

The Dinoflagellate Genera *Brachidinium*, *Asterodinium*, *Microceratium* and *Karenia* in the Open SE Pacific Ocean

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The morphometry and distribution of the unarmoured dinoflagellates *Brachidinium capitatum* F.J.R. Taylor, *Asterodinium gracile* Sournia, *Microceratium orstomii* Sournia and the toxic species *Karenia papilionacea* Haywood *et Steidinger* have been investigated in open waters of the SE Pacific Ocean. The genus *Microceratium* Sournia is recorded for the first time since the initial description. These taxa showed a high morphological similarity and they may correspond to life stages of a highly versatile single species that is able to project body extensions. *Karenia papilionacea* showed the higher abundance in the surface waters of the more productive areas (the Marquesas Archipelago and the Perú-Chile Current). *Brachidinium capitatum* and *K. papilionacea* often co-occurred, predominating *B. capitatum* in offshore surface waters. *Asterodinium gracile* was recorded at the bottom of the euphotic zone (down to 210 m depth), with a shallower distribution in more productive areas. Intermediate specimens of *Asterodinium-Brachidinium-Karenia*, with variable disposition and size of the body extensions were illustrated.

Key Words: *Asterodinium*, *Brachidinium*, harmful algae bloom, *Karenia papilionacea*, *Microceratium*, phytoplankton, SE Pacific Ocean

INTRODUCTION

Most of the species of the genus *Gymnodinium* Stein were described during the late 1800's and early 1900's. Very little progress has been made since then and the taxonomic system has therefore remained almost unchanged since the 19th century. Biecheler (1934) using a silver-impregnation method observed for the first time the apical groove in *Gymnodinium*. Takayama (1985) based on scanning electron microscopy (SEM) showed several types of apical grooves in unarmoured dinoflagellates. Daugbjerg *et al.* (2000) based on light microscopy, SEM, pigment composition and LSU rDNA sequences split *Gymnodinium* into four genera: *Gymnodinium sensu stricto*, *Akashiwo* G. Hansen *et Moestrup*, *Karlodinium* J. Larsen and *Karenia* G. Hansen *et Moestrup*. Since then, the description of new species of *Karenia* characterized by a short straight apical groove, with fucoxanthin and lacking peridinin, has proliferated. In some cases, a single species has been described under different names such as *K. bicuneiformis* Botes, Sym *et*

Pitcher and *K. bidigitata* Haywood *et Steidinger* and other taxa may be conspecific such as *K. longicanalis* Yang, Hodgkiss *et* G. Hansen and *K. umbella* de Salas, Bolch *et* Hallegraeff (Yang *et al.* 2001; Botes *et al.* 2003; de Salas *et al.* 2004; Haywood *et al.* 2004).

Among the recently described species, *Karenia papilionacea* Haywood *et Steidinger* showed several peculiar characteristics in cultures with an unusual plasticity and high size variability. In culture, *K. papilionacea* is also able to move forward the prominent apical process (Haywood *et al.* 2004, p. 170). Other close species, *K. bicuneiformis*, showed pointed or bulbaceous antapical tips in natural waters that were rounded when the species is cultured (Haywood *et al.* 2004, p. 173). The species of *Karenia* were described based on abundant materials cultured under optimal conditions for growth that does not reproduce the low turbulence and oligotrophic conditions of the open ocean. Consequently little is known on the morphology and the life cycle of species such as *K. papilionacea* under natural conditions.

