plankton biology & ecology © The Plankton Society of Japan 2000

# Summer phytoplankton bloom in Manazuru Harbor, Sagami Bay, central Japan

Fumio Satoh, Koji Hamasaki<sup>1</sup>, Tatsuki Toda & Satoru Taguchi

Faculty of Engineering, Soka University, 1-236 Tangi-Cho, Hachiouji 192–8577, Japan <sup>1</sup>Present address: Faculty of Applied Biological Science, Hiroshima University, 1–4–4 Kagami-yama, Higashi-Hiroshima 739–8528, Japan

Recieved 26 July 1999; accepted 26 April 2000

**Abstract:** Chlorophyll-*a* (Chl-*a*) concentration and carbon fixation rate in pico- (2.0–0.2  $\mu$ m: Pico) and total- (<183  $\mu$ m: Total) particle fractions were determined weekly for surface water in Manazuru Harbor, Sagami Bay, Japan from May 1995 to March 1997. Nitrate and silicate showed the highest and lowest concentrations, respectively, in summer. Distinct summer increases in Chl-*a* concentration was observed for both size fractions with a low contribution by the Pico fraction to the Total (15±6.6%). The surface phytoplankton population responded to a 3–4-d period of continuous precipitation (>200 mm) by increasing Chl-*a* concentrations to higher than 40 mgChl *a* m<sup>-3</sup> during the period leading to warmer water temperatures in both the summers of 1995 and 1996. Carbon fixation rates reached the maximum value of 13 mgC m<sup>-3</sup> h<sup>-1</sup> during the Chl-*a* peak in summer. However, the maximum photosynthetic rate (2.8 mgC [mgChl *a*]<sup>-1</sup> h<sup>-1</sup>) was observed one week earlier than the Chl-*a* peak. These abrupt increases were due to larger phytoplankton such as the dinoflagellate *Ceratium furca* rather than the picoplankton, which were usually dominant in a stratified shallow mixed layer with low nutrient concentrations.

Key words: dinoflagellate, Ceratium furca, chlorophyll a, precipitation, summer bloom

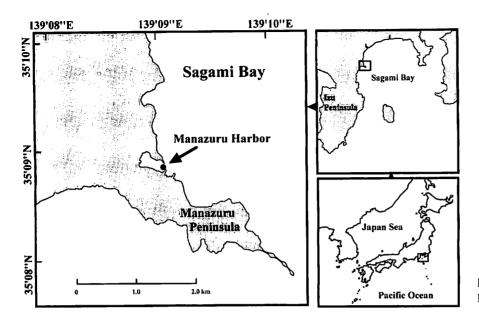
#### Introduction

Phytoplankton populations generally show an abrupt increase in spring and fall in temperate coastal waters (Taguchi et al. 1977; Maita & Odate 1988; Cloern 1991; Falkowski & Raven 1997). The standing stock of phytoplankton is usually relatively low in summer due to a shallow surface mixed layer caused by increases in surface water temperature leading to low nutrient supply (e.g., Mc-Carthy et al. 1977). One of the most persistently dominant group of phytoplankton in these periods are the picoplankton (Joint & Pomeroy 1983; Douglas 1984; Takahashi et al. 1985; Joint et al. 1986; Sondergaard et al. 1991; Iriarte & Purdie 1994; Hamasaki et al. 1999). Another dominant group is various red tide forming species that sporadically appear under similar conditions in summer (Anderson 1997). Their ecological success is dependent upon their life histories, which include a cyst stage (Loeblich & Loeblich 1984; Donoghay & Osborn 1997). However their high levels of abundance are not maintained throughout the summer. The summer bloom is distinguished from the spring and fall blooms based on its size and duration (Takahashi et al. 1977).

Nearshore waters in Japan occasionally receive heavy runoffs of freshwater due to precipitation by seasonal storms in summer. High precipitation may increase the vertical stratification of a water column and provide ample nutrient supplies from runoff to the surface water layer. A sudden supply of nutrients, particularly nitrate, is usually responded to by large phytoplankton such as diatoms (Barber & Smith 1981). Under enhanced oceanographically stable conditions dinoflagellates may dominate when nutrients are supplied (Huntsman et al. 1981; Thomas & Gibson 1990). Dinoflagellates such as Ceratium furca (Ehrenberg) Claparede & Lachmann have been observed not only inside Manazuru Harbor but also along the coast of Sagami Bay in summer (Kikuchi, personal communication). Extensive blooms of this species were reported along the Pacific coast of central Japan in 1997 (Machida et al. 1999). This species has also been reported to form red tides along the west coast of North America (Rensel & Prentice 1980).

