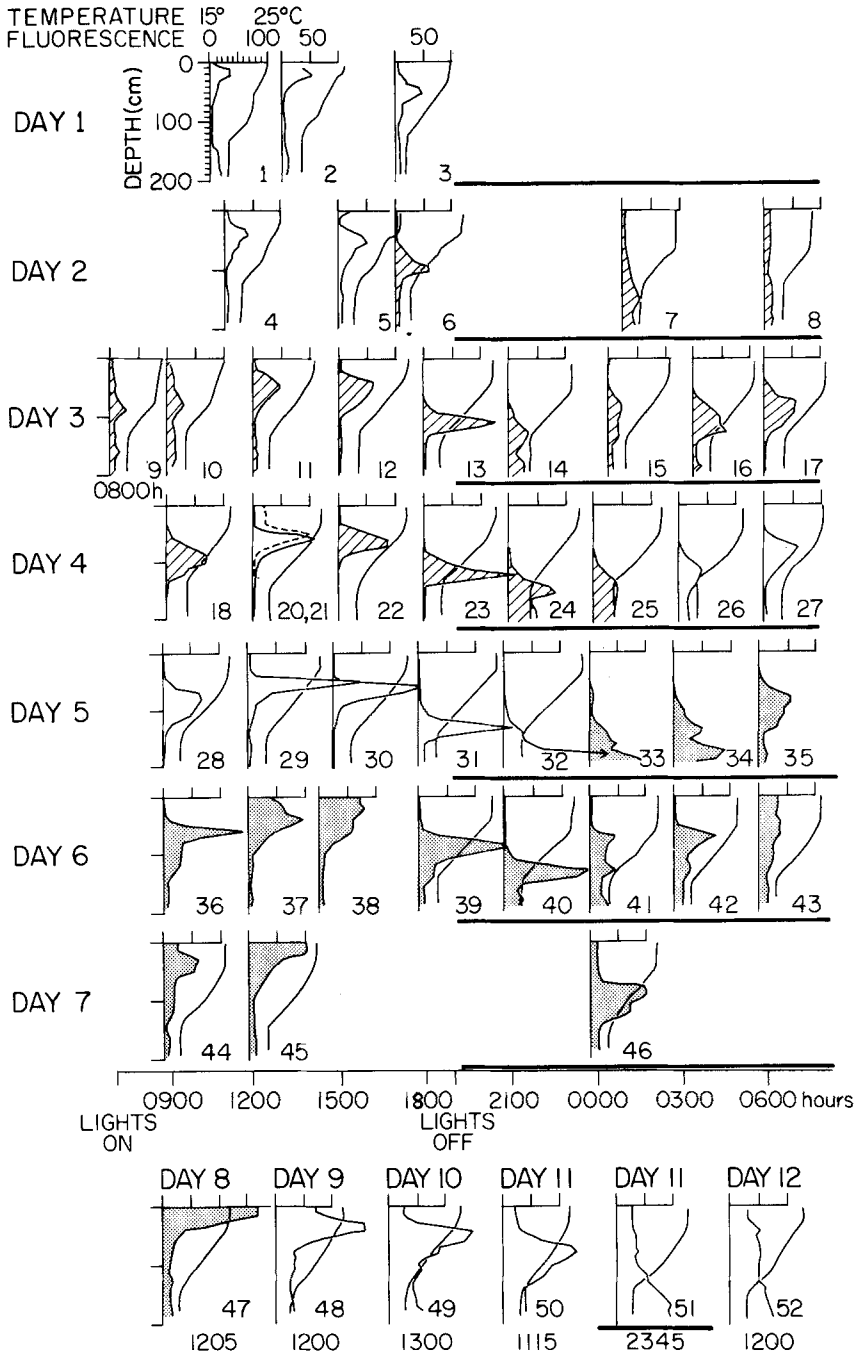

Fig. 1. *Gymnodinium splendens*: fluorescence profiles. Time of sampling is indicated by position of depth axis. Hatched profiles (and Profiles 20 and 21) indicate sampling when nitrate was present only near bottom of tank; stippled profiles indicate sampling when nitrate was > 1.0 μM throughout tank; nitrate was depleted when the remaining profiles were taken. Profile 21 was taken at 14.30 hrs after 1.5 h under reduced irradiance (see "Results – Behavior and Physiological Patterns under Different Conditions")

ments showed that ammonia was usually < 0.5 μM and always < 1.0 μM in the tank. Nitrite concentrations were low (approximately 0.06 μM) and uniform throughout the experiment.