The dinoflagellate *Brachidinium capitatum* F.J.R. Taylor is a flattened unarmoured taxon easily identifiable by the four radiating elongate antapical extensions, apical process, numerous yellow-green chloroplasts and promi-

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nent nucleus. However, the partially erroneous description by Taylor (1963) based on formalin-preserved specimens induced a mysterious character to *Brachidinium* F.J.R. Taylor. Taylor described *Brachidinium* as a laterally compressed, with no cingulum or sulcus, non-motile dinoflagellate placed in the order Dinococcales Pascher (coccolid or parasitic dinoflagellates). Sournia (1972b) found more specimens of *B. capitatum* with variable morphology and based on single or a few fixed specimens described two new species: *B. taylorii* Sournia and *B. brevipes* Sournia. From the same location, Sournia (1972a, b) described two closely related genera: *Asterodinium* Sournia with the species *A. gracile* Sournia and *A. spinosum* Sournia and *Microceratium* Sournia with the species *M. orstomii* Sournia. *Asterodinium* differs from *Brachidinium* on having two elongate extensions radiating from the hyposome and three extensions from the episome. In comparison with *Asterodinium*, *Microceratium* Sournia has only one extension in the episome and two extensions in the hyposome. Co-occurring with these records, Sournia found gymnodinioid cells that he considered close to *Brachidinium*, illustrating the species recently described as *Karenia papilionacea* (Sournia 1972b, p. 157; Haywood *et al.* 2004, p. 171). Later Sournia (1986, p. 49) with the sentence "il pourrait s'agir ici de stades de développement d'autres dinoflagellés plus notoires" was hypothesizing that the brachidiniaceans, members of the genera *Brachidinium*, *Asterodinium* and *Microceratium*, constitute life stages of more common dinoflagellates.

The brachidiniaceans have remained under-investigated during decades. Gómez *et al.* (2005a, b) based on light and scanning electron microscopy revealed the morphological similarities among *Brachidinium capitatum*, *Asterodinium gracile* and *Karenia papilionacea*. These three taxa coincided in distinctive morphological characters such as the straight apical groove, cingulum-sulcus juncture, prominent nucleus in the left hyposome, numerous yellow-green chloroplasts, among other characters (Gómez *et al.* 2005b). Consequently the Sournia's (1986) hypothesis reappeared and the brachidiniaceans may be life stages of common coastal species that are able to project body extensions. In coastal waters, brachidiniaceans with no extensions may be polled as unidentified gymnodinioid cells under routine microscopical analysis or referred as *Karenia brevis*-like cells before the description of *K. papilionacea* (Iizuka 1975; Fraga and Sánchez 1985; Nézan 1998).

Within this context, a cruise along a transect of 7500 Km from the Marquesas Archipelago to the Chilean

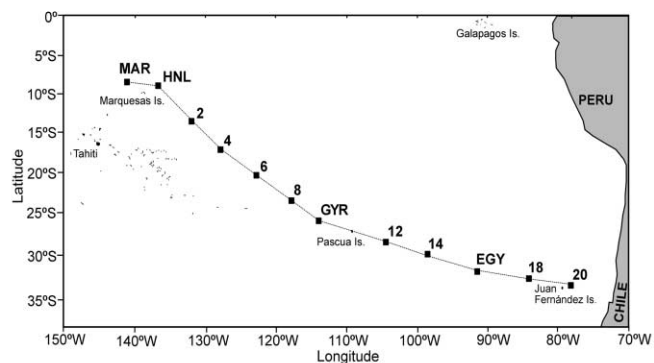


Fig. 1. Map of the sampling stations during the BIOSOPE cruise in the SE Pacific Ocean.

coasts through the severe oligotrophic waters of the South Pacific Gyre (Claustre and Maritorena 2003) provides the opportunity to investigate the distribution of the brachidiniaceans and *K. papilionacea* under different trophic regimes. The present study also investigates the morphometry of *Brachidinium capitatum*, *Karenia papilionacea* and *Asterodinium gracile*. *Microceratium orstomii* has been recorded for the first time since the initial description. Intermediate specimens among these genera, with variable disposition and size of the body extensions are illustrated. The hypothesis of the conspecificity of these taxa is reported.

