

三河湾の夏季における一次生産者サイズ組成の変化

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Changes in Size Composition of Summer Primary Producers in Eutrophic Mikawa Bay, Japan^{1), 2)}

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Abstract

Size-fractionation observations were carried out during the summer of 1981 to compare chlorophyll *a* biomass and productivity in the <25 and <10 μm size fractions with those of the total phytoplankton community in eutrophic Mikawa Bay on the southern coast of central Japan. Nanoplankton of <10 μm size dominated during the summer stratified period. However, because the stratification in this shallow bay was disturbed by stormy weather, larger phytoplankton (>25 μm) blooms were temporarily formed after nutrient supply, which is accelerated by vertical mixing. The <10 μm size fraction occupied 61.8-92.1% (average: 79.4%) of the chlorophyll *a* biomass and 59.5-100% (average: 81.2%) of the surface production during June-early August, when the stratification was well developed. In May and early August-September, when seasonal and temporal vertical mixing was induced by wind action, the >25 μm size fraction accounted for 51.3-73.0% (av.: 60.6%) and 22.4-78.6% (av.: 47.6%) of the chlorophyll *a* biomass, and 33.8-60.6% (av.: 42.2%) and 36.2-71.1% (av.: 57.5%) of the surface production, respectively. The mean assimilation number of <10 μm fraction ($7.3 \text{ mgC} \cdot \text{mgChl. } a^{-1} \cdot \text{h}^{-1}$) in the stratified condition rarely varied from that of the total community ($6.8 \text{ mgC} \cdot \text{mgChl. } a^{-1} \cdot \text{h}^{-1}$), whereas ones dominated by >25 μm fraction frequently showed negative rates. The result indicated that vertical water movement in summer influences the size composition of phytoplankton populations even in a highly eutrophied bay.

The size of marine phytoplankters varies widely from less than one micrometer to a few millimeters in the largest dimension. It is well known that the size of phytoplankton cells plays an important role in phytoplankton population dynamics and in the trophic interactions between phytoplankton and herbivorous zooplankton (e.g., MALONE 1980, SOURNIA 1982). Size composition of natural phytoplankton assemblages has been studied by size-fractionation in coastal and oceanic waters (SAIJO 1964, SAIJO & TAKESUE 1965, MALONE 1971, McCARTHY et al. 1974, DURBIN et al. 1975, HALLEGRAEFF 1981, FURNAS 1983, FURUYA & MARUMO 1983). The results indicate that the nanoplankton, which is usually defined as the fraction passing through fine mesh nets (10-65 μm), is predominant in oligotrophic waters, whereas net plankton, which is retained by the nets, tends to predominate in eutrophic waters. Vertical water movements also affect the size composition of phytoplankton; upward motion of water produces large-sized populations and vice versa (SEMINA 1972, PARSONS & TAKAHASHI 1973). In shallow coastal areas, weak stratification or spring vertical mixing of water extending to the bottom enhances diatom blooms, but under well-stratified conditions in summer the diatom

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²⁾ 三河湾の夏季における一次生産者サイズ組成の変化

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bloom rarely occurs (MALONE & CHERVIN 1979, MALONE 1980).

The aim of the present study is to estimate the nanoplankton contribution to total phytoplankton biomass and production during the stratified period in summer in a highly eutrophied embayment. During the course of the study intermittent diatom blooms in summer were also documented.

Materials and Methods

Mikawa Bay, located on the southern coast of central Japan, is one of the typical shallow embayments which have been highly eutrophied in the last ten or more years. The mean depth is 9.2m and the surface area is 604 km². Two stations were set up in the bay, i.e., St. 1 (6-7m depth) in the inner part and St. 2 (17-18m depth) in the central part (Fig. 1).

The preliminary observations were made at both stations from May 1978 to February 1979 to illustrate the seasonal trends in total biomass and the size composition of phytoplankton populations throughout the year. Seawaters were taken from the surface, weekly or biweekly during the summer, and monthly during the rest of the period. Frequent samplings, at least once a week, were performed at St. 2 to investigate in short-term changes during the summer of 1981. Seawater samples were collected around 10 a.m. with a 5 liter Van Dorn sampler from 0, 2, 5, 10 and 15 m depths. Water temperature and underwater light intensity were measured with a thermometer (Tohodentan) and a submersible lightmeter (Rigosha), respectively. Data on wind velocity recorded near the mouth of the bay were provided by the Nagoya Meteorological Observatory.