Vertical migration patterns of *Gymnodinium splendens* were correlated with the distribution of nitrate in the tank. With nitrate throughout the water column, the daytime peak in dinoflagellate abundance was at the surface, where light intensity was approximately 850 $\mu E\ m^{-2}\ s^{-1}$, and temperature was 27° to 28 °C. In the experiment with higher incident irradiance, *G. splendens* migrated to the surface during the day where temperature was 22 °C and irradiance was 1 100 $\mu E\ m^{-2}\ s^{-1}$. Migration to the surface was not observed when nitrate was depleted or present only at the bottom. Instead, a subsurface maximum was found near 50 cm, where light intensity was about 250 $\mu E\ m^{-2}\ s^{-1}$. During the afternoon of Day 4, we decreased incident irradiance fourfold for 1.5 h by placing a screen over the tank. The thermal structure was not affected, but some of the dinoflagellates moved upward (Profile 21, Fig. 1). We could distinguish no difference between

the daytime behavior of *G. splendens* when nitrate was depleted throughout the container compared to daytime behavior when nitrate was present only at the bottom, with the exception of Day 12, when the capacity for DVM was lost, apparently because of extended nutrient depletion (cf. Eppley *et al.*, 1968).

An intensified nighttime migration to the bottom of the tank was observed on Day 5, when nitrate was depleted throughout. We do not have enough information to determine if the presence of nitrate limits the extent of migratory descent.

The particulate carbon:nitrogen ratio of *Gymnodinium splendens* was sensitive to changes in nutrient conditions (Fig. 2). With nitrate present throughout, the atomic ratio was between 5 and 6, a value characteristic of phytoplankton growing under nutrient-saturated conditions (Redfield *et al.*, 1963) and similar to the ratio for exponential phase *G. splendens* in our 15-liter batch cultures. C:N increased rapidly under nitrate depletion, reaching values of about 8 within 24 h (Day 5). With nitrate at the bottom only, C:N reverted to 5.65 by the end of Day 4.

The relationships between photosynthesis and irradiance were measured on batch cultures and samples from the dinoflagellate peaks in the tank and are expressed as μg carbon fixed μg particulate carbon^{-1} h^{-1} (Fig. 3). The amount of labelled organic carbon in the filtrate was less than 5% of the total and was not included in the calculations.

The highest photosynthetic rates were attained at 500 μE m^{-2} s^{-1} in each of the light period experiments, but photosynthetic activities at half that irradiance were nearly as high. A non-parametric analysis of variance with replicates (Tate and Clelland, 1957) and *a posteriori* comparisons by least-significant range (Sokal and Rohlf, 1969) indicated that the photosynthesis rate at the 4 high light levels was higher than that at the lower two, but the rate at none of the 4 could be distinguished as being significantly higher than the others. Thus, we will consider 250 μE m^{-2} s^{-1} to be saturating light intensity and the mean of the measurements at the 4 high light levels as P_{max}, the photosynthetic capacity.

The midday photosynthetic capacity of *Gymnodinium splendens* was higher in the tank with nitrate throughout (25 °C) than in exponential-phase batch cultures, and more than double the photosynthetic capacity under nitrate depletion. When nitrate was present only at the bottom, and C:N was still high (Fig. 2), P_{max} had an intermediate value. A diurnal rhythm in P_{max} has been demonstrated in dinoflagellates (Prézelin *et al.*, 1977), and our P versus I curves suggest that *G. splendens* also has such a rhythm, with lowest rates in the middle of the dark period (Fig. 3C).

