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NOTE

# Grazing impacts of the heterotrophic dinoflagellate *Polykrikos kofoidii* on a bloom of *Gymnodinium catenatum*

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ABSTRACT: In 1998, a red tide of the paralytic shellfish poisoning (PSP)-producing dinoflagellate *Gymnodinium catenatum* Graham occurred in Yatsushiro Sea, western Japan. The dramatic decline of dominant *G. catenatum* cells occurred during the field and laboratory assessments, accompanied with growth of the heterotrophic dinoflagellate *Polykrikos kofoidii* Chatton. Microscopic observations on both field and laboratory cultured bloom water revealed that >50% of *P. kofoidii* predated on the natural population of *G. catenatum*, and 1 to 8 *G. catenatum* cells were found in food vacuoles of *P. kofoidii* pseudocolonies. Our results suggest that predation by *P. kofoidii* contributes to the cessation of a *G. catenatum* bloom.

KEY WORDS: PSP · *Gymnodinium catenatum* · *Polykrikos kofoidii* · Harmful algal bloom · Predation · Heterotrophic dinoflagellate

Recent increases in toxic dinoflagellate blooms and subsequent shellfish poisoning have led to social and industrial concern worldwide (Shumway 1990, Hallegraeff 1993, Anderson 1994). The chain-forming toxic dinoflagellate *Gymnodinium catenatum* Graham is one of the causative species responsible for paralytic shellfish poisoning (PSP) outbreaks in Australia (Hallegraeff et al. 1989), Japan (Ikeda et al. 1989, Matsuoka & Fukuyo 1994), Mexico (Mee et al. 1986), and Spain (Fraga et al. 1988, Sampayo 1989). An apparent increase of PSP outbreaks due to *G. catenatum* blooms has occurred worldwide in the last 2 decades (Hallegraeff 1993). Therefore, data on the hydrographic and ecological mechanisms controlling *G. catenatum* blooms are urgently needed.

In January 1998, a massive bloom due to *Gymnodinium catenatum* occurred for the first time in Yatsushiro Sea, western Kyushu Island, Japan. We designed an assessment of the natural population of *G. catenatum* coupled with a laboratory incubation experiment to evaluate the bloom fate. We present data showing considerable predation by the pseudocolonial heterotrophic dinoflagellate *Polykrikos kofoidii* Chatton on the dominant *G. catenatum* population, and discuss the ecological importance of the genus *Polykrikos* and its grazing impact on harmful algal blooms.

**Materials and methods.** ***Filed population surveys:*** The *Gymnodinium catenatum* bloom occurred from 19 January to 5 February in Miyano-Gawachi Bay, western Yatsushiro Sea, Kyushu Island (Fig. 1). Five cruises were carried out to survey plankton during the bloom period. Seawater samples were collected by Niskin water samplers and stored in plastic bottles until counting (ca 3 h). Water temperatures and salinities were measured by a conductivity, temperature, depth profiler (CTD); TSURUMI SEIKI Model 3-G. For each cruise, duplicate samples were examined microscopically for identification and abundance of plankton cells using Sedgewick-Rafter chambers. When cell density was less than $10^3$ $l^{-1}$, seawater samples (100 ml) were gently concentrated on nylon mesh (10 µm pore size) and counted immediately. This procedure was performed without sample fixation.

***Laboratory experiment:*** In order to evaluate the succession of phytoplankton and other microorganisms in the bloom water, a simulated bloom experiment was designed in the laboratory. On 22 January, 20 l of seawater was collected from 0.5 m depth (water temperature 13.0°C) and transferred to an acid-rinsed (1 N HCl) opaque tank. The sample was sent overnight by car to the National Research Institute of Fisheries and Environment of Inland Sea (16:00 to 08:30 h). 10 l of this bloom water was then transferred into a transparent plastic vessel (Ø0.8 × 0.95 m) and cultured for 11 d in a photo chamber (SANYO, MBCR-2525CP) at