Water samples were immediately brought back to the laboratory and filtered through a

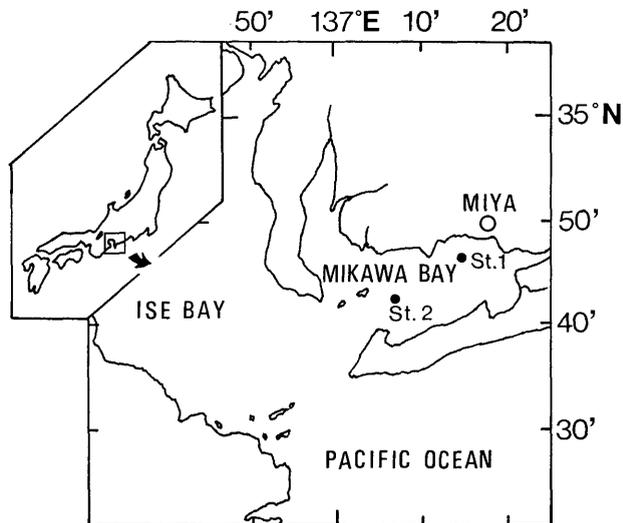


Fig. 1. Map of Mikawa Bay, showing positions of the two sampling stations (Sts. 1 & 2).

330 μm netting in order to remove large zooplankton (unfiltered sample). Aliquots of the surface water were filtered through 10 and 25 μm nets. Three size categories, i.e., 10 μm , 25 μm and total (unfiltered), were used for primary productivity measurements as well as for chlorophyll *a* analyses.

Primary productivity was estimated by the light-dark oxygen bottle method, with incubation for 4 hrs under constant fluorescent lighting at 18 Klx in an incubation chamber. The temperature was adjusted around the in situ surface temperature. Dissolved oxygen was determined by the Winkler titration technique. Daily primary production in the water column under 1 m² was calculated using an empirical equation proposed by STEEMANN NIELSEN & JENSEN (1957). When the photosynthetic quotient, (O_2/CO_2), is equal to 1.0, 1 mg of O_2 produced corresponds to 0.375 mg of organic carbon photosynthesized.

Concentrations of chlorophyll *a* and pheopigments were determined by the spectrophotometric method using the equation of LORENZEN (1967) after extraction in 90% acetone from the samples collected on Whatman GF/C filters. Identification of dominant phytoplankters was done immediately in the living state under an inverted microscope. Salinity was determined by a salinometer (Autolab 601-MK2). Reactive silicate and reactive phosphate were determined by the methods of MULLIN & RILEY (1955) and MURPHY & RILEY (1962), respectively, nitrite after BENDSCHNEIDER & ROBINSON (1952), nitrate by the copper-cadmium reduction method of WOOD et al. (1967), ammonia after SAGI (1966), and urea by the procedure of NEWELL et al. (1967).

Results

1. Seasonal changes in total biomass and size composition of phytoplankton in 1978-1979

Marked seasonal changes in total biomass and its size composition in terms of chlorophyll *a* were observed at the surface (Fig. 2). Although the vernal blooming (March-April) was missed in the present investigation, two major and one minor blooms were detected. Among major ones, an early bloom which was dominated by the large size class $>25 \mu\text{m}$ occurred in late June, and the second dominated by the small size class $<10 \mu\text{m}$ occurred in mid-September. The early one was mainly consisting of long-chained diatoms such as *Skeletonema costatum* and *Chaetoceros* spp., and the second was of $<10 \mu\text{m}$ fraction communities (over 70% of total biomass), including photosynthetic microflagellates. While the species were not identified in the present study, the microflagellates were mainly composed of species belonging to Euglenoida, Cryptomonadida, Chrysomonadida and Dinoflagellida (AICHI PREF. unpublished). It is also noticeable that the large class temporarily formed minor blooms during the summer period, e.g., in early August. During winter (January-February), the total biomass was small and the larger size ($>25 \mu\text{m}$) was dominant.

From autumn to early winter, the surface water began to cool, the convective turnover started in October, then the autumn bloom was initiated and gradually peaked at over 13 mg Chl. *a*·m⁻³. Although a peak in late November was dominated by the small size class $<10 \mu\text{m}$ (Fig. 2), microscopic examinations revealed that this bloom was exclusively formed by