Field Observations

The behavior of *Gymnodinium splendens* was recently observed in the field. On May 11, 1980, at 01.10 hrs, a subsurface layer of *G. splendens* was observed at 18 m, where temperature was 14.0 °C and potential density was 1.0250 (Fig. 4A). Beginning at 10.00 hrs, 4 profiles were performed over 1 h, and several analyses were made on discrete samples. Fig. 4B shows one of the profiles in which density structure was similar to the nighttime observation. The layer of maximum dinoflagellate abundance had moved upward into nitrate-depleted water at 14 m, potential density = 1.0247. In addition to the vertical migration of *G. splendens* which brought the peak closer to the surface, internal wave activity displaced the daytime dinoflagellate peak vertically between 14 and 9 m, causing its associated irradiance to vary between 90 and 540 μE m^{-2} s^{-1}. The profiles in Fig. 4 demonstrate a vertical migration from a depth near the nitracline upward to an irradiance level near that which saturates photosynthesis, in excellent agreement with our laboratory results. The biomass

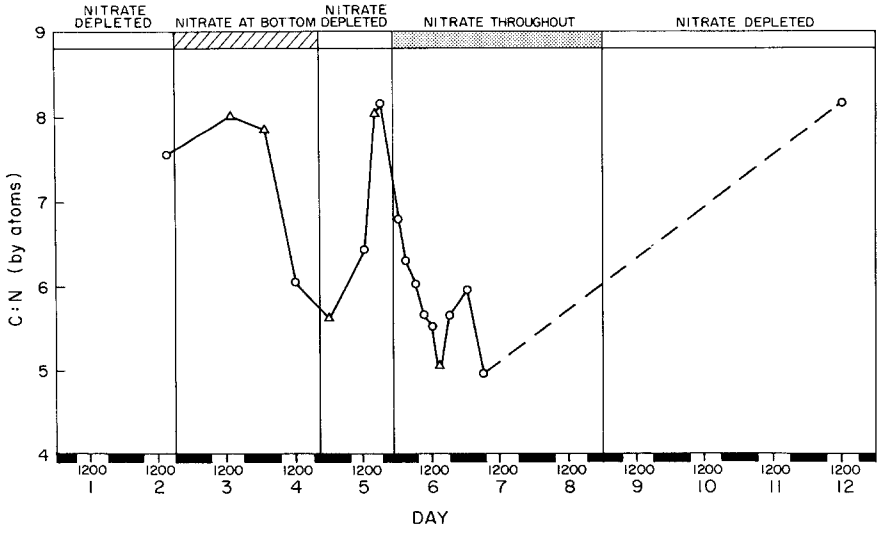

Fig. 2. *Gymnodinium splendens.* Carbon to nitrogen ratios during course of the experiment. Open circles indicate average values for water column and incorporate data from 3 to 5 depths. Triangles are determinations from the peak of dinoflagellate abundance. Black bars on abscissa indicate dark periods