MATERIALS AND METHODS

Samples were collected at 12 stations from 5 to 270 m depth during the BIOSOPE (Biogeochemistry and Optics South Pacific Experiment) cruise on board *R/V L'Atalante* from 26 October to 12 December 2004 (Fig. 1). Eighty three samples collected by Niskin bottles were preserved with acidified Lugol's solution and stored at 5°C. Samples of 500 mL were concentrated via sedimentation in glass cylinders. Along 6 days, the top 450 mL of sample was progressively slowly siphoned off with small-bore tubing. Fifty mL of concentrate representing 500 mL whole water was settled in composite settling chambers. The entire chamber was scanned at 200× with an IX71 inverted Olympus microscope equipped with a DP70 Olympus digital camera and each specimen was photographed and measured at 400× with the DP70-BSW software (Olympus, Tokyo, Japan).

The percentage of surface irradiance at each depth was calculated from underwater PAR (Photosynthetic Active Radiation, 400-700 nm) profile performed by a PNF-300 Profiling Natural Fluorometer sensor (Biospherical Instruments, San Diego, U.S.A.). The limit of the euphot-

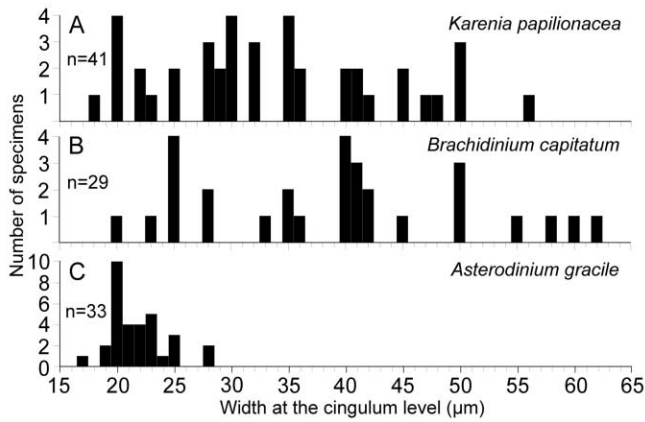


Fig. 2. Histograms of the width at the cingulum level of the records of A. *Karenia papilionacea*, B. *Brachidinium capitatum* and C. *Asterodinium gracile*.

ic zone corresponds to the depth where PAR is reduced to 1% of its surface value. The variables represented in the section plots were produced by interpolation between casts using the kriging as the gridding method in the Surfer software (Golden Software, Golden, U.S.A.).

RESULTS

Karenia papilionacea

A total of 41 specimens have been ascribed to the “standard” *K. papilionacea*. The width at the cingulum level ranged from 18 to 56 μm with an average width of $33.7 \pm 10 \mu\text{m}$ (Fig. 2A). *Karenia papilionacea* and *B. capitatum* often co-occurred and the former predominated in the surface waters of productive regions (MAR and St. 20) whereas *B. capitatum* prevailed in oligotrophic off-

shore stations (Figs 3A, B). The highest abundance of *K. papilionacea*, 12 cells L^{-1} , was recorded at 15 m depth in open waters of the Perú-Chile Current near the Juan Fernández Archipelago and 8 cells L^{-1} near the Marquesas Archipelago (Fig. 3A). However, in these regions the abundance was higher if the specimens that cannot be strictly ascribed to *K. papilionacea* are included (Figs 4I, J)

Brachidinium and *Asterodinium* are easily identifiable due to the distinctive body extensions. The cell body of *K. papilionacea* corresponded to that of *Brachidinium* lacking the extensions, maintaining the distinctive apical process, the prominent round to oval nucleus located in the left hyposome and the yellow-green pigmentation. The cell outline of the “standard” *K. papilionacea* showed a butterfly (Figs 4A-C) or Mexican-hat shape (Figs 4D-F). As reported in the cultures, in the present study large specimens ($>40 \mu\text{m}$ wide) of *K. papilionacea* co-occurred with the smaller ones (Figs 4G, H). Other specimens with an elongate ellipsoidal shape and an apex that varied greatly from a pointed process to a prominent overhanging apical process could not be strictly assigned to *K. papilionacea* (Figs 4I, J). One of these specimens showed a nucleus that occupied most of the hyposome (Fig. 4I).