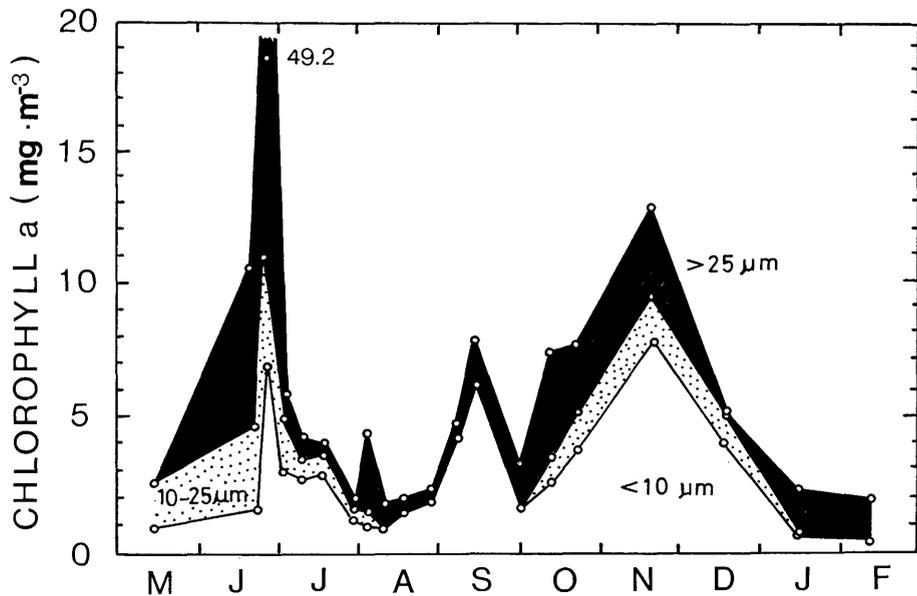


Fig. 2. Seasonal changes in chlorophyll *a* concentration of three different size fractions in the surface water at St. 2 in the central part of Mikawa Bay, from May 1978 through February 1979.

several diatom species, i.e., *Coscinodiscus asteromphalus*, *Ditylum brightwellii*, *Rhizosolenia calcar-avis*, etc., which belong to the larger size classes. We could not determine the cause for this disagreement, though a defect seemed to exist in the filter funnels used in size fractionation rather than in the microscopic examinations.

These results indicate that nanoplankton contribution to total phytoplankton biomass is important in summer even in the eutrophic embayments as in oligotrophic oceanic waters. However, its relative contribution is sometimes dropped to a greater extent by the temporal blooms of large-sized diatoms. Therefore, an extensive investigation during summer was designed to obtain the precise picture of the general importance of summer nanoplankton populations and the temporal diatom increases. Besides chlorophyll *a* analysis, the measurement of photosynthetic potential was attempted for three size fractionated samples during the summer of 1981.

2. Biomass and productivity of different size classes during summer

Hydrographic conditions during summer when the study was done can be summarized as follows. The seawater was vertically mixed throughout the water column until late May. In the following two months, the discontinuity layers of temperature and salinity gradually developed and ascended until they reached 5 m depth in late July. Then they weakened and descended in August (Fig. 3A & B). Consequently, the pycnocline was formed and shifted vertically between 5 and 10 m depths from June to August. During the course, the stratified structure was temporarily weakened or destroyed by strong winds caused by low atmospheric pressures and typhoons (Fig. 3C).