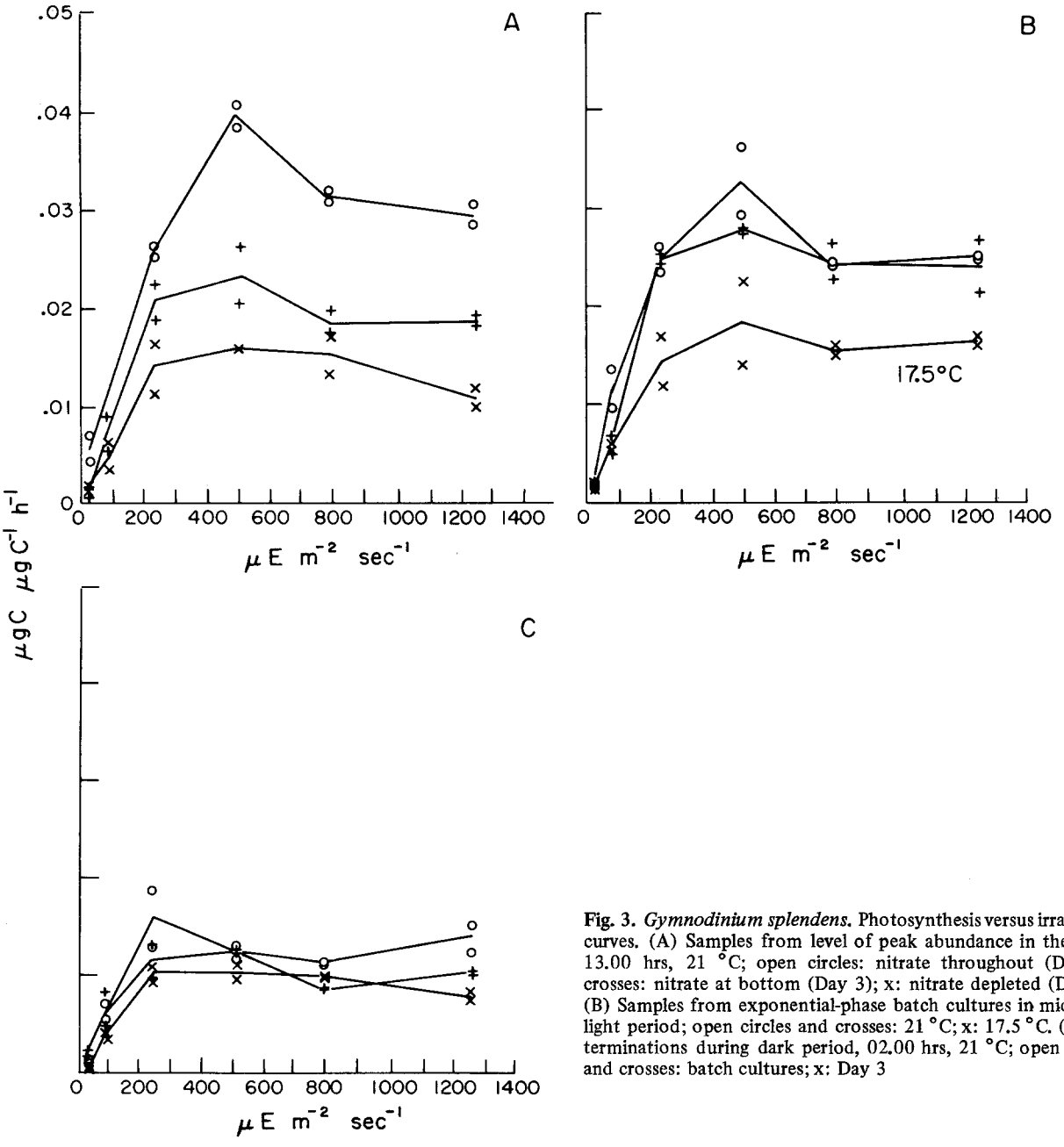

Fig. 3. *Gymnodinium splendens.* Photosynthesis versus irradiance curves. (A) Samples from level of peak abundance in the tank, 13.00 hrs, 21 °C; open circles: nitrate throughout (Day 6); crosses: nitrate at bottom (Day 3); x: nitrate depleted (Day 5). (B) Samples from exponential-phase batch cultures in middle of light period; open circles and crosses: 21 °C; x: 17.5 °C. (C) Determinations during dark period, 02.00 hrs, 21 °C; open circles and crosses: batch cultures; x: Day 3

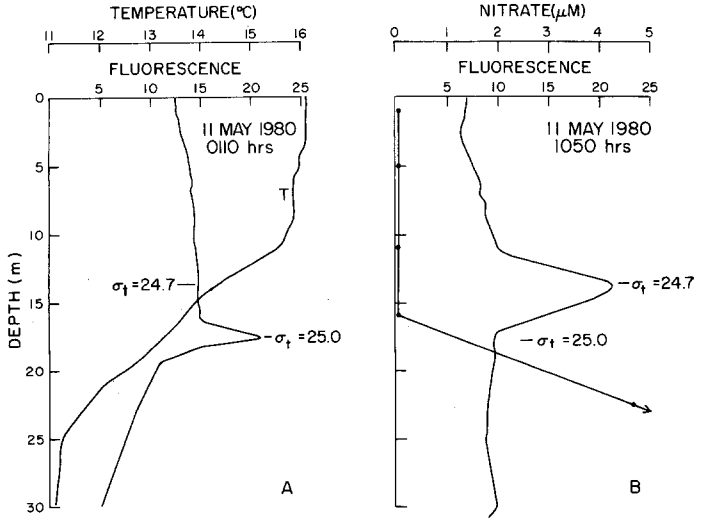

Fig. 4. Fluorescence profiles at a field station (33°28'N; 117°48'W) where a subsurface layer of *Gymnodinium splendens* was present; σ_t = density. In (A) temperature curve, T, is shown; in (B), nitrate concentrations are indicated by filled circles

Table 1. *Gymnodinium splendens.* Measurements from subsurface chlorophyll maximum layer dominated by *G. splendens* and from samples taken from *G. splendens* abundance peak in laboratory experiments

