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The role of phagotrophic dinoflagellates in marine ecosystems

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Abstract

Phagocytosis as a means of heterotrophic nutrition in dinoflagellates, mainly in non-thecate forms devoid of photosynthetic pigments, is described on the basis of a year of observations at two fixed stations and other records from the natural habitat. The phagocytosed inclusions in the cell cytoplasm may show the remnants of the prey organisms in various stages of digestion as distinct from food vacuoles which are normal products of cell metabolism. Most of the larger phagotrophic dinoflagellates, such as *Noctiluca miliaris*, *Polykrikos kofoidii* and *Gyrodinium* spp., were recorded chiefly at the Secchi disk depth in the preserved samples. Among the more fragile non-theccates which were recorded and observed, mainly in live samples, many specimens showed phagotrophic inclusions. The role of these holozoic dinoflagellates in the pelagic ecosystem is discussed.

Introduction

Phagotrophy as a method of nutrition in dinoflagellates has been reported by several investigators over the years. Most noteworthy among these contributions is the monograph by KOFOID and SWEZY (1921) on non-thecate dinoflagellates based on observations of plankton samples collected off La Jolla, California. Some of the more recent papers describing phagotrophy in thecate and non-thecate dinoflagellates are by BIECHELER (1952), ENOMOTO (1956), NORRIS (1969), BEERS et al. (1975), SEKIGUCHI and KATO (1976) and KIMOR (1979, 1981).

The instances of phagotrophy described below are derived from records and observations carried out by the author during a one-year study of the seasonal and bathymetric distribution of dinoflagellates at two fixed stations off La Jolla and at other sampling sites in the same general area of southern California. Like his predecessors KOFOID and SWEZY (1921), the author found the Scripps Pier to be a convenient site for plankton sampling at frequent time intervals and for examination of the dinoflagellates alive soon after collection. This was particularly important in the case of some of the larger non-thecate dinoflagellates which do not withstand preserving fluids such as formalin and lose their shape beyond recognition or disintegrate completely.

It is the purpose of this contribution to focus attention on the relative abundances of thecate to non-thecate dinoflagellates at a selected site. The author also deals specifically with a number of occurrences where phagotrophy as a form of nutrition in this group of protists, mainly in non-thecate forms, had a major impact on the pelagic ecosystem either of a short-term or a long-term nature. This approach seemed particularly timely in view of the fact that most of the earlier contributions dealing with