Brachidinium capitatum

A total of 29 specimens of *B. capitatum* were observed. The width at the cingulum level ranged from 20 to 62 μm with an average value of $39.1 \pm 11.5 \mu\text{m}$ (Fig. 2B). The largest dimension of *Brachidinium* ranged from 65 to 130 μm with an average value of $98.4 \pm 27.1 \mu\text{m}$.

All the specimens of *Brachidinium* appeared in the

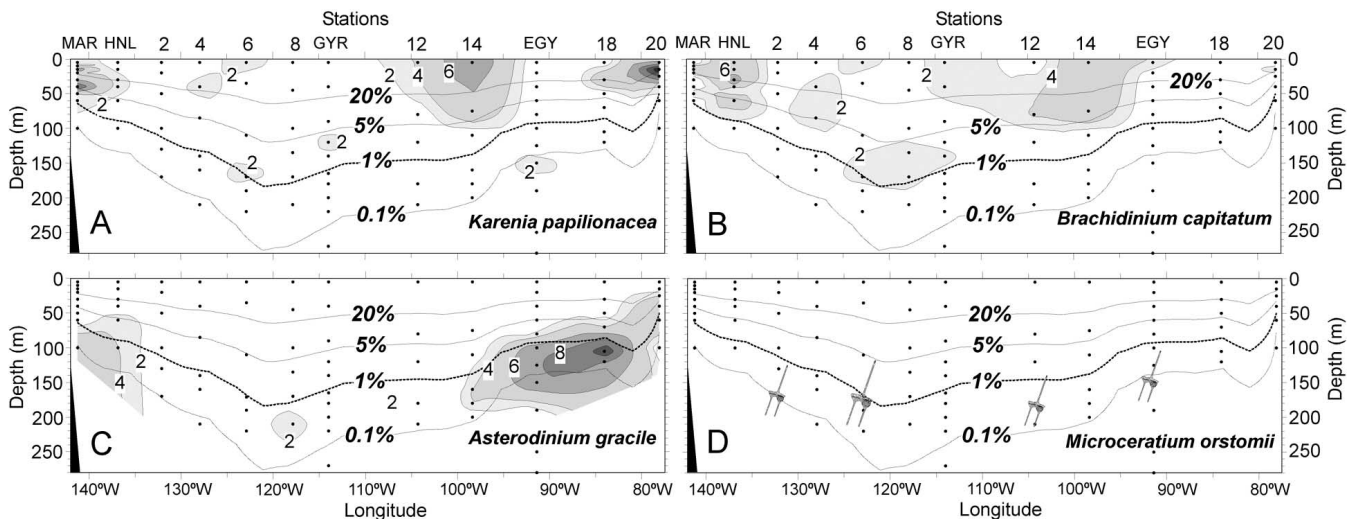


Fig. 3. Section plots of the distribution of A. *Karenia papilionacea*, B. *Brachidinium capitatum*, C. *Asterodinium gracile* and D. *Microceratium orstomii*. Abundance expressed as cells L^{-1} . The dashed lines represent the percentage of the surface irradiance.