In this study size-fractionated Chl-a concentrations and

Corresponding author: Satoru Taguchi; e-mail, staguchi@t.soka.ac.jp



carbon fixation rates of the phytoplankton population were determined weekly from 1995 to 1997 to identify the persistent occurrence of summer dinoflagellate blooms in the nearshore waters of Manazuru Harbor.

# **Materials and Methods**

## Sampling

Surface seawater samples were collected at ca. 1200 h with a bucket in Manazuru Harbor (35°08.9'N, 139°09.1'E; maximum depth, 5.5 m) in Sagami Bay on a weekly basis from 26 May 1995 to 25 March 1997 (Fig. 1). The shape of Manazuru Harbor approximates that of a rectangle 0.53 km long and 0.17 km wide. The watershed adjacent to Manazuru Harbor covers 1.4 km<sup>2</sup>, about 4 times the area of the harbor, and no major tributaries enter the harbor. Surface temperature was measured with a mercury thermometer and salinity was obtained using a refrectometer. Collected water samples were prescreened through  $183-\mu m$  nylon mesh to eliminate large zooplankton and debris, and brought back to the laboratory. Precipitation was measured every day during the sampling period with a rain gauge located on the roof of the Manazuru Municipal Office (35°09'15"N, 139°08'26"E).

## Chlorophyll a and nutrient analysis

Duplicate subsamples of 100 ml each were filtered serially through 2.0- $\mu$ m polycarbonate filters and Whatman GF/F glass fiber filters for analysis of chlorophyll concentrations in the 2.0-0.2  $\mu$ m size fraction (Pico fraction). Further subsamples of 100 ml each were filtered onto GF/F filters to determine the total chlorophyll concentrations (Total fraction). A vacuum pump at <100 mm Hg pressure was employed for the filtration (Li & Dickie 1985). Each sample collected on a filter was extracted in N,N-Dimethylform-

Fig. 1. Location of the sampling station in Manazuru Harbor, Sagami Bay, Japan.

amide (DMF) at 4°C for 24 h (Suzuki & Ishimaru 1990). Chlorophyll concentration was determined fluorometrically on a Turner Design fluorometer using procedures described in Holm-Hansen et al. (1965). Nitrate and silicate concentrations of the samples collected from 26 May 1995 to 30 November 1995 were measured using a calorimetric method as described in Strickland & Parsons (1972). The samples from 6 December 1995 to 26 March 1997 were analyzed on a Bran+Lubbe AASC II Autoanalyzer (Parsons et al. 1984). Intercalibration between the two methods confirmed results to be comparable.

# **Carbon fixation rate**

Subsamples were also collected for the measurement of carbon fixation rates using stable <sup>13</sup>C isotopes (Hama et al. 1983). Subsamples were dispensed into 4-liter black and clear polycarbonate bottles which were incubated with 118- $\mu$ M <sup>13</sup>C-sodium bicarbonate within 3 h of sampling. Incubations were made in the laboratory at an irrandiance of  $150 \,\mu\text{E}\,\text{m}^{-2}\,\text{s}^{-1}$  on a 12L:12D cycle provided by coolwhite fluorescent lamps. This irradiance was employed to provide a light-saturated photosynthetic rate. Incubation temperature was 20°C which was equal to the annual mean of surface seawater temperature at the site in the present study. After the incubation, duplicate aliquots of 200 ml were filtered onto GF/F filters precombusted at 450°C for 4 h to determine the bulk carbon fixation rate. Parallel duplicate aliquots of 300 ml prefiltered through 2.0-µm polycarbonate filters were also filtered onto precombusted GF/F filters to determine the carbon fixation rate for the Pico fraction. Each sample captured on GF/F filters was dried at 54°C for 12 h. The concentrations of particulate organic carbon and the isotopic ratios of <sup>13</sup>C and <sup>12</sup>C were determined by a Finningan TracerMat mass spectrometer combined with a Fisions NA 1500 CNS elemental analyzer.