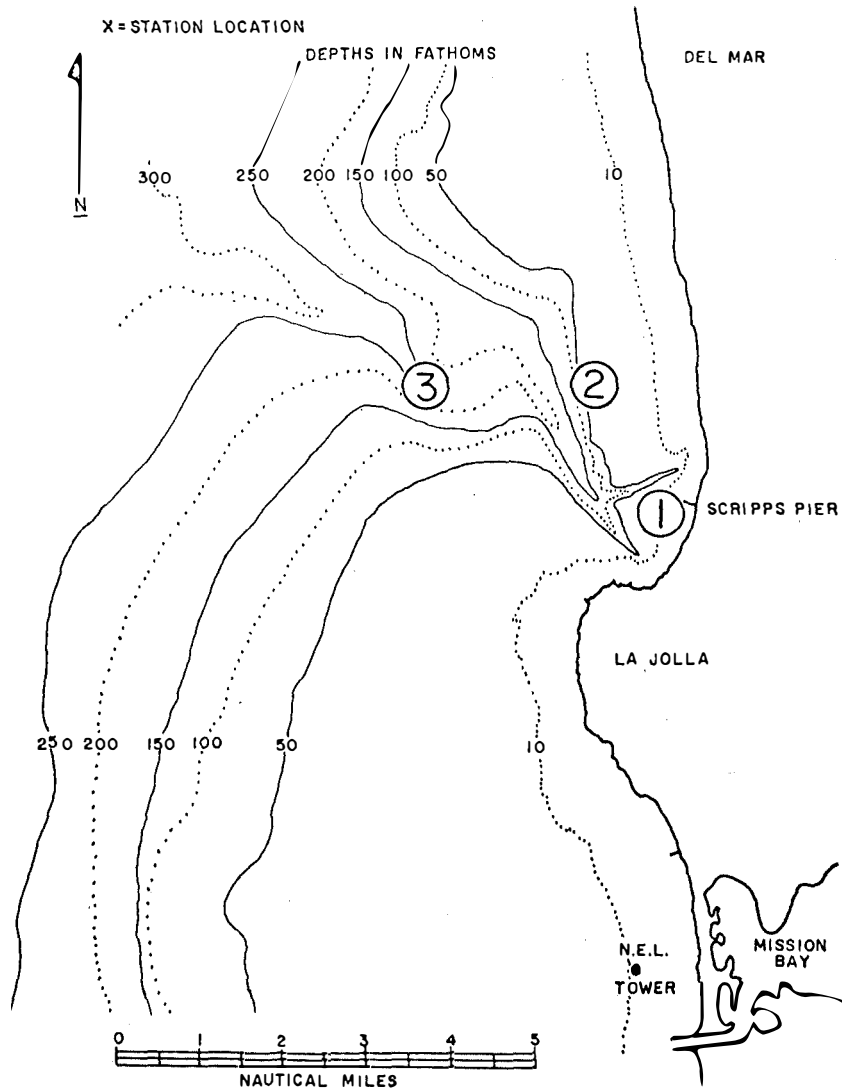


Figure 1

Location of stations 1–3. Basic map after STRICKLAND et al. 1970

red tides and mass development of dinoflagellates relate to thecate species such as *Gonyaulax polyedra*, *Prorocentrum micans*, etc. However, there is increasing evidence now that heterotrophic non-thecate forms such as *Cochlodinium catenatum*, *Gyrodinium* spp. and *Noctiluca miliaris* can also constitute, at times, significant components of the dinoflagellate standing crop and are likely to have impact on the production of other plankters in the food web through phagotrophic nutrition.

Materials and methods

Two stations, designated as 2 and 3, located off La Jolla, California, were occupied approximately every two to three weeks for a one-year period, beginning in December

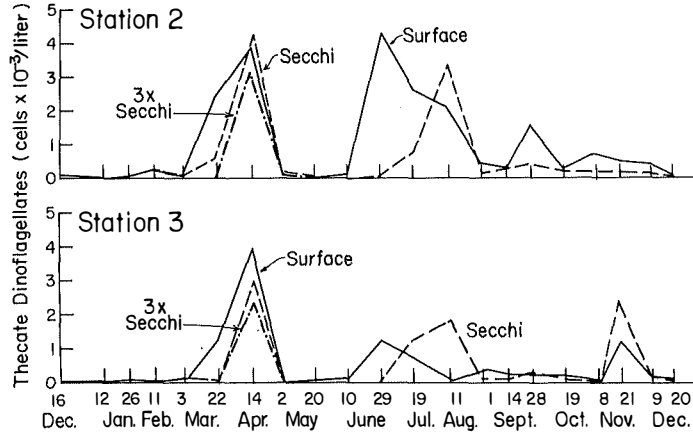


Figure 2

Spatial and temporal abundances of non-thecate dinoflagellates (cells x 10⁻³/litre) December 1976 to December 1977