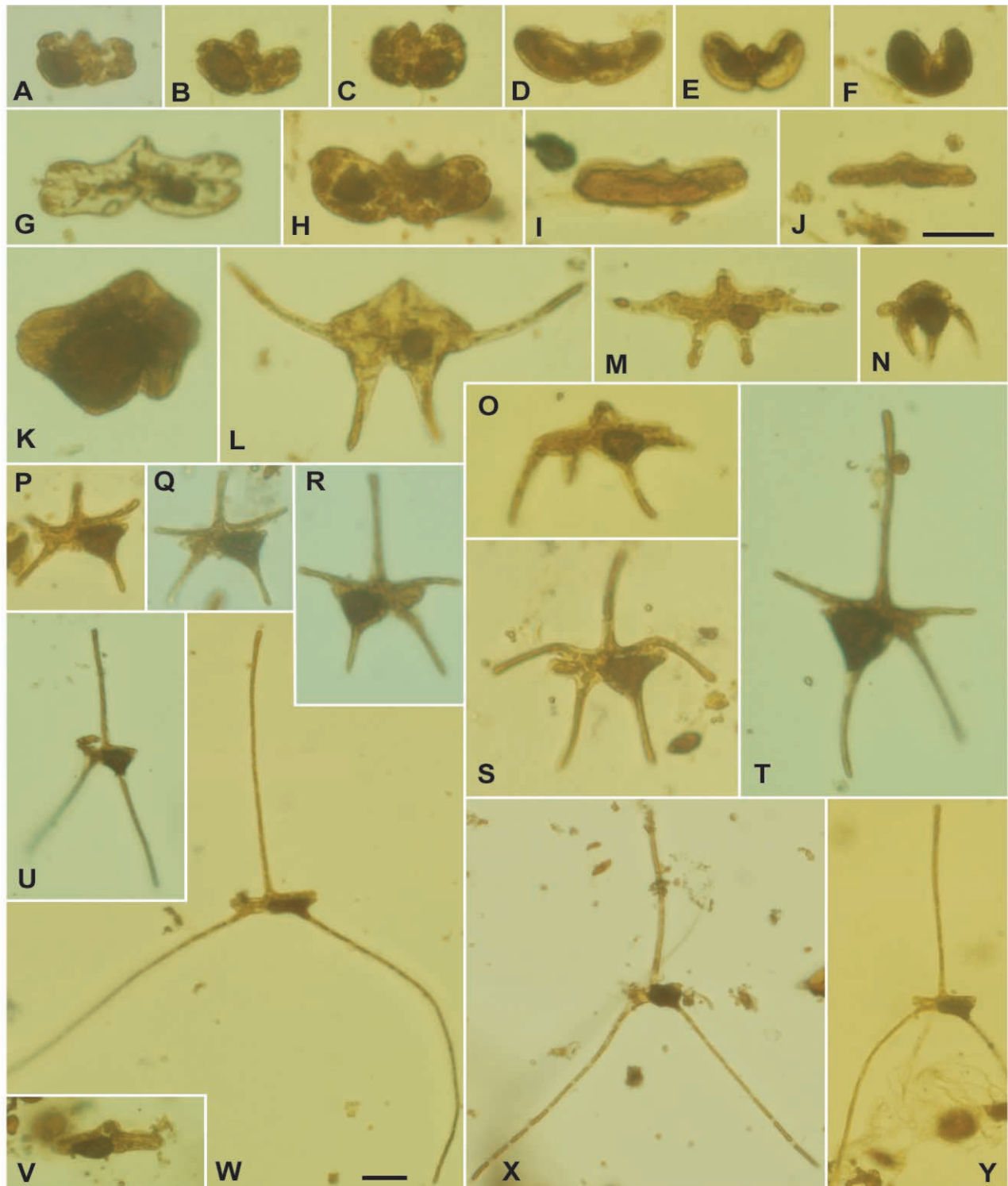


Fig. 4. Photomicrographs of brachidiniacean-*Karenia*, bright field optics. A-C. Butterfly-shaped *Karenia papilionacea*, D-F. Mexican hat-shaped *K. papilionacea*, G-H. Large cells of *K. papilionacea*, I-J. Unidentified ellipsoidal *Karenia* (note the large nucleus in Fig. 4I), K. Unidentified *Karenia* with the conical episome, L. Unidentified *Brachidinium* with the conical episome, M. *Brachidinium capitatum*, N. Unidentified small *Brachidinium* with a round episome, O. *B. capitatum* with extensions of different size, P-T. Specimens of *Asterodinium* with variable degree of development of the extensions, U. W-Y, *Microceratium orstomii*, V. Unidentified *Karenia*-like cell occurring with Fig. 4W. Location (see Fig. 1) and depth of the records: A. HNL 40 m, B. St. 20 15 m, C. GYR 120 m, D. MAR 40 m, E. St. 14 5m, F. MAR 40 m, G. St. 14 5 m, H. MAR 15 m, I. EGY 150 m, J. St. 18 30 m, K. St. 20 60 m, L. EGY 75 m, M. GYR 5 m, N. MAR 20 m, O. St. 14 5 m, P. MAR 100 m, Q. HNL 60 m, R. EGY 150 m, S. St. 8 210 m, T. St. 20 60 m, U. EGY 150 m, V-W. St. 6 170 m, X. St. 2 170 m, Y. St. 12 180 m. All the photomicrographs at the same magnification, except the figures U-Y that are reduced by a factor of 1.6. Scale bars: 20 μ m.

euphotic zone. Its vertical distribution was wider in open waters and shallower near the Marquesas Archipelago and the Perú-Chile Current. The deepest record occurred at 170 m depth in the clearest waters associated with the South Pacific Gyre. The highest abundance, 6 cells L⁻¹, was recorded at 30 m depth in the surrounding waters of the Marquesas Archipelago (Fig. 3B). The length of the extensions showed a high variability. Nearly all the specimens had four extensions of similar length that can be interpreted as a synchronic growth of the body extensions (Fig. 4M). Exceptionally one of the specimens showed two alternate extensions longer than the other ones (Fig. 4O). If a non-synchronic growth of the extensions is discarded, it can be speculated that *Brachidinium* transforms into *Asterodinium* by the retraction of two of the four antapical extensions and the projection of the apical process. Nearly all the specimens of *Brachidinium* showed the distinctive apical process with variable degree of