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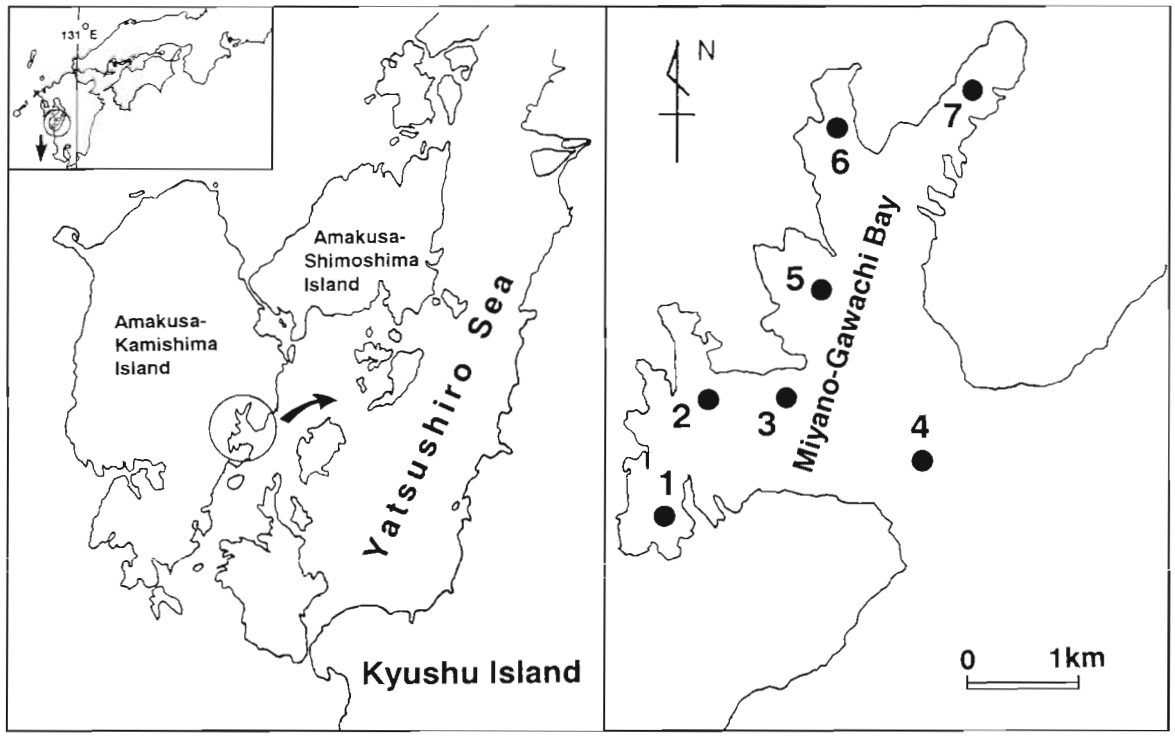



Fig. 1. Sampling station in Miyano-Gawachi Bay, located in western Kyushu Island

13.0 ± 1.3°C, with a 10:14 h L:D cycle under illumination of ca 60 µE $m^{-2}$ $s^{-1}$ provided by cool-white fluorescent lamps. Constant stirring and shaking of the medium were not performed during the experiment. 100 ml of the seawater was gently concentrated on a nylon mesh as described above and plankton cells were counted each day. In order to determine the frequency of *Polykrikos kofoidii* predation on *Gymnodinium catenatum* cells, observations were carried out using an epifluorescent microscope (OLYMPUS IX70) attached to a VTR system (IKEGAMI time lapse video recorder TVR-7480, Victor color video monitor TM-150S, SONY camera adapter CMA-D2) and a PANASONIC color video printer (NV-MP50). On 30 January, the number of spherical autofluorescence bodies in *P. kofoidii* food vacuoles which were assumed to be captured *G. catenatum* cells were counted individually (= 245 *P. kofoidii* pseudocolonies) under blue light excitation. The *P. kofoidii* cells were immobilized using nickel chloride treatment at a final concentration of ca 40 µg $l^{-1}$ (Matsuyama et al. 1997). Plankton cell size and volume were determined on the immobilized cells. Cell volume of plankton was calculated on the basis of their linear dimensions, assuming simple geometrical shapes. Biomass (µg C $l^{-1}$) conversions were estimated by applying equations published elsewhere (Mullin et al. 1966, Strathmann 1967, Edler 1979, Lessard 1991, Verity et al. 1992). The calculation of cell volumes in *P. kofoidii* was carried out based on the measurement on non-*G. catenatum* prey individuals. Cell ingestion rate $I_C$ (*G. catenatum* cells $d^{-1}$) during the experiment was calculated using the following equation (Goldman et al. 1989): $I_C = \Delta N_{GC}/\bar{N}_{PS}\Delta t$ where $\Delta N_{GC}$ is decrease in *G. catenatum* cell density; $\bar{N}_{PS}$ is ln average cell density of *P. kofoidii* during the experiment; $\Delta t$ is length of experiments (days). Calculation of $I_C$ was carried out using the data sets obtained from 27 through 31 January. In this case, all decreases in concentration of *G. catenatum* during the experiment is assumed to be due to *P. kofoidii* predation.