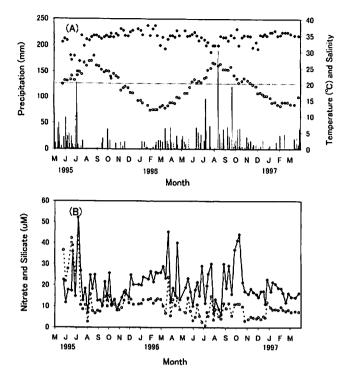


Fig. 2. Temporal variation of abiotic factors and nutrient concnetrations in Manazuru Harbor, Sagami Bay from May 1975 to March 1977. A. Temperature ( $\bigcirc$ ), salinity ( $\blacklozenge$ ) and precipitation (bar); dotted line indicates the annual mean of seawater temperature. B. Silicate ( $\diamondsuit$ ) and nitrate ( $\bigcirc$ ).

Carbon fixation rate was calculated using the procedures described in Hama et al. (1983). After the incubation, chlorophyll samples were also taken. The photosynthetic rate (mgC [mgChla]<sup>-1</sup>h<sup>-1</sup>) for the Total- and Pico fractions were calculated using the Chl-*a* concentrations for each fraction at the end of the incubations.

## Results

#### Abiotic factors

The water temperature ranged from 11.8 on 31 January 1996 to 28.8°C on 23 August 1995, and salinity from 24.0 on 6 July 1995 to 38.0 PSU on 24 January 1996 (Fig. 2A). The highest value of precipitation on one single day was 191 mm and was measured on 12 August 1996 at the end of the period of warming surface water temperatures. The largest value for continuous precipitation amounted to 261 mm and was measured during the period from 3 to 5 July 1995 (Fig. 2A). The second largest value for continuous precipitation amounted to 191 mm and was observed during the period from 6 to 9 July 1996. Decrease in salinity larger than 4 over the course of one week occurred during these continuous periods of heavy precipitation. These decreases in salinity occurred during the period of warming surface temperatures.

Nitrate concentrations ranged from  $0.86 \,\mu\text{M}$  on 6 July 1996 to 43  $\mu\text{M}$  on 6 July 1995, with a mean value (±one

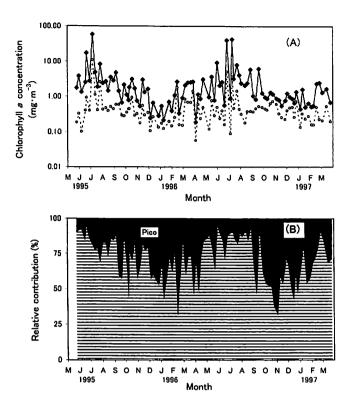


Fig. 3. Temporal variation of Chl-*a* concentrations of the Total ( $\blacklozenge$ ) and Pico fractions ( $\bigcirc$ ) (A) and the relative contribution of the Chl-*a* concentration of the Pico fraction to the Total concentration (B) in Manazuru Harbor, Sagami Bay from May 1975 to March 1997.

standard deviation) of  $11\pm 8.4 \,\mu$ M (Fig. 2B). Silicate concentrations ranged from  $6.1 \,\mu$ M on 19 August 1996 to  $52 \,\mu$ M on 6 July 1995, with a mean concentration of  $20\pm 9.8 \,\mu$ M. Both the highest and lowest nutrient concentrations were observed in summer.

# Chlorophyll-a concentration

Chl-a concentrations of the Total fraction ranged from  $0.19 \text{ mgChl} a \text{ m}^{-3}$  on 4 April 1996 to 59 mgChl  $a \text{ m}^{-3}$  on 6 July 1995 and those within the Pico fraction ranged from  $0.057 \text{ mgChl} a \text{ m}^{-3}$  on 4 April 1996 to 11 mgChl  $a \text{ m}^{-3}$  on 6 July 1995 (Fig. 3A). Peak concentrations were almost 15 times higher than the maximum concentrations (about  $4 \text{ mgChl} a \text{ m}^{-3}$ ) at a station in the center of Sagami Bay (35°07'N, 139°22'E) observed by Noda & Ichimura (1967). The definition of "bloom" has not yet become well established in the literature (see Smayda 1997). However, a distinct summer bloom, revealed by exceptionally high Chl-a cocentrations, higher than the usual high level of about  $20 \text{ mgChl} a \text{ m}^{-3}$ , was observed in July in both 1995 and 1996. Those blooms mainly consisted of the dinoflagellate Ceratium furca (Taguchi, unpublished data). The shortest and longest axis of those cells were  $35\pm4$  and  $175\pm24\,\mu\text{m}$ (n=50), respectively (Hirano, unpublished data). This species was almost totally confined to the fraction larger