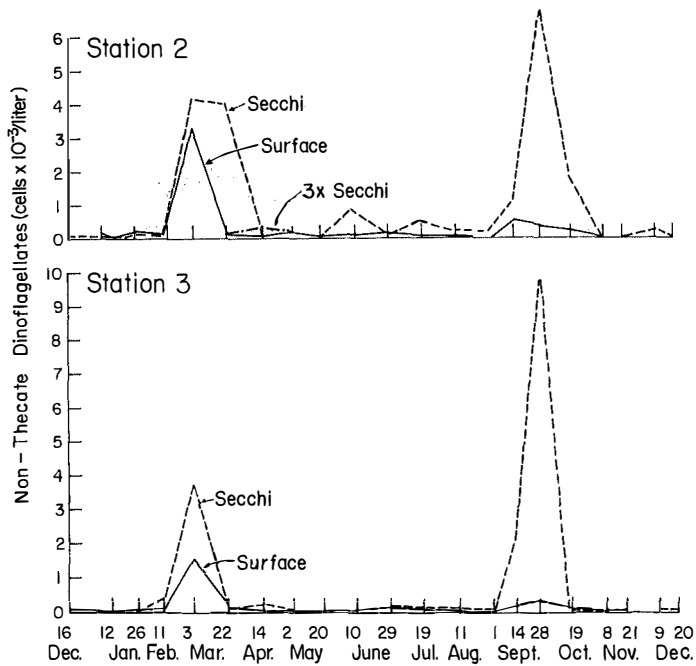


Figure 3

Spatial and temporal abundances of thecate dinoflagellates (cells x 10⁻³/litre) December 1976 to December 1977

1976 (Fig. 1). Station 1, at the end of the Scripps Pier, was used extensively for the collection of living organisms and for records of some physical and chemical parameters.

Sampling was based on transparency data along a depth profile including surface, 1 x Secchi depth (about 20 % of the surface illumination) and 3 x Secchi depth (about 1 % of the surface illumination).

As described in KIMOR (1981), Niskin bottles (5 litres) were deployed at the three levels and used to capture water for the preserved material. Reagent grade formalin was used for the preservation of the samples at a final concentration of 5 %. Aliquots from the concentrated samples were used for establishing the numerical abundance of the dinoflagellates larger than 50 μm by the UTERMÖHL method (1932).

Live material for immediate examination in the laboratory (generally within one hour of collection) was collected with a small plankton net of 1/4 m mouth opening and 35 μm mesh.

In addition, the author had the opportunity to study a dinoflagellate bloom in a small lagoon located on the campus of the University of California, Santa Barbara, during a visit with Dr. Beatrice M. Sweeny of the Department of Biology, in December 1976. Lastly, a series of zooplankton samples was kindly put at the author's disposal by Dr. M.M. Mullin of the Institute of Marine Resources at the University of California, San Diego. The analysis of these samples provided material for a quantitative study of the role of *Noctiluca miliaris* in controlling, through phagotrophy, the abundance of eggs in the plankton of the calanoid copepod *Acartia tonsa* (KIMOR 1979).

Results

The monitoring of the dinoflagellates at Stations 2 and 3 (Fig. 1) during the one-year sampling program referred to above pointed to an alternation of peaks of leading thecate and non-thecate species (Figs. 2, 3). Moreover, the non-thecate species, many of which showed evidence of holozoic inclusions, were generally more abundant at the Secchi disk depth than at the surface (Fig. 3).

For a better assessment of the relative shares of the two groups of dinoflagellates in time and space, throughout the sampling period, a few large ($> 65 \mu\text{m}$) dominant species of each group were selected in the final analysis of the data. These were: *Ceratium cf. dens*, *C. furca*, *C. fusus*, *Dinophysis fortii*, *Peridinium depressum* and *P. divergens* of the thecates and *Cochlodinium catenatum*, *Gyrodinium* spp. and *Torodinium robustum* of the non-thecates. It should be noted that even among the thecates, two species: *Peridinium depressum* and *P. divergens*, are considered non-photosynthetic (REID et al. 1970). These, with the three leading species of non-thecates, would add to the heterotrophic component of the total dinoflagellate populations. Considering the very conspicuous peaks caused mainly by the heterotrophic and potentially phagotrophic *Cochlodinium catenatum* in March and September 1977, at the Secchi disk level (Figs. 3, 4a), the role of these members of the phytoplankton community appears to be particularly significant. However, the three leading species of non-thecate dinoflagellates mentioned above are among those not adversely affected by formalin in the preserved samples. Among other species of known phagotrophic capability recorded in the course of the same study as being similarly resistant but far less abundant in the samples were: *Achradina sulcata*, *Erythroopsis minor*, *Kofoidinium velleloides*, *Noctiluca miliaris*, *Polykrikos kofoidii*, *Pronoctiluca pelagica*, *P. spinifera*, *Warnowia (Pouchetia) sp.* and *Balechina coerulea* (Fig. 4).