**Results.** ***Field observations:*** The *Gymnodinium catenatum* bloom reached a maximum density of 6.27 × $10^5$ cells $l^{-1}$ on 28 January. The highest density of this alga was observed in the innermost part of Miyano-Gawachi Bay (Fig. 2.), and seawater appeared to be dark brown in color (red tide). Water temperatures and salinities ranged from 13 to 15°C and from 31 to 32 psu, respectively. During the *G. catenatum* bloom, massive PSP toxin levels were observed in filter-feeding bivalves: 65.6 MU (mouse unit) $g^{-1}$ in short-necked clam *Ruditapes philippinarum* and 438 MU $g^{-1}$ in Pacific oyster *Crassostrea gigas*. PSP data from shellfish were obtained from the local government (Kumamoto Prefecture, AOAC methods).

Recently, *Gymnodonium nolleri* Ellegaard et Moestrup, which were thought to have a great morphological similarity with *G. catenatum*, were found along the Denmark coast (Ellegaard et al. 1993, Ellegaard & Oshima 1998). Based on the laboratory culture and HPLC analysis, it has been shown that the culture strain of *G. catenatum* obtained from Miyano-Gawachi Bay forms long chains (16 to 32 cells) and produces PSP toxins (S. Sakamoto pers. comm.). Therefore, the present bloom-forming *G. catenatum* is identical with widespread *G. catenatum* species causing PSP outbreaks (Hallegraeff 1993).

Fig. 3A shows the changes in cell densities of *Gymnodinium catenatum*, and the co-occurring heterotrophic dinoflagellate *Polykrikos kofoidii* pseudocolonies (equivalent spherical diameter [ESD = ca 50 µm]) in Miyano-Gawachi

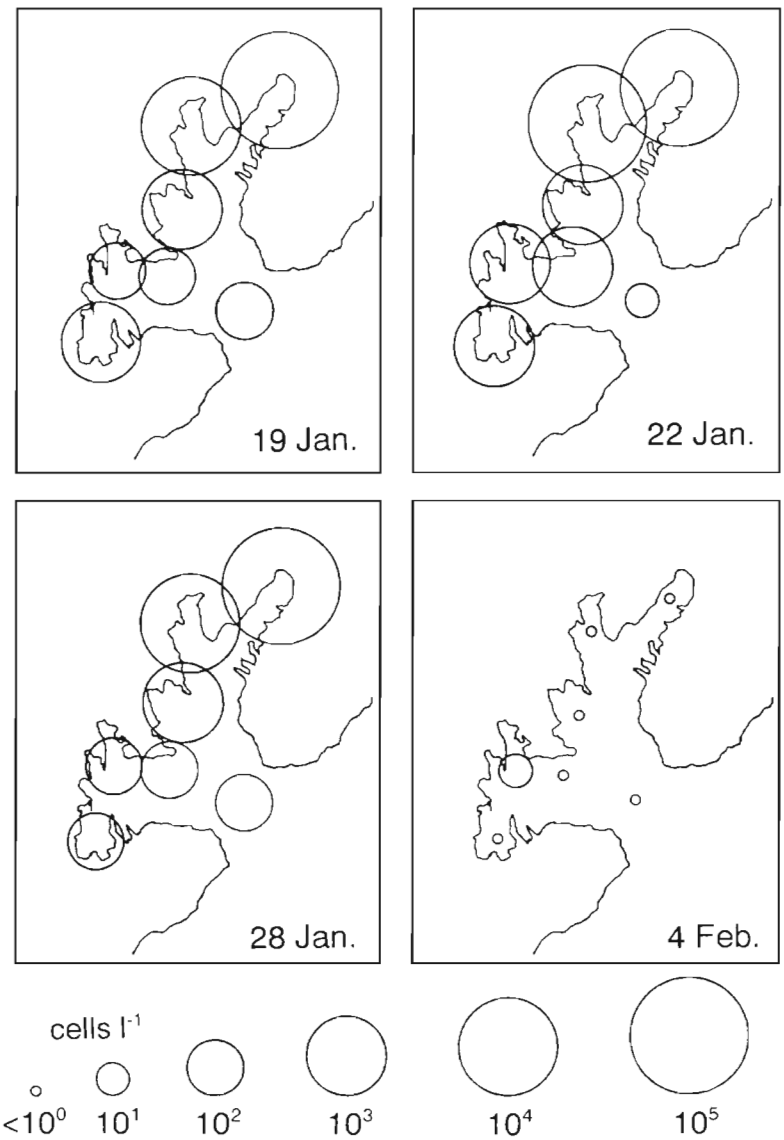



Fig. 2. Temporal changes of horizontal distribution of *Gymnodinium catenatum* in Miyano-Gawachi Bay, from 19 January to 4 Feburary. Cell densities (*G. catenatum* cells l$^{-1}$) are expressed as mean cell count in the water column (0.5, 2, 5 m depth). Seawater samples for laboratory incubation were collected at 0.5 m depth at Stn 7 on 22 January