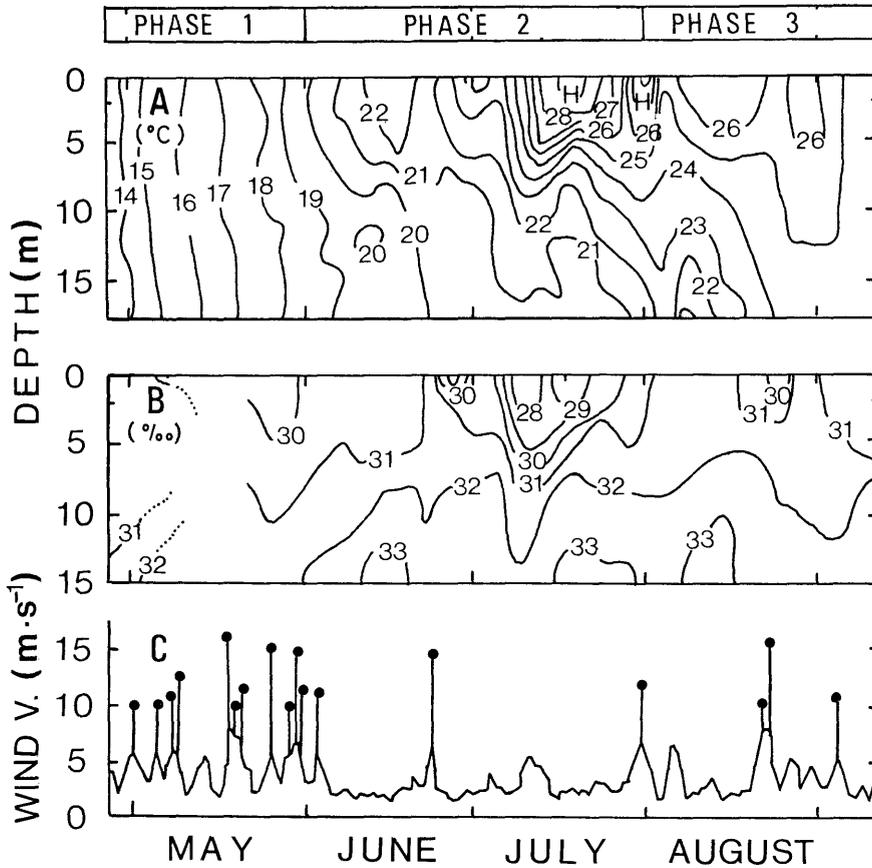


Fig. 3. Changes in water temperature (A) and salinity (B) at St. 2 in Mikawa Bay, and average wind velocity (solid line) and maximum wind velocity beyond $10\text{ m}\cdot\text{sec}^{-1}$ (solid circle) (C) recorded near the mouth of the bay, during the summer of 1981.

According to these temporal hydrographic changes, we divided the period into the following three phases. Phase 1 was from late April to the end of May, when convective turnover of water occurred. Phase 2 was from June to late July, when the pycnocline was formed and developed, ascending from about 10 m to 5 m depth. Phase 3 was from August to mid-September, when the pycnocline gradually descended, and vertical stability of water was weakened and finally destroyed. Throughout these phases, the depth of 1% relative light level, which approximately corresponds to the lower limit of the euphotic layer, was located mostly between 10 m and 15 m.

The concentration of nutrients, ammonia, nitrate, nitrite, phosphate and silicate, decreased in the upper layer above the pycnocline, but increased in the bottom layer (Fig. 4). In the surface layer, the level of nutrients, especially phosphate ($0.00\text{--}0.03\ \mu\text{M}$) and silicate ($0.3\text{--}3.5\ \mu\text{M}$), was low in phase 1, probably because of an active consumption during the preceding spring bloom. During phase 2, while the level of silicate slightly recovered ($1.7\text{--}33.7\ \mu\text{M}$),