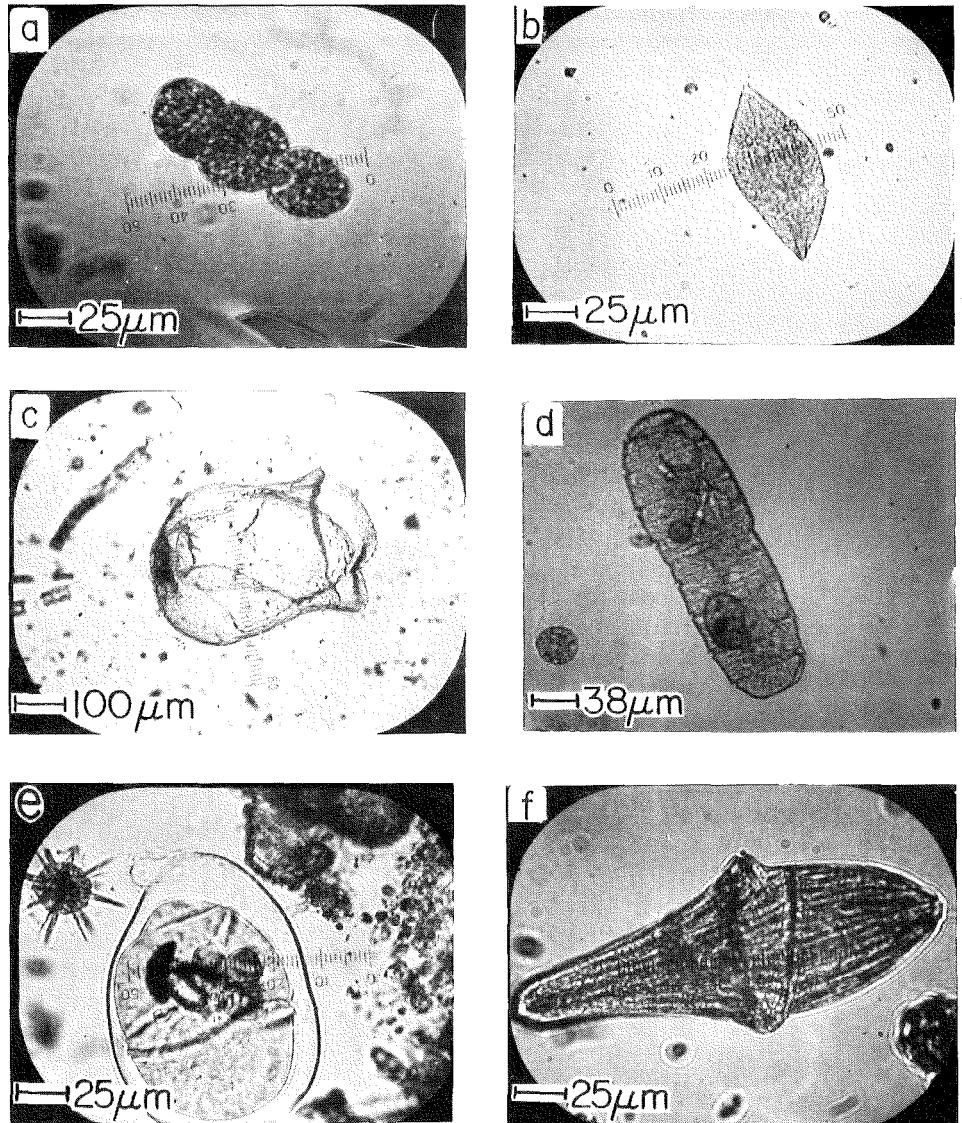


Figure 4

Holozoic non-thecate dinoflagellates recorded in preserved samples: a. *Cochlodinium catenatum*, b. *Gyrodinium* sp., c. *Kofoidinium velleoides*, d. *Polykrikos kofoidii*, e. *Warnowia* sp., f. *Balechina coerulea*