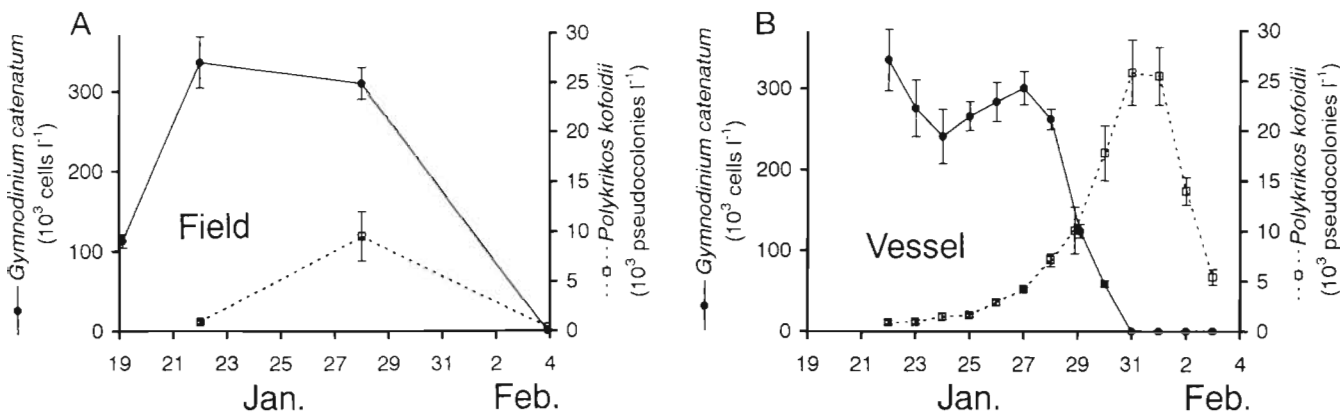



Fig. 3. Changes in cell density of *Gymnodinium catenatum* and co-occurring *Polykrikos kofoidii* in field (A; Stn 7) and in vessel (B). Field data is expressed as mean cell density of the water column at Stn 7 (see Fig. 1). Bars indicate duplicate counting errors (SE)

Table 1. Changes in the estimated species-specific biomass (µg C $l^{-1}$) in the vessel culture

| | Date | | |
|---|---|---|---|
| | Jan 23 | Jan 27 | Jan 31 |
| Diatoms | | | |
| *Actinoptychus* sp. | 0.1 | 0.2 | 0.1 |
| *Cerataulina* spp. | 0.3 | | |
| *Chaetoceros* spp. | 0.5 | 0.3 | 1.0 |
| *Coscinodiscus wailesii* | 0.9 | 3.7 | 29 |
| *Coscinodiscus* sp. | 0.1 | 0.2 | 1.5 |
| *Detonulla pumila* | 2.0 | 2.0 | 3.9 |
| *Ditylum brightwellii* | 0.3 | 0.2 | 0.7 |
| *Eucampia zodiacus* | 5.9 | 1.9 | 1.4 |
| *Guinardia flaccida* | 0.3 | 0.001–0.1 | 0.001–0.1 |
| *Hemiaulus* spp. | | | 0.1 |
| *Leptocylindrus danicus* | 0.001–0.1 | 0.001–0.1 | 0.2 |
| *Nitzschia* spp. | 0.001–0.1 | 0.001–0.1 | 0.001–0.1 |
| *Odontella longicruris* | | | 0.1 |
| *Pleurosigma* sp. | 0.001–0.1 | 0.1 | 0.001–0.1 |
| *Pseudo-nitzschia* sp. | 0.001–0.1 | 0.001–0.1 | 0.1 |
| *Rhizosolenia* sp. | 0.001–0.1 | 0.001–0.1 | 0.1 |
| *Skeletonema costatum* | 0.3 | 0.6 | 3.5 |
| *Stephanopyxis palmeriana* | | | 0.2 |
| *Thalassiosira* spp. | 1.1 | 0.3 | 0.6 |
| *Thalassionema* sp. | 0.001–0.1 | 0.001–0.1 | 0.001–0.1 |
| *Thalassiothrix* sp. | 0.001–0.1 | 0.001–0.1 | 0.1 |
| Flagellates | | | |
| *Dinophysis acuminata* | | 0.001–0.1 | 0.001–0.1 |
| *Distephanus speculum* | 0.1 | 0.3 | 1.5 |
| *Eutreptiella gymnastica* | 1.8 | | |
| *Gonyaulax spinifera* | 0.001–0.1 | | |
| *Gonyaulax verior* | 0.4 | 0.1 | |
| *Gymnodinium catenatum* | 899 | 981 | 0.7 |
| *Gymnodinium sanguinum* | 0.2 | 0.1 | |
| *Gyrodinium dominans* | 2.4 | 1.2 | 1.6 |
| *Polykrikos kofoidii* | 23 | 105 | 643 |
| *Protoperidinium pentagonia* | 2.3 | 1.4 | 0.5 |