development (Figs 4L-O). One large specimen showed a conical episome, lacking the apical process (Fig. 4L). The contour of its episome resembled that of unidentified *Karenia* specimens that often co-occurred (Fig. 4K). One of the specimens of *Brachidinium* showed the smallest dimensions observed with only 16 µm wide and one of the lateral extensions was incompletely developed. The shape of the episome, round and lacking the apical process (Fig. 4N), resembled that in *Karenia bicuneiformis*. Both species of *Karenia*, *K. papilionacea* and *K. bicuneiformis* are very close genetically and coincided in the main morphological characters (Haywood *et al.* 2004). Despite the shape and position of the nucleus is not usually conservative in some species of *Karenia*, the nucleus in *K. papilionacea*, *K. bicuneiformis*, *Asterodinium*, *Brachidinium* and *Microceratium* was invariably located in the left hyposome.

Asterodinium gracile

A total of 33 specimens of *Asterodinium gracile* were observed. The width at the cingulum level ranged from 17 to 28 µm with an average value of 22.2 ± 4 µm, showing less size variability than in *B. capitatum* and *K. papilionacea* (Fig. 2C). The largest dimension of *Asterodinium* ranged from 35 to 200 µm (85.3 ± 57.1 µm). Nearly all the specimens were collected below the euphotic zone with the deepest record at 210 m depth (St. 8, Fig. 4S), coinciding with clearest waters (Fig. 3C). None specimen appeared in surface waters and the vertical distribution of the records of *Asterodinium* was shallower in more eutrophic stations (Fig. 3C). Some of the shallower

records of *A. gracile* coincided with the deeper records of *B. capitatum*. *Karenia papilionacea* and *A. gracile* did not usually co-occur in open waters, except a few records of elongated cells of *K. papilionacea* below the euphotic zone (Fig. 3A). The highest abundance of *A. gracile* was recorded at St. 18 with 10 cells L⁻¹ at 100 m depth (Fig. 3C). The variable degree of development of the body extensions in *A. gracile* is shown in Figs 4P-T. In well-developed specimens, the right hyposome was reduced and the cell body contents were expanded into the adjacent body extensions. However, the left hyposome cannot be reduced due to containing the prominent nucleus (Fig. 4T).