Additional species among the non-theccates, devoid of photosynthetic pigments, belonging chiefly to the genera *Gymnodinium* and *Gyrodinium*, were recorded mainly in the live samples collected at the three stations (Fig. 5a–c). This is because they were adversely affected by formalin and as a result were not recorded in the counts of the preserved samples.

In some species, such as *Balechina coerulea*, both chromatophores as well as holozoic inclusions were detected, suggesting myxotrophic nutrition (Fig. 4f).

A distinct case of phagotrophy was noted in the photosynthetic dinoflagellate *Gyrodinium dorsum* recorded on December 16, 1976 as blooming in a small lagoon adjoining the Marine Laboratory of the University of California, Santa Barbara. Examination of the plankton samples from the lagoon revealed the presence, in addition to *G. dorsum*, of lower numbers of the larger holozoic non-thecate dinoflagellate *Gyrodinium spirale*. These cells contained brown inclusions of the same color and shape as *G. dorsum* (Fig. 6a–c). The inclusions were seen to be extruded via the hypocone when *G. spirale* was placed on a microscope slide. It may be inferred that *G. spirale* was actively feeding on the smaller photosynthetic dinoflagellate *G. dorsum*. Although two attempts to confirm phagotrophy in culture were made, it was not possible to establish cultures of *G. spirale*, either alone or in combination with *G. dorsum*. The latter organism has been maintained in culture for some time both at Scripps Institution of Oceanography and at the University of California, Santa Barbara.

A case of large-scale predation of *Acartia tonsa* eggs by the non-thecate dinoflagellate *Noctiluca miliaris* was studied by the author in two sets of samples collected by Dr. M.M. Mullin and E. Brooks from two ships, R/V „David Starr Jordan” and R/V „Townsend Cromwell”, off Del Mar California, in May 1976 (KIMOR 1979).