Bay during the bloom are shown in Fig. 3. *G. catenatum* was dominant (86.8% as cell density, 95.5% as carbon) in the water column on 23 January (Table 1). The bloom (>$10^5$ cells $l^{-1}$) occurred from 19 through 28 January but was not observed on 4 February or thereafter. *P. kofoidii* was first observed on 22 January, at a density of 925 pseudocolonies $l^{-1}$ and increased to 9250 pseudocolonies $l^{-1}$ on 28 January. In field samples, numerous *P. kofoidii* had spherical brown bodies in their food vacuoles (Fig. 4B, C) by 4 February. The population of *P. kofoidii* decreased to 340 pseudocolonies $l^{-1}$. On this date, almost all *P. kofoidii* had less material in their food vacuoles. No *G. catenatum* or *P. kofoidii* were found in samples collected on 10 February (data not shown).

***Interaction of both dinoflagellates under laboratory conditions:*** *Gymnodinium catenatum* maintained its population during the initial 6 d but rapidly declined with increasing density of *Polykrikos kofoidii*, as in the field observations. Microscopic observations revealed that *P. kofoidii* was an active predator (Fig. 3B) on *G. catenatum* (Fig. 5): 50 to 70% of the total *P. kofoidii* pseudocolonies contained autofluorescent bodies (16 to 50 µm diameter) in their food vacuoles which were probably captured *G. catenatum*. It was difficult to confirm whether or not the autofluorescent bodies found in *P. kofoidii* food vacuoles were captured *G. catenatum*. However, the dominant *G. catenatum* was the only component of the phytoplankton having a cell size of ca 16 to 50 µm. Thus, 1 fluorescent body in *P. kofoidii* food vacuoles is thought to be 1 captured *G. catenatum*. During the rapid decreasing phase of the *G. catenatum* bloom, 1 to 8 captured *G. catenatum* cells were frequently observed in *P. kofoidii* pseudocolonies (Fig. 6). When almost all *G. catenatum* had disappeared from the water sample, the composition of *P. kofoidii* food vacuoles markedly decreased and the vacuoles gradually became small.

There are few quantitative studies on the ecological importance of the colonial heterotrophic dinoflagellates *Polykrikos* and *Phaepolykrikos* on phytoplankton, despite their likely importance in coastal ecosystems (Smetacek 1981, Hansen 1991). Nakamura et al. (1992) reported that a heterotrophic dinoflagellate *Gyrodinium* sp. (described as *Gyrodinium dominans* Hulburt) preys upon the raphidophyte *Chattonella antiqua* (Hada) Ono at a rate of 3.6 to 4.8 *C. antiqua* cells $d^{-1}$. According to our preliminary $I_C$ estimation, a *P. kofoidii* pseudocolony preys on *Gymnodinium catenatum* at a rate of 2.7 to 16.2 *G. catenatum* cells $d^{-1}$ (mean 6.3 *G. catenatum* cells $d^{-1}$). Direct microscopic observations confirmed that *P. kofoidii* is likely able to prey on 2 to 8 cells of chained *G. catenatum* (see Fig. 6). This ability probably contributes to the comparatively high estimate of ingestion rates. On the other hand, our estimation of ingestion rates is probably an overestimate because other organisms such as ciliates and copepods may prey on *G. catenatum*, and other causes of mortality in *G. catenatum* were not examined. In addition, the prey growth also gives low ingestion rates in our estimation. However, Blackburn et al. (1989) revealed that *G. catenatum* showed poor growth at 14.5°C and could not grow under 12.5°C. In our study, water temperature in laboratory cultures was kept at 13°C, so that the condition would give little or no growth response to *G. catenatum*, even in a nutrient-rich and photo-provided condition (Blackburn et al. 1989). However, further laboratory experiments