Microceratium orstomii

Four *Asterodinium*-like specimens with only 3 extensions, intermediate between *Asterodinium* and *Brachidinium* in terms of body extensions, corresponded to the description of *M. orstomii* (Sournia 1972a). From the episome only arose the elongate apical process or central apical extension and from the hyposome arose 2 antapical extensions (Figs 4U, W-Y). The extensions of *Microceratium* tended to be longer than in the common 5-extensions *Asterodinium*. The width at the cingulum level of *Microceratium* with values between 20-25 µm was similar to that of *A. gracile*. Exceptionally one of the specimens reached 310 µm of total length and 40 µm wide at the cingulum level, being the largest brachidiniacean observed (Fig. 4W). This specimen co-occurred with one specimen of a large elongated unidentified *Karenia* (Fig. 4V). The specimens of *Microceratium* appeared at 150 m (Fig. 4U), 170 m (Figs 4W, X) and 180 m depth (Fig. 4Y; Fig. 3D).

DISCUSSION

Trends in the distribution of the brachidiniaceans-*Karenia papilionacea*

The type species of *Brachidinium* and the other species, *B. taylorii* and *B. brevipes*, were described from surface samples. The two species of *Asterodinium* and *Microceratium orstomii* were collected at 100 m and 75 m depth, respectively (Taylor 1963; Sournia 1972a, b). From the same location, Sournia (1972b) also illustrated *K. papilionacea* collected from surface waters. In the offshore waters of the NE Africa upwelling, Margalef (1975) found exceptionally high abundances (up 4000 cells L⁻¹) of *B. capitatum* in the upper 30 m depth. In the same region, Estrada (1976, 1978) reported up 10000 cells L⁻¹ of *B. capitatum* coinciding with 20000 cells L⁻¹ of flattened

Karenia brevis-like cells in offshore surface waters. Gómez (2003) and Gómez *et al.* (2005a, b) found *Brachidinium* and *Asterodinium* at an average depth of 35 and 85 m, respectively, in several regions of the NW and Equatorial Pacific Ocean. The same pattern was observed in the present study in the SE Pacific Ocean (Figs 3B, C).

Haywood *et al.* (2004) reported that the abundance of *K. papilionacea* was lower than 1000 cells L⁻¹ in the late austral summer in the coasts of New Zealand. In the European Atlantic coasts *Karenia brevis*-like cells also appear in summer with abundances that never exceeded 1500 cells L⁻¹ (Nézan 1998). Yeung *et al.* (2005) found *K. papilionacea*-like cells with an abundance of 10 cells L⁻¹ in the pier of the Hong Kong University. In the present study in open waters, the higher abundances of *K. papilionacea*, 10 cells L⁻¹, were found in the more productive regions.

Adaptation to light availability

The brachidiniaceans and *Karenia* are characterized by an unusual yellow-green bright pigmentation. *Brachidinium* and *Karenia* were encountered in the surface and *Asterodinium* and *Microceratium* below the euphotic zone. The records below the euphotic zone and surface waters of tropical seas required highly versatile pigment composition to adapt to different light regimes. Most of dinoflagellates have chloroplasts that contain chlorophyll *c*₂ and peridinin as the major carotenoid. However, the chloroplasts of *Karenia* have chlorophylls *c*₁ + *c*₂ and fucoxanthin-derived carotenoid but lacks peridinin (Tangen and Bjørnland 1981), originated from a haptophyte tertiary endosymbiosis in an ancestral peridinin-containing dinoflagellate (Yoon *et al.* 2002). *Karenia brevis* (Davis) G. Hansen *et* Moestrup, responsible of massive toxic blooms in the Gulf of México, is the best known species of the genus. This species has a robust photosynthetic capability and accumulation of diadinoxanthin and diatoxanthin depending of the irradiance with minor adjustments in chlorophyll *a* and fucoxanthin contents that facilitate acclimation to variable irradiance regimes (Evens *et al.* 2001). This pigment plasticity could explain that *Asterodinium* can survive near the nutricline below 200 m depth with less than 0.1% of the surface irradiance. The availability of nitrate near the nutricline also favored the pigment accumulation as observed in *Asterodinium* (Gómez 2003; Gómez *et al.* 2005b). In addition, the cell shape of *A. gracile* with a strongly flattened cell body and elongate extensions seems to be an adaptation to increase the cross-section in light limiting condi-

tions. Other shade flora members such as *Ceratium platycorne* Daday have highly pigmented wide flattened extensions (Sournia 1982).