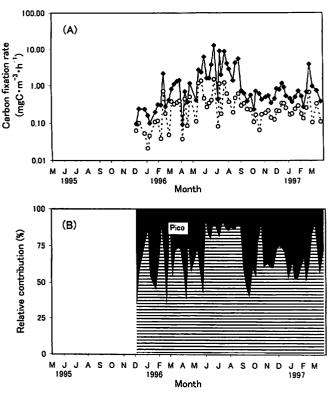


Fig. 4. Temporal variation of carbon fixation rate of the Total  $(\spadesuit)$  and Pico fractions  $(\bigcirc)$  (A) and the relative contribution of the carbon fixation rate of the Pico fraction to the Total carbon fixation rate (B) in Manazuru Harbor, Sagami Bay from May 1995 to March 1997.

than Pico during the present study. The contribution of the Pico fraction to Total Chl-a concentration varied between 5.3% on 20 June 1995 and 69% on 15 February and 4 November 1996 (Fig. 3B).

## **Carbon fixation rate**

Carbon fixation rates ranged from 0.091 mgC m<sup>-3</sup> h<sup>-1</sup> on 4 April 1996 to 13 mgC m<sup>-3</sup> h<sup>-1</sup> on 26 June 1996 for the Total fraction, and from 0.037 mgC m<sup>-3</sup> h<sup>-1</sup> on 4 January 1996 to 1.5 mgC m<sup>-3</sup> h<sup>-1</sup> on 26 June 1996 for the Pico fraction (Fig. 4A). Peak values did not differ greatly from the 5–10 mgC m<sup>-3</sup> h<sup>-1</sup> reported from offshore stations in Sagami Bay (Noda & Ichimura 1967). Percent contribution of Pico to Total varied from 7.2% on 30 May 1996 to 65% on 4 December 1995 (Fig. 4B), with a mean value of  $31\pm16\%$ . Seasonal changes in the Pico contribution to Total carbon fixation rate were similar to those for Chl-*a* concentration.

Photosynthetic rate ranged from  $0.15 \text{ mgC} [\text{mgChl }a]^{-1}$ h<sup>-1</sup> on 17 September 1996 to 2.8 mgC [mgChl  $a]^{-1}$ h<sup>-1</sup> on 18 June 1996 for the Total fraction, and from 0.083 mgC [mgChl  $a]^{-1}$ h<sup>-1</sup> on 7 February 1996 to 1.5 mgC [mgChl  $a]^{-1}$ h<sup>-1</sup> on 18 June 1996 for the Pico fraction (Fig. 5). These maximum values are within the range reported for the surface phytoplankton population of Sagami Bay

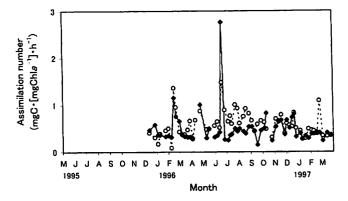


Fig. 5. Temporal variation of photosynthetic rate of the Total  $(\blacklozenge)$  and Pico  $(\bigcirc)$  fractions in Manazuru Harbor, Sagami Bay from December 1996 to March 1997.

(Noda & Ichimura 1967; Shimura & Ichimura 1972). These maximum photosynthetic rates for the Total and Pico fractions on 18 June 1996 occurred one week earlier than the summer peak in Chl-*a* concentrations. At that peak the photosynthetic rate was relatively low, being about 0.3 mgC  $[mgChl a]^{-1}h^{-1}$  for the Total fraction and 0.8 mgC  $[mgChl a]^{-1}h^{-1}$  for the Pico fraction.