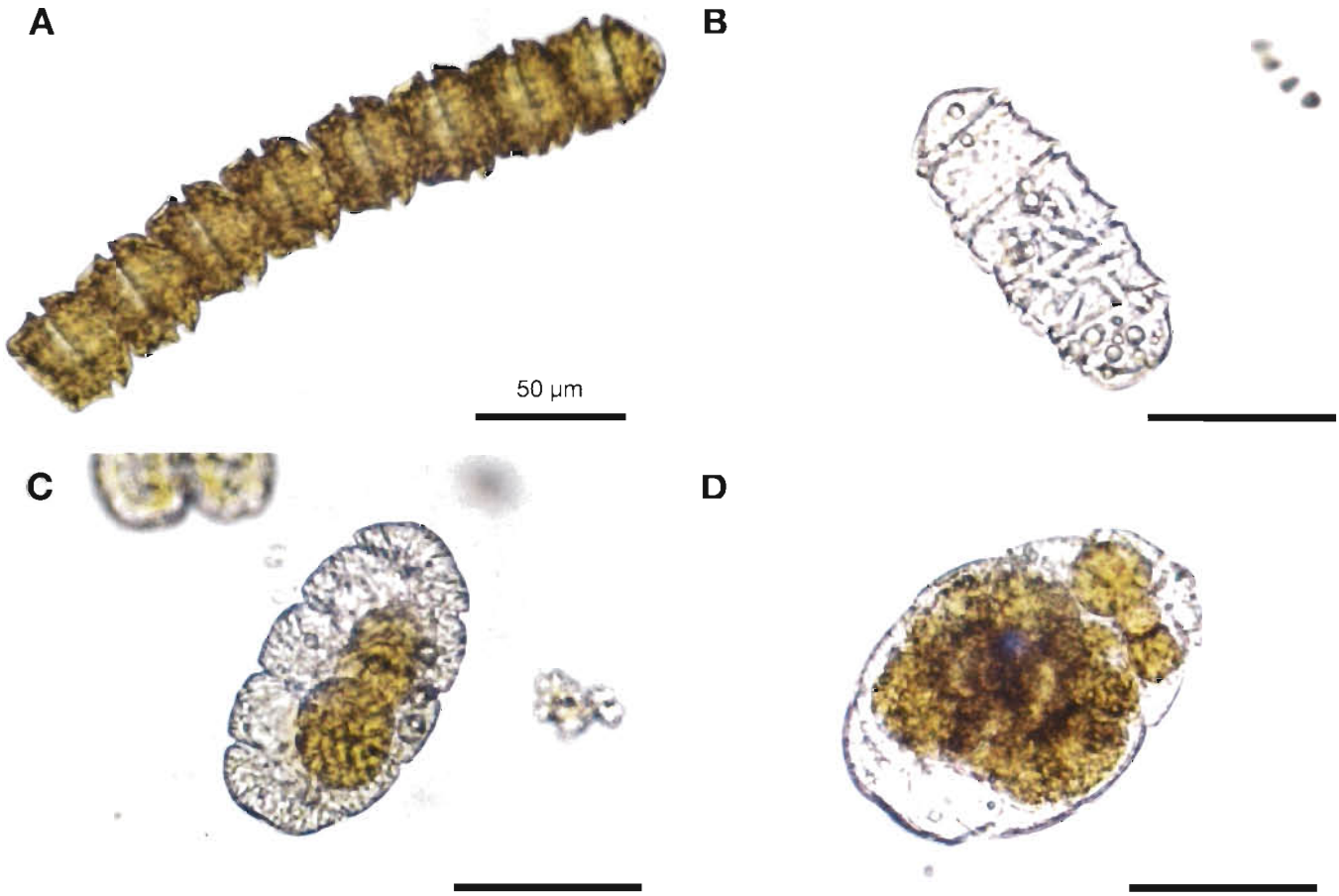
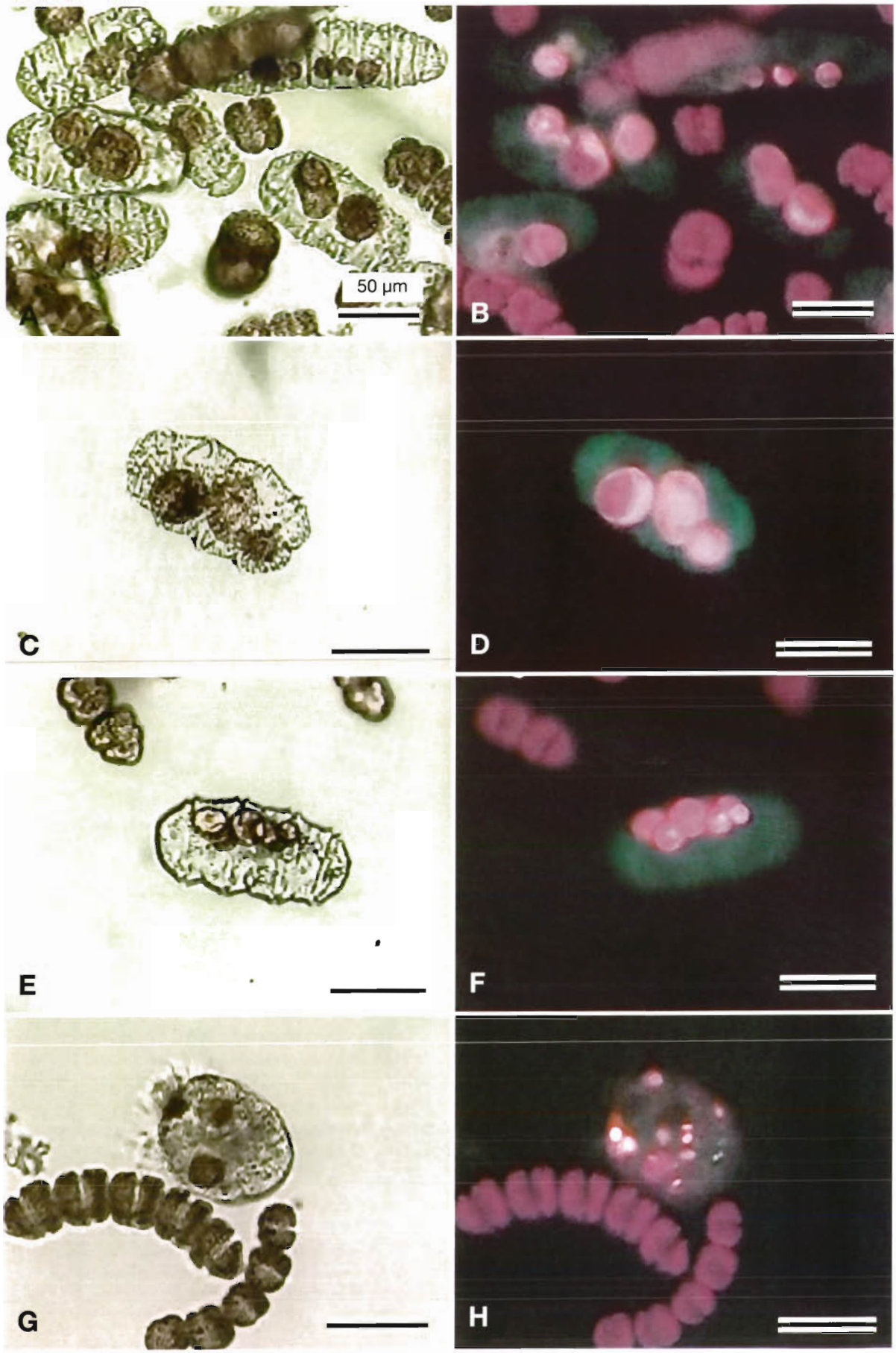