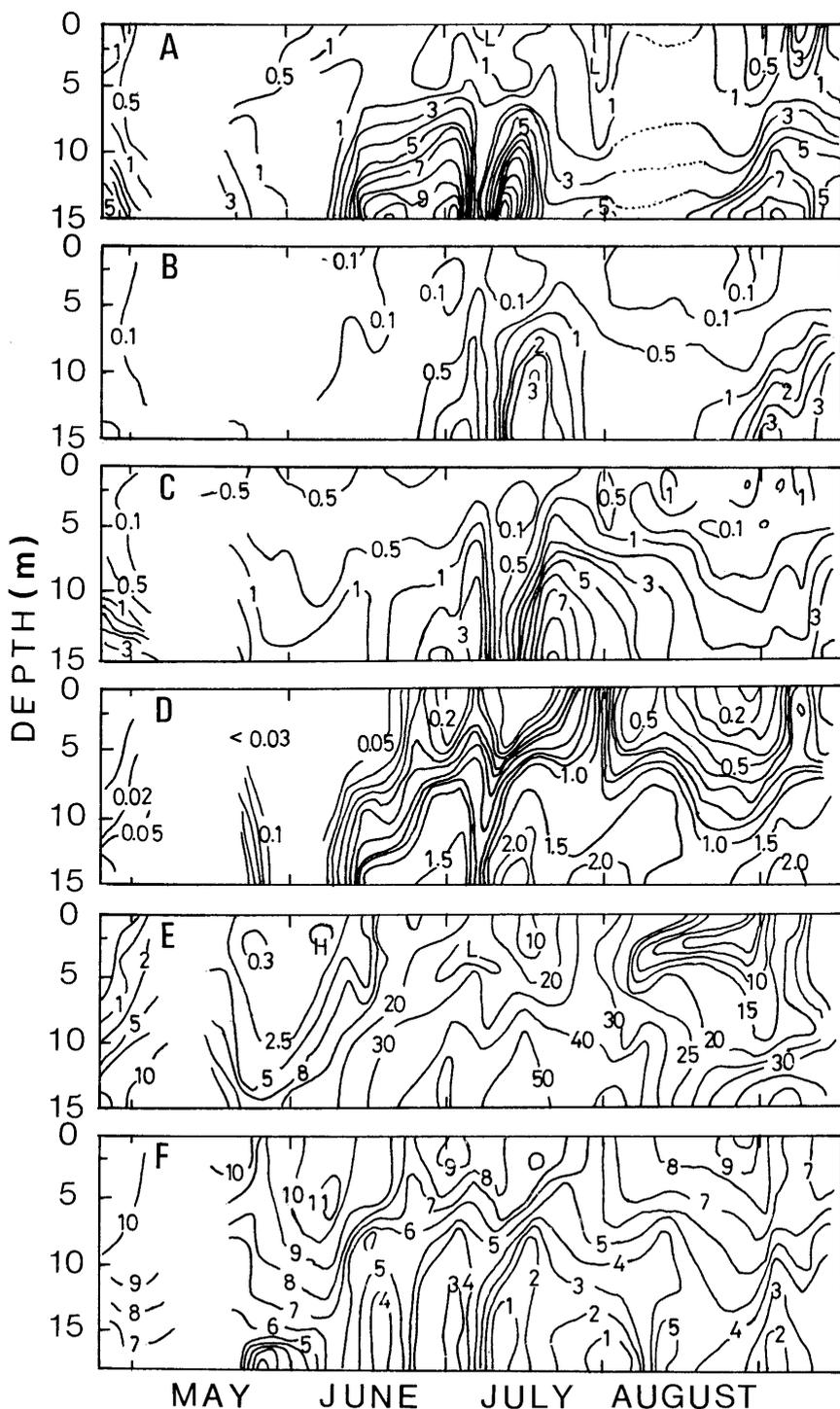


Fig. 4. Changes in ammonium nitrogen, μM (A), nitrite nitrogen, μM (B), nitrate nitrogen, μM (C), reactive phosphate, μM (D), reactive silicate, μM (E) and dissolved oxygen, $\text{mg}\cdot\text{l}^{-1}$ (F) at St. 2 in Mikawa Bay during the summer of 1981.

the phosphate concentration was still low ($<0.34 \mu\text{M}$). It should be noted, however, that slight increases were also recorded in phosphate on and June 26 and July 6. The latter might be attributable to temporal vertical mixing of water, which did not extend to the sea bottom and was induced by strong winds on those days (Fig.3 C). Such a wind-driven vertical mixing became intense and sometimes reached the sea bottom in phase 3, so the level of nutrients in the surface layer was as high as $0.08\text{--}1.11 \mu\text{M}$ or $1.4\text{--}36.8 \mu\text{M}$. All these indicate that the surface nutrient concentration was variable in the stratified summer period despite being controlled positively by the temporal replenishment by vertical mixing of water and negatively by the rapid consumption by phytoplankton growth. In other words, nutrient depletion during summer, if any, may not be severe in this bay.

In the bottom layer below the pycnocline, concentrations of nutrients increased from phases 1 to 2, but decreased from phases 2 to 3 (Fig. 4A-E). This indicates that regenerated nutrients in the bottom layer were accumulated in phases 1 and 2 but brought up to the surface layer in phase 3. The isolation of the bottom layer in phase 2 is also indicated by the fact that the time lags of a few days between the bottom maxima of ammonia, nitrite and nitrate in this order were accompanied by gradual decrease of dissolved oxygen concentration (Fig. 4F).

Figure 5 shows the changes of dominant phytoplankters and chlorophyll *a* throughout the study period. Chlorophyll *a* concentrations varied remarkably from 0.43 to $55.4 \text{ mg}\cdot\text{m}^{-3}$, and