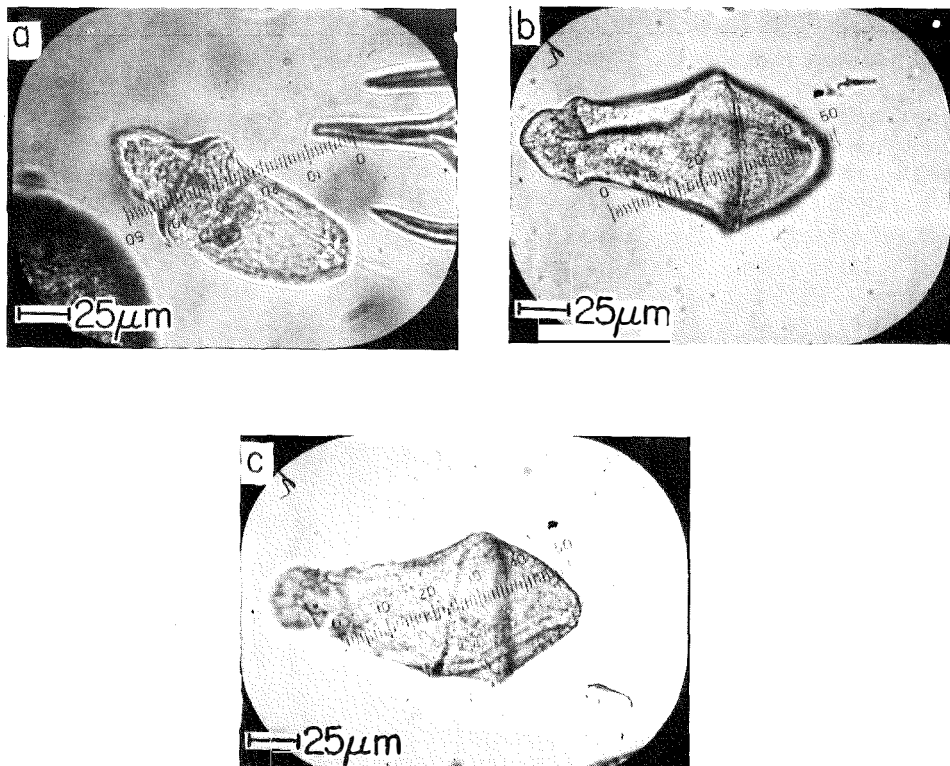


Figure 5

Holozoic non-thecate dinoflagellates recorded only in live samples: a–c. *Gymnodinium* spp.

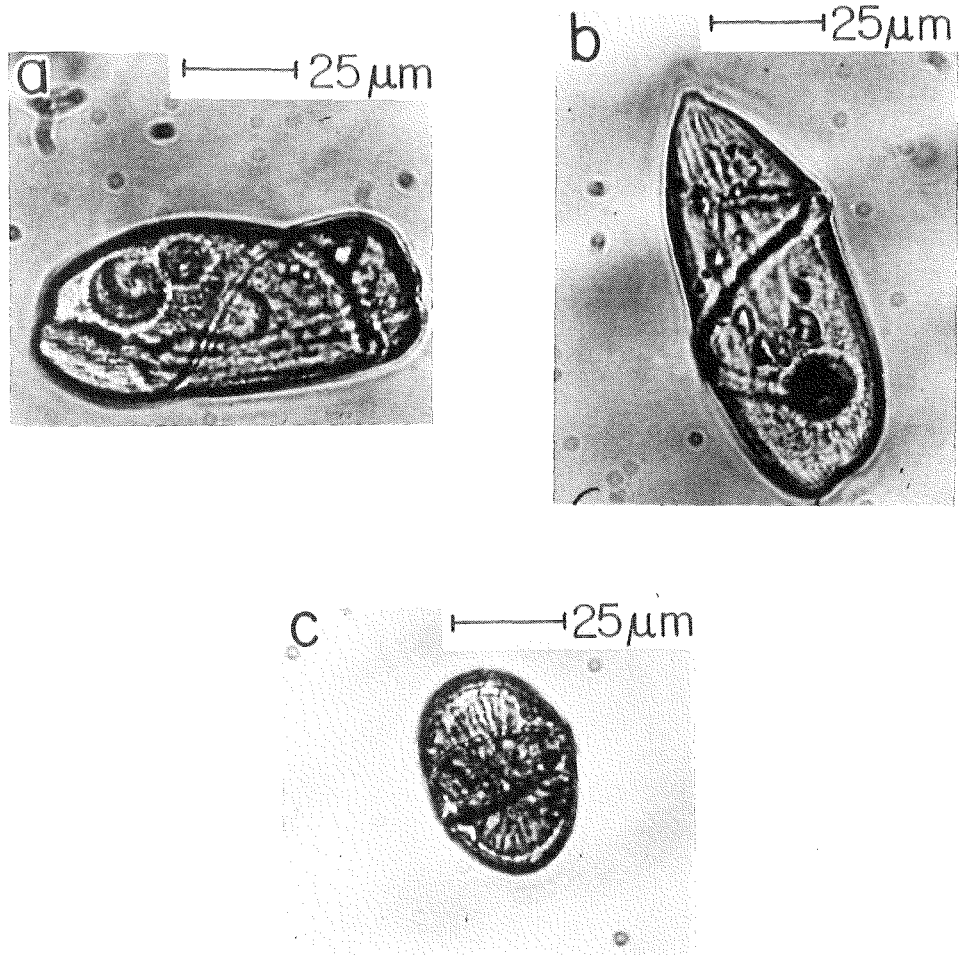


Figure 6

Phagotrophy in *Gyrodinium spirale* (live material): a–b. *G. spirale* with ingested *G. dorsum* cells, c. *G. dorsum* – free cell