Fig. 4. *Gymnodinium catenatum* and *Polykrikos kofoidii* in field sample collected on 28 January (A) vegetative cells of *G. catenatum*; (B) *P. kofoidii* pseudocolony; (C, D) *P. kofoidii* pseudocolony containing *G. catenatum* cells in their food vacuole

using culture strains are needed in order to clarify the certain effect of *P. kofoidii* on *G. catenatum*.

During the experiment, considerable growth of several ciliates (*Strobilidium* spp., *Tiarina* sp., *Undella* sp., and *Tintinnopsis* spp.) and copepods were also observed (Table 2). Of these, *Strobilidium* spp. contained large fluorescent bodies which probably were captured *Gymnodinium catenatum* in their food vacuoles (Fig. 5G, H), but this was not common (less than 8% of the total cells). A similar low removal by oligotrichine ciliates was also mentioned in a red tide of the naked dinoflagellate *Gymnodinium mikimotoi* Miyake et Kominami ex Oda (Nakamura et al. 1995). Furthermore, the available food cell size for tintinnid ciliates is generally considered to be about half of their lorica oral diameter (e.g. Heinbokel 1978). The oral diameter of tintinnids found in our laboratory experiments ranged from 18 to 31 µm, and they showed little predation on chain-forming *G. catenatum* cells. Other major predators, e.g. copepods, were found at a density of 10 copepods $l^{-1}$ in the vessel, but fluorescence in copepod guts was very weak and approximately 60% of copepods died within 8 d. Hence, we concluded that the effect of ciliate and copepod predation (grazing) on *G. catenatum* was low and considerably less than that of *P. kofoidii* during the present experiment. The rapid *G. catenatum* bloom cessation in field and laboratory appears to be due to the extreme proliferation of *P. kofoidii*.