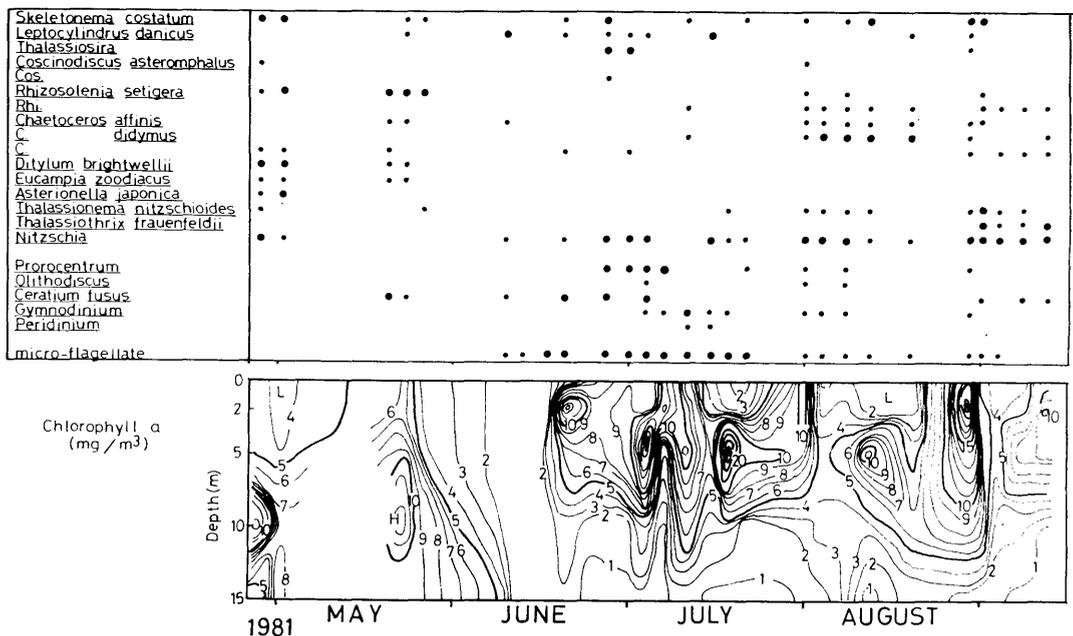


Fig. 5. Vertical distribution of chlorophyll *a* concentration (unfiltered) and changes of phytoplankton species in the surface layers (0-5 m) at St. 2 in Mikawa Bay during the summer of 1981. Large dots indicate that dominant species occurred in considerable numbers; small dots indicate that other species occurred in relatively large numbers.

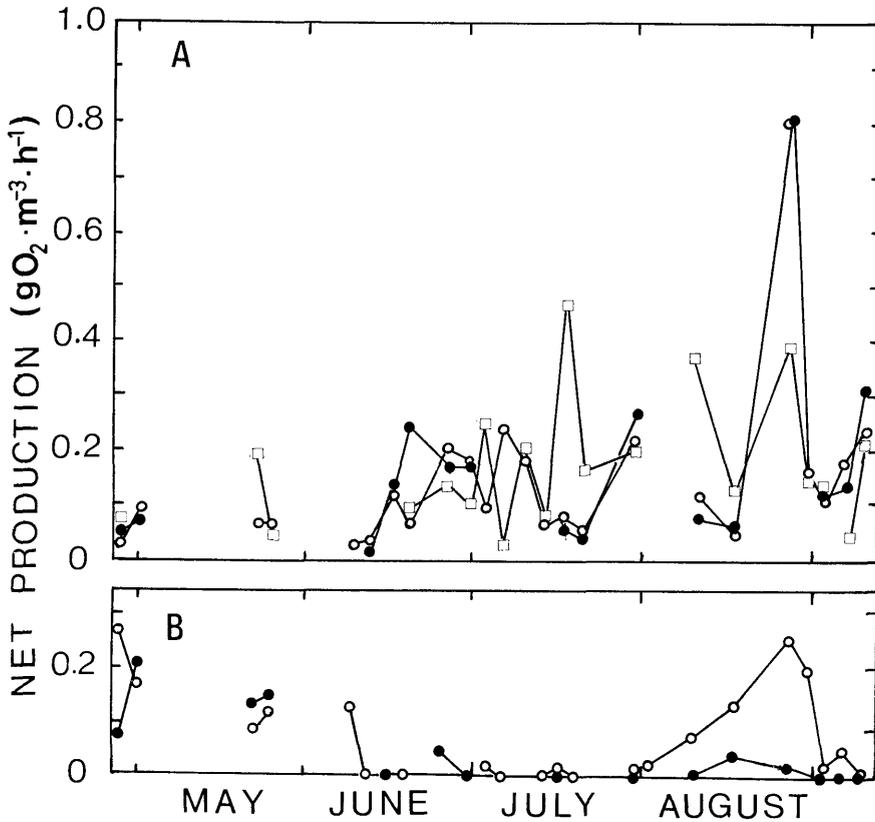


Fig. 6. Changes in net production rate of phytoplankton in water samples collected at the surface layers (A), 0 m (open circle), 2 m (solid circle) and 5 m (open square) and the bottom layers (B), 10 m (open circle) and 15 m (solid circle) at St. 2 in Mikawa Bay during the summer of 1981.

eight distinct maxima were recorded in the surface layer above the pycnocline. The dominant species at these maxima changed as follows: *Skeletonema costatum*, *Ditylum brightwellii* and *Nitzschia* sp. in late April (phase 1), *Rhizosolenia setigera* in late May (phase 1), microflagellates and *Ceratium fusus* in mid June (phase 2), microflagellates, *C. fusus* and *Prorocentrum* sp. in early July (phase 2), *Chaetoceros didymus* in mid-August (phase 3), *Nitzschia* spp. and *Thalassiothrix frauenfeldii* in late August (phase 3), and *Thalassionema nitzschioides* and *Th. frauenfeldii* in mid-September (phase 3). In summary, the dominant taxa changed from diatoms in phase 1 through mixed populations of microflagellates and dinoflagellates in phase 2 to diatoms again in phase 3.