## Discussion

In temperate coastal waters the stratified shallow surface mixed layer in summer is usually characterized by nutrientlimited conditions and dominated by small-sized phytoplankton such as the Pico fraction (Joint & Pomeroy 1983; Douglas 1984; Takahashi et al. 1985; Joint et al. 1986; Sondergaard et al. 1991; Iriarte & Purdie 1994; Jacquet et al. 1998). Abundance of the Pico fraction is reportedly controlled by water temperature in temperate coastal waters (Odate 1989; Miyazono et al. 1992; Iriarte & Purdie 1994) but not nutrient concentrations (Kousa 1991). In this cases a close coupling exists among the different compartments of the microbial loop (Azam et al. 1983; Kudoh et al. 1990). However, the well documented characteristics of temperate coastal waters have been perturbed by a distinct regional climatic event, particularly in the nearshore regions in the present study. Heavy rain storms and typhoons usually pass through the present area every summer. As storms approach the coastal area, upwelling occurs by wind-induced mixing (Zeeman 1985; Furnas et al. 1988; Fogel et al. 1999). This upwelling, as well as an increase in water temperature, could enhance the excystment of dinoflagellates from inshore cysts, usually at the bottom depths shallower than 100 m, to seed the surface population (Abbott & Albee 1967). Storms also provide heavy rain that can contribute to the formation of a pycnocline containing ample nutrients from runoff although the effect of precipitation can not be expected to be of event-scale because of the ratio (about 4) of watershed to harbor area in the present study. However, nitrate reached 40  $\mu$ M in the surface water several times during the present study. Stratification due to

pycnocline has been recognized as a precondition for the development of dinoflagellates (Donaghav & Osborn 1997). Once a storm passes, quiescent periods, influxes of runoff, and sunny days often follow. All these factors tend to increase vertical stratification. A shallow thermocline was often observed during these periods in the present study area (data not shown). Consequently the seeded population could form a layer of high concentration above the pycnocline. When vertical mixing in the pycnocline decreases to the point where directional swimming motion relative to the water can overcome the vertical dispersive effects of small-scale mixing, then swimming behavior alone could serve to concentrate dinoflagellate cells such as Ceratium furca into such a layer, as suggested by Donagahy & Osborn (1998). This effect may be enhanced by local growth of those motile cells that make brief excursions into deeper waters to take up nutrients (Eppley et al. 1968; Cullen & Horrigan 1981) and by suppression of grazing (Gentien & Arzul 1990).

A portion of the Pico fraction that would have spread throughout the water column due to the vertical mixing during storms can also bloom above the pycnocline under similar favorable conditions. They can reach densities higher than  $10 \text{ mgChl} a \text{ m}^{-3}$ , as observed in the present study. The small size of plankters in the Pico fraction provides a large surface area to volume ratio that must be beneficial for nutrient uptake (Banse 1976). However, in some respects they are not as flexible in their nutrient-gathering abilities as motile cells such as *Ceratium furca*, since they lack swimming ability and therefore utilize only nutrients at the depth in which they exist.

Chl-a concentrations in summer during the present study reached the maximum values following heavy precipitation, although the apparent relationship between the peak in Chla concentrations and nutrient concentrations is different between 1995 and 1996. The response of phytoplankton to increased nutrient supply could be faster than the one week interval between samplings adopted during the present study. Summer blooms were only able to be detected by sampling every two days in Saanich Inlet, Canada (Takahashi et al. 1977). As also pointed out by Nielsen et al. (1990), standard coarse-scale sampling methods have probably prevented the detection of, or led to underestimation of peak concentrations in layered blooms. High precipitation of 191 mm within a single day was observed on 12 August 1996 but it may not have lasted long enough to concentrate phytoplankton cells above the pycnocline and enhance phytoplankton production. Alternativly the seed population may already have been exhausted during earlier period of heavy precipitation since a period when water temperatures warmed considerably has passed.

Chl-a concentrations during the summer phytoplankton bloom in nearshore waters were considerably higher than those reported for the offshore waters of Sagami Bay (Noda & Ichimura 1967; Shimura & Ichimura 1972), although the photosynthetic rate was similar. The area of the summer phytoplankton bloom can be estimated as 10% of the total surface area of Sagami Bay (2,700-km<sup>2</sup> surface area) since a narrow band (2-km width) of these blooming plankton along the coast (130-km length of shoreline) has been observed during summer (Kikuchi, personal communication). The annual surface primary production for the bloom band can be estimated as  $6 \text{ gC m}^{-3} \text{ year}^{-1}$  from the present study. The annual primary production of about  $1.8 \text{ gC m}^{-3} \text{ year}^{-1}$  reported for the surface waters of Sagami Bay (Aruga 1977) increases by about 20%. However, this value has to be considered to be a first order estimation pending further studies.