Eggs of *A. tonsa* constituted the most conspicuous inclusions in *Noctiluca* cells throughout the water column, with predation decreasing with depth at both stations, over the 35 m water column. Grazing pressure by *Noctiluca* on *A. tonsa* eggs was greatest in the upper 20 m, with the percentage of ingested eggs reaching over 75 % in one of the two sets of samples (Figs. 7, 8). The fact that the *A. tonsa* eggs, shed singly into the water, had a spiny covering characteristic of this species did not prevent their ingestion by *Noctiluca*, possibly due to a protective sheath over the spines, noted in some of the eggs (Fig. 8c). Up to 12–14 eggs were recorded in some of the *Noctiluca* cells, a fact which points to the capacity of this voracious and non-selective predator to graze heavily on whatever food particles of adequate size are present in the plankton in sufficiently high concentrations. In this particular case, the preying by *Noctiluca* on

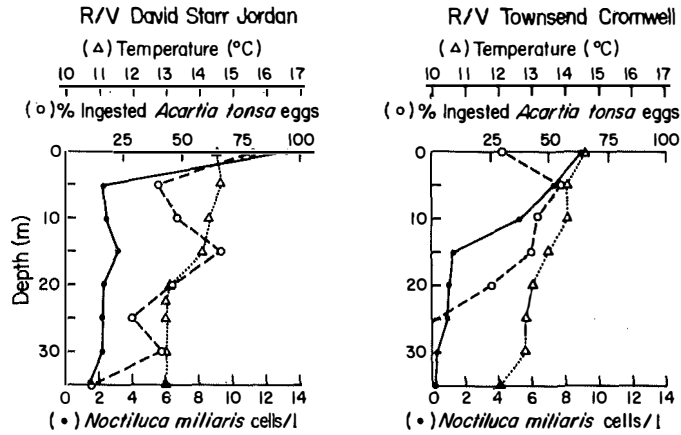


Figure 7

Numbers of *Noctiluca miliaris*, percentage of ingested eggs and temperature profiles during a two-ship cruise, 20 March 1976