Sample	Depth (m)	Irradiance (μE m^{-2} s^{-1})	Temperature (°C)	Nitrate (μM)	C:N (at)	C:chlorophyll *a* (g g^{-1})
Field sample						
10.50 hrs, 11 May 1980	9–14	90–540	15.0	0.01	7.72	80.1
Laboratory experiment						
Day 3, 13.00 hrs nitrate at bottom	0.6	175	24.1	0.10	8.04	122.9
Day 4, 12.00 hrs nitrate at bottom	0.5	235	25.2	0.05	6.30	104.1
Day 5, 13.00 hrs nitrate depleted	0.5	250	26.2	0.10	8.07	103.9
Day 6, 13.00 hrs nitrate throughout	0.4	350	26.5	8.0	5.02	88.7

of *G. splendens* from the fluorescence peak was quite high (particulate organic carbon, POC = 1 138 μg l^{-1}, chlorophyll = 14.2 μg l^{-1}), so particulate analyses should be representative of the dinoflagellates' chemical composition. Measurements on samples from the peak can be compared with those from our laboratory experiments (Table 1).

Discussion and Conclusions

Many dinoflagellate species undergo diurnal vertical migration, and, for *Gymnodinium splendens* this behavior has been observed both in the field (Kiefer and Lasker, 1975) and in the laboratory (Kamykowski, 1981). Our results are in general agreement with previous studies and add to the list of dinoflagellate behaviors that appear to involve geotaxis and diel rhythms in addition to phototaxis (Eppley *et al.*, 1968; Weiler and Karl, 1979; Kamykowski, 1981). The upward swimming of *G. splendens* in sealed tubes is an especially interesting observation on possible geotaxis because it cannot be explained by orientation to chemical or light gradients. Movement through thermoclines is restricted in some dinoflagellates (Kamykowski and Zentara, 1977), but in agreement with Kamykowski (1981), we have shown that *G. splendens* will swim through large temperature gradients.

The behavior of *Gymnodinium splendens* is interesting and ecologically relevant in its response to different nutrient regimes. Like *Cachonia niei* (Eppley *et al.*, 1968) and *Gonyaulax polyedra* (Heaney and Eppley, in press), *Gymnodinium splendens* migrated to the surface during the light period when nitrate was present throughout the tank, but formed a subsurface layer during the light period when nitrate was depleted. This subsurface aggregation formed under an irradiance (250 μE m^{-2} s^{-1}) comparable to the light levels at which *C. niei* (0.25 cal cm^{-2} min^{-1}) and *Gonyaulax polyedra* (150 μE m^{-2} s^{-1}) formed layers. Such intensities are close to saturating for photosynthesis; Harris *et al.* (1979) found that *Ceratium hirundinella* also formed subsurface layers where irradiance was optimal for photosynthesis. An irradiance of 250 μE m^{-2} s^{-1} is about 10% summer sunlight, and is similar to the light levels measured at the chlorophyll maximum layers of the Southern California Bight (Cullen and Eppley, 1981).

Among physiological parameters differing between the nitrate-saturated and nitrate-depleted conditions, the C:N ratio is a good indicator of nutritional status (Myers, 1951; Eppley and Renger, 1974). In our experiment, this ratio changed as if nitrate were the most important form of inorganic nitrogen for the phytoplankton: the ratio was low when nitrate was present, but high when nitrate was depleted. Photosynthetic capacity also followed a trend indicating that when nitrate was depleted throughout the tank, growth was nitrogen-limited. Thus, two behavioral and physiological patterns have been described: (1) a nutrient-saturated pattern with high P_{max}, low C:N, and ascent to strata with high light intensity during the light period; (2) a nitrate-limited pattern with low P_{max}, high C:N, and daytime aggregation at a depth corresponding to about 10% natural surface irradiance. These two patterns for behavior and C:N are identical to those observed for *Cachonia niei* (Eppley *et al.*, 1968; Strickland *et al.*, 1969) and *Gonyaulax polyedra* (Heaney and Eppley, in press).

The response of migrating dinoflagellates to stratified conditions with nitrate present only at depth has been studied in the red-tide forming *Gonyaulax polyedra* (Heaney and Eppley, in press). In that experiment, the addition of nitrate to the bottom of the nitrate-depleted tank resulted in a rapid (1 d) change in C:N ratio from 8.5 to 6.5, and resumption of vertical migration into the surface layer (incident photosynthetically active radiation, I_o = 1130 μE m^{-2} s^{-1}). Addition of nitrate to the deep layer in the experiment with *Gymnodinium splendens* elicited a similar, but slower

response in C:N, and a partial reversion of P_{max} toward the nutrient-saturated value, but a contrasting behavioral response. With nitrate available only at depth, *G. splendens* continued to avoid the surface, maintaining a position at a light level indistinguishable from that preferred when nitrate was depleted.