**Discussion and conclusions.** ***Significance of heterotrophic dinoflagellates in harmful algal blooms:*** Previous studies have demonstrated that various toxic dinoflagellates are rejected as food by active predators such as crustacean zooplankton (Huntley et al. 1986, Ives 1987, Uye & Takamatsu 1990 ) and ciliates (Abe & Hirayama 1979, Hansen 1989, Hansen 1995). This physiological aspect appears to have a significant ecological effect of reducing the grazing pressure during the course of bloom formation in harmful dinoflagellates (Uye & Takamatsu 1990). On the other hand,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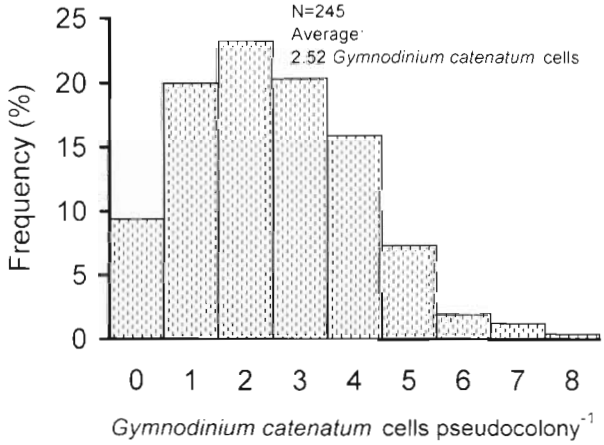


Fig. 6. Frequency of captured *Gymnodinium catenatum* cells in food vacuoles of *Polykrikos kofoidii* in a vessel measured on 30 January

recent research has revealed that harmful dinoflagellate blooms are greatly regulated by the co-occurrence of heterotrophic dinoflagellates (Lessard 1991, Jacobson & Anderson 1996). Natural blooms of the naked dinoflagellate *Gymnodinium mikimotoi*, which is a major nuisance species associated with finfish and shellfish mortalities along the Japanese coast (Honjo 1994), have been shown to be significantly affected by the growth of the heterotrophic dinoflagellate *Gyrodinium dominans* (Nakamura et al. 1995). Some previous studies have noted the co-occurrence of the colonial heterotrophic dinoflagellate *Polykrikos* during the course of PSP-causing dinoflagellate blooms. Carreto et al. (1986) briefly reported that *Polykrikos schwartzii* Bütschli was abundant in a red tide of *Gonyaulax excavata* (formally *Alexandrium tamarense* Balech). They suggested that *P. schwartzii* was the major active predator on the natural *A. tamarense* populations. Recently, Sampayo (1998) reported that *G. catenatum* blooms and subsequent PSP outbreaks in shellfish which occurred around Lisbon, Portugal, frequently ceased due to the proliferation of *P. kofoidii*. Sampayo (1998) was the first to reveal interactions between *G. catenatum* and pseudocolonial heterotrophic dinoflagellates. Our observation of considerable predation by *P. kofoidii* on a natural *G. catenatum* bloom in geographically distant areas suggests that populations of toxic dinoflagellates are often regulated by the proliferation of heterotrophic dinoflagellate predators worldwide.

Table 2. Changes in microzooplankton and copepod densities (ind. $l^{-1}$) observed in the vessel culture

| | Date | | |
|---|---|---|---|
| | Jan 23 | Jan 27 | Jan 31 |
| *Strobilidium* sp. | 100 | 420 | 1200 |
| *Tiarina* sp. | <10 | <10 | 20 |
| *Tintinnopsis* sp. | 20 | 40 | 350 |
| *Undella* sp. | 10 | 10 | 80 |
| Copepods | 10 | 10 | <10 |

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Fig. 5. (A–F) Fluorescent microscopic observations on *Polykrikos kofoidii* in the vessel. (A) *Gymnodinium catenatum* and *P. kofoidii* assemblages; (B) the same assemblages under blue light excitation; (C–F) *P. kofoidii* pseudocolony observed by light microscope and blue light excitation; (G) *Strobilidium* sp. under the light microscope; (H) the same *Strobilidium* sp. under blue light excitation

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