One of the more complicated aspects of dinoflagellate dynamics is that summer blooms of dinoflagellates such as *Ceratium furca* are known to exhibit specific vertical structures in coastal water colums (Eppley et al. 1968; Taguchi 1982; Franks & Anderson 1992). Information on more detailed spatial and temporal scales is required to fully understand the dynamics of summer dinoflagellate blooms, for example, the analysis of satellite image (Cullen et al. 1997). Such efforts will facilitate estimating the contribution of bloom-forming dinoflagellates to the total primary production of Sagami Bay.

# Acknowledgments

We thank Dr T. Kikuchi and the staff at Manazuru Marine Laboratory for Science Education, Yokohama National University, for their kind cooperation and support in collecting samples and for information on the watershed adjacent to Manazuru Harbor. Unpublished data were kindly provided by T. Hirano. We also thank the Manazuru Municipal Office for offering data on precipitation. This study was supported partially by a grant from the National Space Development Agency of Japan.

#### Literature cited

- Abbott, D. P. & R. Albee 1967. Summary of thermal conditions and phytoplankton volumes measured in Monterey Bay, California 1961–1966. *Calif. Coop. Oceanic Fish. Invest. Rep.* 11: 155–156.
- Anderson, D. M. 1997. Bloom dynamics of toxic Alexandrium species in the northeastern U. S. Limnol. Oceanogr. 42: 1009– 1022.
- Aruga, Y. 1977. Productivity of phytoplankton in Suruga Bay and Sagami Bay, p. 127–133. In *Productivity of Biocenoses in Coastal Regions of Japan*, JIBP Synthesis vol. 14. (eds. Hogetsu, K., M. Hatanaka, T. Hanaoka & T. Kawamura). Univ. Tokyo Press, Tokyo.
- Azam, F., T. Fenchel, J. G. Field, J. S. Gray, L. A. Meyer-Reil & F. Thingstad 1983. The ecological role of water-column microbes in the sea. *Mar. Ecol. Prog. Ser.* 10: 257–263.
- Banse, K. 1976. Rates of growth, respiration and photosynthesis of unicellular algae as related to cell size-a review. J. Phycol. 12: 135-140.
- Barber R. T. & W. O. Smith, Jr. 1981. The role of circulation,

sinking, and vertical migration in physical sorting of phytoplankton in the upwelling center at 15°S, p. 366–371. In *Coastal Upwelling* (ed. Richards, F. A.). Am. Geophys. Union, Washington, D. C.