These contrasting behaviors are apparently important in determining the distributions of *Gonyaulax polyedra* and *Gymnodinium splendens* in the Southern California Bight. *Gonyaulax polyedra* often occurs in dense surface patches of nitrate-depleted water overlying a shallow thermocline and nitrate supply (Eppley and Harrison, 1974). The results of Heaney and Eppley (in press) demonstrate a mechanism to account for these field observations. *Gymnodinium splendens*, however, is found in subsurface layers during periods of stratification off the southern California coast (Fig. 4 and Kiefer and Lasker, 1975; Lasker, 1975; Cullen and Renger, 1979), which would be predicted from our laboratory results.

We have demonstrated, in *Gymnodinium splendens*, a range of responses to different conditions which can work together to adapt the dinoflagellate to different conditions in stratified water. A somewhat different suite of responses exists for *Gonyaulax polyedra*, and other species of phytoplankton no doubt have equally complex behavioral patterns. Steele (1964) stated that there was no reason to expect large losses of phytoplankton due to sinking from stratified tropical waters. We suggest that there is no reason to expect that phytoplankton in well-stratified water are found anywhere but their behaviorally determined preferred depths (cf. Hasle, 1950; Blasco, 1978; Harris *et al.*, 1979). Experiments and field studies can determine to what extent this supposition holds.

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Literature Cited

Anderson, G. C. and R. P. Zeutschel: Release of dissolved organic matter by marine phytoplankton in coastal and offshore areas of the northeast Pacific Ocean. Limnol. Oceanogr. *15*, 402–407 (1970)

Blasco, D.: Observations on the diel migration of marine dinoflagellates off the Baja California Coast. Mar. Biol. *46*, 41–47 (1978)

Cullen, J. J. and R. W. Eppley: Chlorophyll maximum layers of the Southern California Bight and possible mechanisms of their formation and maintenance. Oceanol. Acta *4* 23–32 (1981)

Cullen, J. J. and E. H. Renger: Continuous measurement of the DCMU-induced fluorescence response of natural phytoplankton populations. Mar. Biol. *53*, 13–20 (1979)

Eppley, R. W. and W. G. Harrison: Physiological ecology of *Gonyaulax polyedra*, a red water dinoflagellate off Southern California. *In*: Proceedings of First International Conference on Toxic Dinoflagellate Blooms, pp 11–22. Ed. by U. R. LeCicero. Wakefield, Mass.: Massachusetts Science and Technology Foundation 1974

Eppley, R. W., R. W. Holmes and J. D. H. Strickland: Sinking rates of marine phytoplankton measured with a fluorometer. J. exp. mar. Biol. Ecol. *1*, 191–208 (1967)

Eppley, R. W., O. Holm-Hansen and J. D. H. Strickland: Some observations on the vertical migration of dinoflagellates. J. Phycol. *4*, 333–340 (1968)

Eppley, R. W. and E. H. Renger: Nitrogen assimilation of an oceanic diatom in nitrogen-limited continuous culture. J. Phycol. *10*, 15–23 (1974)

Forward, R. B.: Light and diurnal vertical migration: photobehavior and photophysiology of plankton. Photochem. Photobiol. Rev. *1*, 157–209 (1976)

Harris, G. P., S. I. Heaney and J. F. Talling: Physiological and environmental constraints in the ecology of the planktonic dinoflagellate *Ceratium hirundinella*. Freshwat. Biol. *9*, 413–428 (1979)

Hasle, G. R.: Phototactic vertical migration in marine dinoflagellates. Oikos *2*, 162–175 (1950)

Heaney, S. I. and R. W. Eppley: Light, temperature, and nitrogen as interacting factors affecting diel vertical migrations of dinoflagellates in culture. J. Plankton Res. (In press)

Heaney, S. I. and T. I. Furnass: Laboratory models of diel vertical migration in the dinoflagellate *Ceratium hirundinella*. Freshwat. Biol. *10*, 163–170 (1980)