Size and shape changes

The high variability of the size of the extensions of the brachidiniaceans has been remarked since the early works. In the description of *Brachidinium*, Taylor (1963) reported "the species is interesting in that the cells appear to exhibit a structural adaptation to their environment, namely, the production of elongate processes ... in this connection it might also be noted the specimen ... in less dense water exhibited a greater elongation of processes". The number of extensions of *Microceratium* (3-extensions) was lower, but the length of each extension was longer than in the typical 5-extensions *Asterodinium* (Figs 4P-Y). In addition to the increase of the cross-section for the photosynthesis, the elongated extensions are supposed to be associated with a reduction of the sinking speed and consequently a reduction of the energy required maintaining the cell in the euphotic zone. The projection of body extensions has been considered as an adaptive strategy for warm water dinoflagellates under low turbulence conditions (Zirbel *et al.* 2000).

Although the cell size is often an important taxonomic character in dinoflagellates, it can be variable. This variability was especially notorious in cultures of *K. papilionacea* with a usual range of width of 18-32 μ m, but also co-occurring with cells 65-90 μ m wide (Haywood *et al.* 2004) that has been also observed in natural waters in the present study (Figs 4G, H). Haywood *et al.* (2004, p. 175) reported "small to large cells present in cultures that were not separated into size classes because of the intergradations between sizes and because the significance of the size classes cannot be addressed until the life cycle of these species is known." *Karenia papilionacea* is also characterized by fast changes of shape and in cultures the apical process contracts forward when the cells are stressed (Haywood *et al.* 2004, p. 170) as already illustrated Sournia (1972b, p. 157). The live cells of *Brachidinium* were able to move the body extensions (Léger 1971; Gómez *et al.* 2005a). *Karenia bicuneiformis* was also able to change its morphology and the pointed or bulbaceous antapical tips observed in natural waters disappeared and the cells are rounder in cultures (Haywood *et al.* 2004, p. 173).

According to Raven (1986) the reduced size of the "small" subpopulations of microalgae allows an optimization of photon capture and nutrient uptake, such

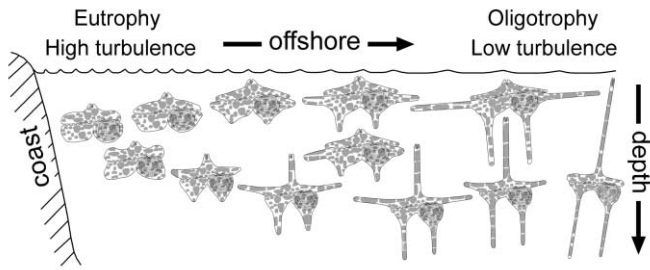


Fig. 5. Scheme of the distribution of the tentative life stages of *Brachidinium capitatum*.

that they may take optimal advantage of the conditions generally prevailing during the blooms (i.e., availability of nutrients, turbulence). In contrast, the “large” forms appeared to be more adapted for survival under non-bloom conditions (Raven, 1986). Consequently under the optimal conditions for growth such as cultures and eutrophic coastal waters, the smaller forms of *K. papilionacea* will predominate, whereas in open waters the projection of body extensions would constitute a competitive advantage (Fig. 5). Toxic species such as *Karenia* have been intensively investigated in high turbulence conditions such as cultures and coastal waters. Little is known on the adaptation of these species to the stratified open ocean.

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