- Cloern, J. E. 1991. Annual variation in river flow and primary production in the south San Francisco Bay Estuary (USA), p. 91–96. In *Estuaries and Coasts: Spatial and Temporal Intercomparisons* (eds. Elliott, M. & J.-P. Ducrotoy). Olsen & Olsen.
- Cullen, J. J., & S. G. Horrigan 1981. Effects of nitrate on the diurnal vertical migration, carbon to nitrogen ratio, and the photosynthetic capacity of the dinoflagellate, *Gymnodinium splendens. Mar. Biol.* 62: 81–89.
- Cullen, J. J., A. M. Ciotti, R. F. Davis & M. R. Lewis 1997. Optical detection and assessment of algal blooms. *Limnol. Oceanogr.* 42: 1223–1239.
- Douglas, D. J. 1984. Microautoradiography-based enumeration of photosynthetic picoplankton with estimates of carbon-specific growth rate. *Mar. Ecol. Prog. Ser.* 14: 223–238.
- Donaghay, P. L. & T. R. Osborn 1997. Toward a theory of biological-physical control of harmful algal bloom dynamics and impacts. *Limnol. Oceanogr.* 42: 1283–1296.
- Eppley, R., O. Holme-Hansen & J. D. H. Strickland 1968. Some observations on the vertical migration of dinoflagellates. J. Phycol. 4: 333–340.
- Falkowski, P. G. & J. A. Raven 1997. *Aquatic Photosynthesis*, Blackwell Science, 375 pp.
- Fogel, M. L., C. Aguilar, R. Cuhel, D. J. Hollander, J. D. Willey, & H. W. Paerl 1999. Biological and isotopic changes in coastal waters induced by Hurrican Gordon. *Limnol. Oceanogr.* 44: 1359–1369.
- Franks, P. J. S. & D. M. Anderson 1992. Alongshore transport of a toxic phytoplankton bloom in a buoyance current: *Alexandrium tamarense* in the Gulf of Maine. *Mar. Biol.* **112**: 153–164.
- Furnas, M. J., T. Okaichi, D. M. Anderson, & T. Nemoto 1989. Cyclonic disturbance and a phytoplankton bloom in a tropical shelf ecosystem, p. 236–276. In *Red tides: Biology, Environmental Science, and Toxicology* (eds. Okaichi, T., D. M. Anderson, & T. Nemoto). Elsevier.
- Gentien, P. & G. Arzul 1990. Exotoxin production by *Gyrodinium* cf. *aureolum* (Dinophyceae). J. Mar. Biol. Assoc. U. K. **70**: 571–581.
- Hama, T., Y. Miyazaki, Y. Ogawa, T. Iwakuma, M. Takahashi, A. Otsuki & S. Ichimura 1983. Measurement of photosynthetic production of a marine phytoplankton population using a stable <sup>13</sup>C isotope. *Mar. Biol.* 73: 31–36.
- Hamasaki, K., F. Satoh, T. Kikuchi, T. Toda & S. Taguchi 1999. Biomass and production of cyanobacteria in a coastal water of Sagami Bay, Japan. J. Plankton Res. 21: 1583–1591.
- Holm-Hansen, O., C. J. Lorenzen, R. N. Holmes & J. d. H. Strickland 1965. Fluorometric determination of chlorophyll. J. Cons. Perm. Int. Explor. Mer 30: 3–15.
- Huntsman, S. A., K. H. Brink, R. T. Barber & D. Blasco 1981. The role of circulation and stability in controlling the relative abundance of dinoflagellates and diatoms over the Peru shelf, p. 375–365. In *Coastal Upwelling* (ed. Richards, F. A.). Am. Geophys. Union, Washington, D. C.
- Iriarte, A. & D. A. Purdie 1994. Size distribution of chlorophyll a biomass and primary production in a temperate estuary

(Southampton Water): the contribution of photosynthetic picoplankton. Mar. Ecol. Prog. Ser. 115: 283-297.