Heaney, S. I. and J. F. Talling: Dynamic aspects of dinoflagellate distribution patterns in a small productive lake. J. Ecol. *68*, 75–94 (1980)

Holligan, P. M.: Dinoflagellate blooms associated with tidal fronts around the British Isles. *In*: Toxic dinoflagellate blooms, pp 249–256. Ed. by D. L. Taylor and H. H. Seliger. New York: Elsevier 1979

Kamykowski, D.: The growth response of a model *Gymnodinium splendens* in stationary and wavy water columns. Mar. Biol. *50*, 289–303 (1979)

Kamykowski, D.: Laboratory experiments on the diurnal vertical migration of marine dinoflagellates through temperature gradients. Mar. Biol. *62*, 57–64 (1981)

Kamykowski, D. and S.-J. Zentara: The diurnal vertical migration of motile phytoplankton through temperature gradients. Limnol. Oceanogr. *22*, 148–151 (1977)

Kiefer, D. A. and R. Lasker: Two blooms of *Gymnodinium splendens*, an unarmored dinoflagellate. Fish. Bull. U.S. *73*, 675–678 (1975)

Lasker, R.: Field criteria for survival of anchovy larvae: the relation between inshore chlorophyll maximum layers and successful first feeding. Fish. Bull. U.S. *73*, 453–462 (1975)

Myers, J.: Physiology of the algae. A. Rev. Microbiol. *5*, 157–180 (1951)

Prézelin, B. B., B. W. Meeson and B. M. Sweeney: Characterization of photosynthetic rhythms in marine dinoflagellates. I. Pigmentation, photosynthetic capacity and respiration. Pl. Physiol., Lancaster *60*, 384–387 (1977)

Provasoli, L.: Recent progress, an overview. *In*: Toxic dinoflagellate blooms, pp 1–14. Ed. by D. L. Taylor and H. H. Seliger. New York: Elsevier 1979

Redfield, A. C., B. H. Ketchum and F. A. Richards: The influence of organisms on the composition of seawater, pp 26–77. *In*: The sea. Ed. by M. N. Hill. New York: Interscience 1963

Seliger, H. H., M. A. Tyler and K. R. McKinley: Phytoplankton distributions and red tides resulting from frontal circulation patterns. *In*: Toxic dinoflagellate blooms, pp 239–248. Ed. by D. L. Taylor and H. H. Seliger. New York: Elsevier 1979

Sharp, J. H.: Improved analysis for "particulate" organic carbon

and nitrogen from seawater. Limnol. Oceanogr. *19*, 984-989 (1974)

Sokal, R. R. and F. J. Rohlf: Biometry. The principles and practice of statistics in biological research, 776 pp. San Francisco: W. H. Freeman & Co. 1969

Solórzano, L.: Determination of ammonium in natural waters by the phenol hypochlorite method. Limnol. Oceanogr. *14*, 799-801 (1969)

Staker, R. D. and S. F. Bruno: Diurnal vertical migration in marine phytoplankton. Botanica mar. *23*, 167-172 (1980)

Steele, J. H.: A study of production in the Gulf of Mexico. J. mar. Res. *22*, 211-222 (1964)

Strickland, J. D. H., O. Holm-Hansen, R. W. Eppley and R. J. Linn: The use of a deep tank in plankton ecology. I. Studies of the growth and composition of phytoplankton crops at low nutrient levels. Limnol. Oceanogr. *14*, 23-34 (1969)

Strickland, J. D. H. and T. R. Parsons: A practical handbook of seawater analysis, 2nd ed. Bull. Fish. Res. Bd Can. *167*, 1-310 (1972)

Tate, M. W. and R. C. Clelland: Nonparametric and shortcut statistics, 171 pp. Danville, Illinois: Interstate Printers & Publishers 1957

Tyler, M. A. and H. H. Seliger: Annual subsurface transport of a red tide dinoflagellate to its bloom area: water circulation patterns and organism distribution in the Chesapeake Bay. Limnol. Oceanogr. *23*, 227-246 (1978)

Weiler, C. S. and D. M. Karl: Diel changes in phased-dividing cultures of *Ceratium furca* (Dinophyceae): nucleotide triphosphates, adenylate energy charge, cell carbon, and patterns of vertical migration. J. Phycol. *15*, 384-391 (1979)

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