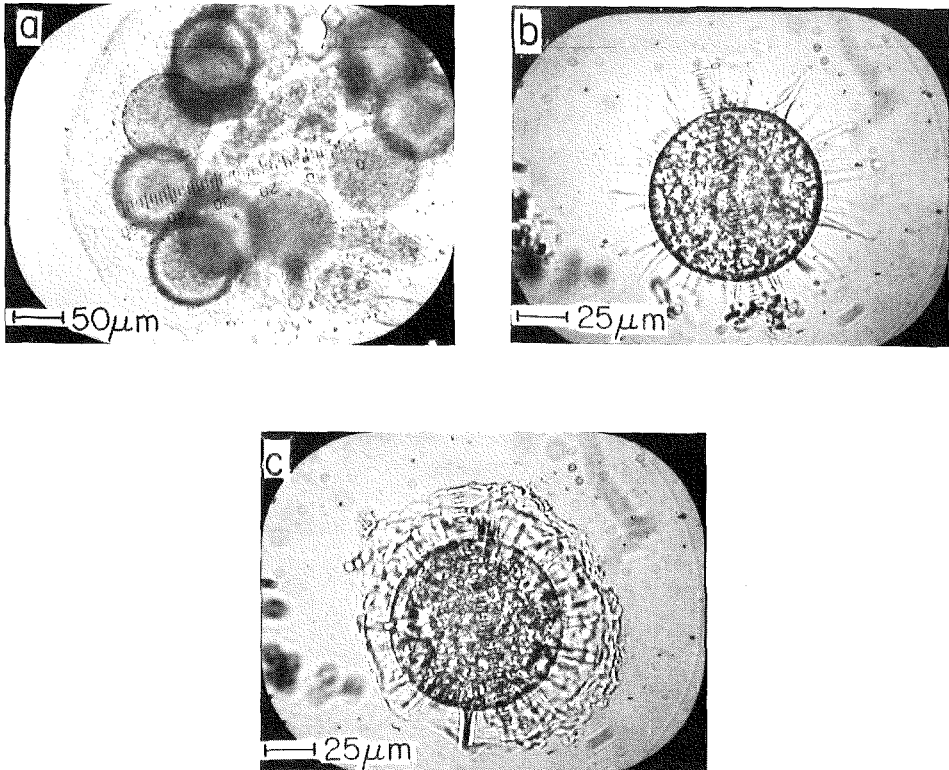


Figure 8

Phagotrophy in *Noctiluca miliaris* (fixed material): a. *N. miliaris* with ingested *A. tonsa* eggs, b. Spiny egg of *A. tonsa*, c. Spiny eggs of *A. tonsa* covered with sheath

such a high proportion of the freely-shed eggs of a single species of copepod common to that area was bound to impact heavily on the ensuing adult population and as a result on the actual structure of the pelagic ecosystem.

Finally, among the few records of phagotrophy in thecate dinoflagellates (HOFENDER 1930; NORRIS 1969), a conspicuous occurrence of *Ceratium massiliense* with an ingested *Gymnodinium* sp. was recorded in one of the samples during the one-year program (Fig. 9). (*Ceratium massiliense* has been identified as the closely-related species *C. deflexum* by M. Elbrächter – personal communication.)

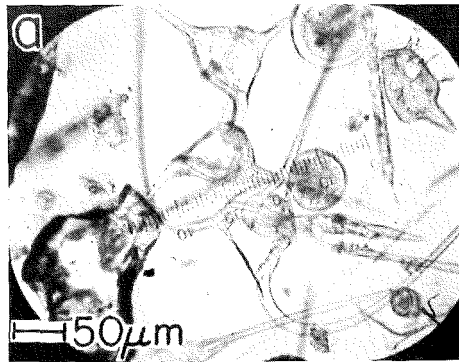


Figure 9

Phagotrophy in *Ceratium massiliense* (fixed material): *C. massiliense* with ingested cell of *Gymnodinium* sp.

Discussion and conclusions

From the evidence presented above it appears that the role of dinoflagellates in general, and of the non-thecate dinoflagellates in particular, is in need of reappraisal. While the dinoflagellates are important contributors to the primary productivity of the seas, they also have significant roles as osmotrophs and phagotrophs.

Not only is holozoic nutrition common among a large number of species of the larger non-thecate dinoflagellates, but also some of the common thecate forms, such as most species of *Peridinium*, are considered non-photosynthetic and may thus add to the heterotrophic component of this heterogeneous group of protists. On the other hand, individual cases of phagotrophy among thecate dinoflagellates do not appear to indicate that it is a significant mode of nutrition in this group.

Of greater consequence to food chain relationships appears to be a large number of non-thecate dinoflagellates, devoid of photosynthetic pigments and presumed to be obligate phagotrophs on the basis of the live observations reported above. These non-thecate dinoflagellates, due to their fragility, disintegrate easily in preserved samples and, as a result, their role as grazers on important prey organisms in the plankton is often overlooked. These fragile forms are particularly conspicuous in the oceanic plankton or in areas where oceanic currents approach the mainland, as in the case of the inshore and offshore waters of southern California. Therefore, special attention should be paid to their sampling and examination alive, if possible, on board ships with adequate laboratory facilities. In this way, a little-known and potentially significant pathway in food chain relationships could be better understood and properly assessed.

Acknowledgement

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