- Jacquet, S., J.-F. Lennon, D. Marie & D. Vaulot 1998. Picoplankton population dynamics in coastal waters of the northwestern Mediterranean Sea. *Limnol. Oceanogr.* 43: 1916–1931.
- Joint, I. R & A. J. Pomeroy 1983. Production of picoplankton and small nanoplankton in the Celtic Sea. Mar. Biol. 77: 19–27.
- Joint, I. R., N. J. P. Owens & A. J. Pomeroy 1986. Seasonal production of photosynthetic picoplankton and nanoplankton in the Celtic Sea. *Mar. Ecol. Prog. Ser.* 28: 251–258.
- Kousa, H. 1991. Picoplanktonic algae in the northern Baltic Sea: seasonal dynamics and flagellate grazing. *Mar. Ecol. Prog. Ser.* 73: 269–276.
- Kudoh, S., J. Kanda & M. Takahashi 1990. Specific growth rate and grazing mortality of chroococcoid cyanobacteria *Synechoccoccus* spp. in pelagic surface waters in the sea. J. Exp. Mar. Biol. Ecol. 142: 201–212.
- Li, W. K. W. & P. M. Dickie 1985. Growth of bacteria in seawater filtered through 0.2 μm Nucleopore membranes: implications for dilution experiments. *Mar. Ecol. Prog. Ser.* **26**: 245–252.
- Loeblich, A. R., III. & L. A. Loeblich 1984. Dinoflagellate cysts, p. 443–480. In *Dinoflagellates* (ed. Spector, D. L.). Academic Press, Orlando.
- Machida, M., M. Fujitomi, K. Hasegawa, T. Kudoh, M. Kai, T. Kobayashi, & T. Kamiide 1999. Red tide of *Ceratium furca* along the Pacific coast of central Japan 1n 1997. *Nippon Suisan Gakkaishi* 65: 755–756. (In Japanese.)
- Maita, Y. & T. Odate 1988. Seasonal changes in size-fractionated primary production and nutrient concentrations in the temperate neritic water of Funka Bay, Japan. J. Oceanogr. Soc. Jpn 44: 268–279.
- Miyazono, A., T. Odate & Y. Maita 1992. Seasonal fluctuations of cell density of cyanobacteria and other picophytoplankton in Iwanai Bay. Hokkaido, Japan. J. Oceanogr. 48: 257–266.
- McCarthy, J. J., W. R. Taylor & J. L. Taft 1977. Nitrogenous nutrition of the plankton in the Chesapeake Bay. I. Nutrient availability and phytoplankton preferences. *Limnol. Oceanogr.* 22: 996–1011.
- Nielsen, T. G., T. Kiorboe & P. K. Bjornsen 1990. Effect of a *Chrysochromulina* polylepis subsurface bloom on the planktonic community. *Mar. Ecol. Prog. Ser.* 62: 21–35.
- Noda, Y. & S. Ichimura 1967. Primary production in Sagami Bay in summer of 1964. *Inf. Bull. Planktol. Jpn.* Commem. No. Dr. Y. Matsue: 183–186. (In Japanese.)
- Odate, T. 1989. Seasonal changes in cell density of cyanobacteria and the picophytoplankton populations in Funka Bay, Japan. *Bull. Plankt. Soc. Jpn* **36**: 53–61.
- Parsons, T. R., Y. Maita & C. M. Lalli 1984. A Manual of Chemical and Biological Methods for Seawater Analysis. Permagon Press, Oxford, 173 pp.
- Rensel, J. E. & E. F. Prentice 1980. Factors controlling growth and survival of cultured spot prawns, *Pandalus platyceros*, in Puget Sound, Washington. *Fish. Bull.* **78**: 781–788.
- Shimura, S. & S. Ichimura 1972. Primary productivity in coastal water adjacent to the Kuroshio off Shimoda. J. Oceanogr. Soc. Jpn 28: 8–17.
- Smayda, T. J. 1997. What is a bloom? A commentary. *Limnol.* Oceanogr. 42: 1132–1136.

- Sondergaard, M., L. M. Jensen & G. Ertebjerg 1991. Picoalgae in Danish coastal waters during summer stratification. *Mar. Ecol. Prog. Ser.* 79: 139-149.
- Strickland, J. D. H. & T. R. Parsons 1972. A Practical Handbook of Sea Water Analysis. 2nd ed. Bull. Fish. Res. Bd Canada, 167 pp.
- Suzuki, R. & T. Ishimaru 1990. An improved method of the determination of phytoplankton chlorophyll using N,N-Dimethylformamide. J. Oceanogr. Soc. Jpn 46: 190–194.
- Taguchi, S. 1982. Seasonal studies of the dinoflagellate Ceratium longipes (BAILEY) GRAN in the Bedford Basin. J. Exp. Mar. Biol. Ecol. 59: 115–131.
- Taguchi, S., K. Iseki, & T. Kawamura 1977. The estimation of annual production by phytoplankton in Akkeshi Bay, Japan, J.

Oceanogr. Soc. Jpn 32: 97-102.

- Takahashi, M., D. L. Seibert, & W. H. Thomas 1977. Occasional blooms of phytoplankton during summer in Saanich Inlet, B. C., Canada. Deep-Sea Res. 24: 775–780.
- Takahashi, M., K. Kikuchi & Y. Hama 1985. Importance of picocyanobacteria biomass (unicellular, blue-green algae) in the phytoplankton population of the coastal waters off Japan. *Mar. Biol.* 89: 63-69.
- Thomas, W. H. & C. H. Gibson 1990. Quantified small-scale turbulence inhibits a red tide dinoflagellate *Gonyaulas polyedra* Stein. *Deep-Sea Res.* 37: 1583–1593.
- Zeeman, S. I. 1985. The effects of tropical storm Dennis on coastal phytoplankton. *Estu. Coast. Shelf Sci.* 20: 403-418.