Hourly net production also showed considerable variation. Active production was recognized in the upper 5 m (Fig. 6A). However, the productivity in the deeper layers below 10 m was also high in exceptional cases in April and late August, when the water mixed vertically (Fig. 6B). In the latter, the highest rate was $0.811 \text{ gO}_2 \cdot \text{m}^{-3} \cdot \text{h}^{-1}$ ($=0.304 \text{ gC} \cdot \text{m}^{-3} \cdot \text{h}^{-1}$), which was attained by the diatom blooms mainly of *Nitzschia* spp. and *Th. frauenfeldii*, occurring in the

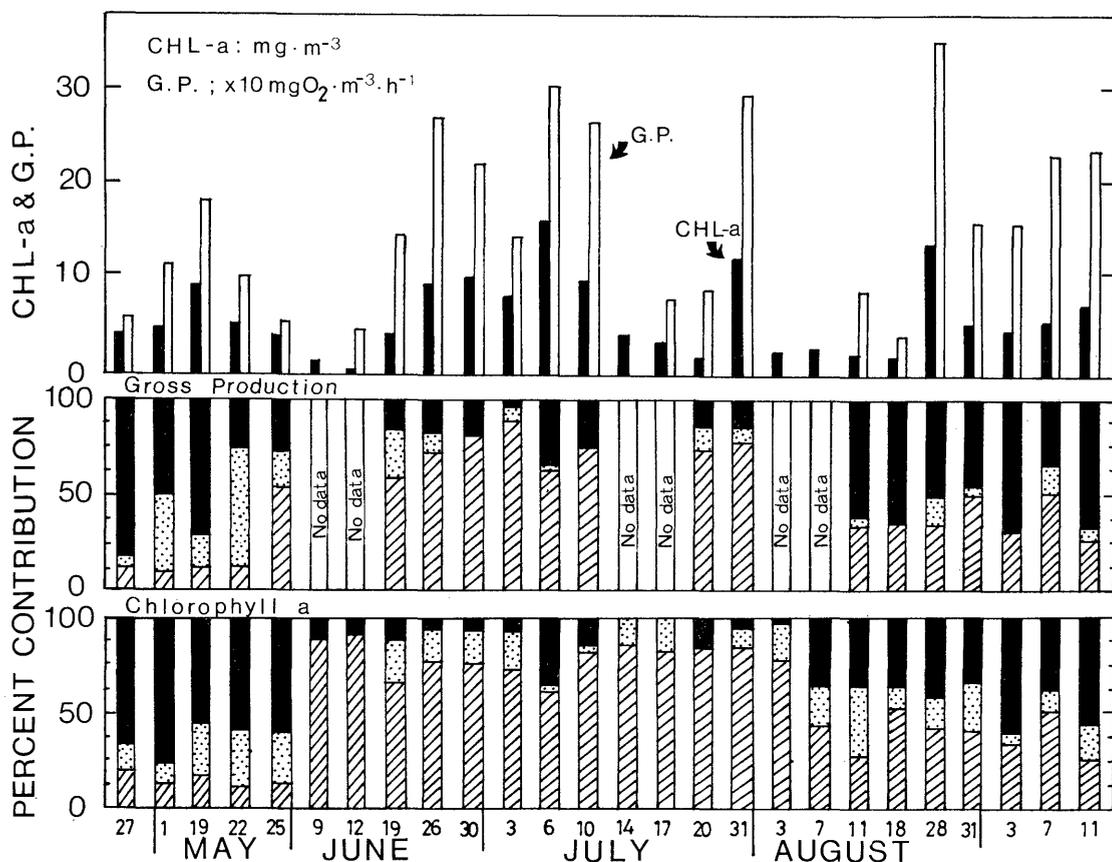


Fig. 7. Total chlorophyll *a* concentration and gross production rate at St. 2 in Mikawa Bay during the summer of 1981. Chlorophyll *a* and gross production rate in three size fractions as percentages in unfiltered samples. Shaded column: $<10 \mu\text{m}$ fraction; dotted column: $10\text{--}25 \mu\text{m}$ fraction; solid column: $>25 \mu\text{m}$ fraction.

upper 2 m. On the other hand, the productivity in mid-July, when the maximum chlorophyll *a* biomass ($55.4 \text{mg} \cdot \text{m}^{-3}$) was recorded by a bloom of unicellular microflagellates, was rather low at $0.466 \text{gO}_2 \cdot \text{m}^{-3} \cdot \text{h}^{-1}$ ($=0.175 \text{gC} \cdot \text{m}^{-3} \cdot \text{h}^{-1}$).

Figure 7 shows the temporal changes in total (unfiltered) chlorophyll *a* biomass and production and their size composition in the surface. The total chlorophyll *a* biomass and gross production at the surface ranged from 1.52 to $15.7 \text{mgChl.a} \cdot \text{m}^{-3}$ and from 0.044 ($=0.016$) to $0.346 \text{gO}_2 \cdot \text{m}^{-3} \cdot \text{h}^{-1}$ ($=0.130 \text{gC} \cdot \text{m}^{-3} \cdot \text{h}^{-1}$), respectively.

Seasonality of size composition in biomass was clear. The $>25 \mu\text{m}$ fraction was mainly composed of diatoms and accounted for 51.3 to 73.0% with an average of 60.6% of the total before late May. The $<10 \mu\text{m}$ fraction composed of small diatoms occupied the greatest part ($61.8\text{--}92.1\%$, average: 79.4%) during June-early August. After mid-August, both the $>25 \mu\text{m}$ and $<10 \mu\text{m}$ fractions occupied equivalent parts, i.e., $33.8\text{--}60.6\%$ (average: 42.2%) and $24.1\text{--}51.9\%$ (average: 38.8%), respectively. The contribution of the $10\text{--}25 \mu\text{m}$ fraction was

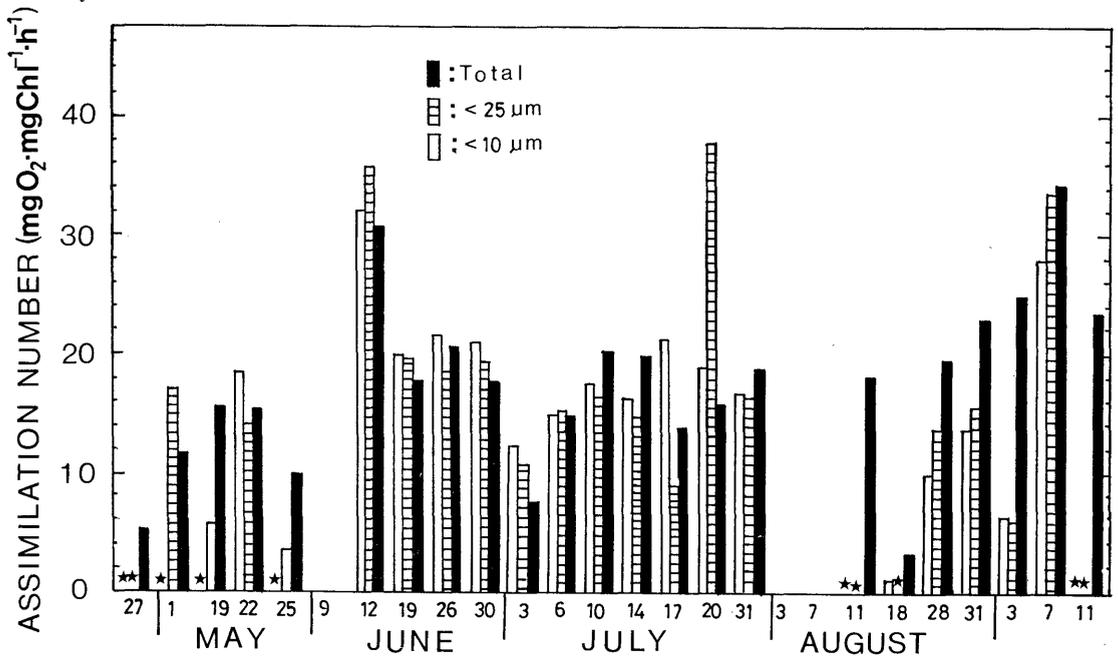


Fig. 8. Assimilation number for unfiltered and two fractionated samples collected at St. 2 in Mikawa Bay during the summer of 1981. Asterisks indicate the negative production rates.

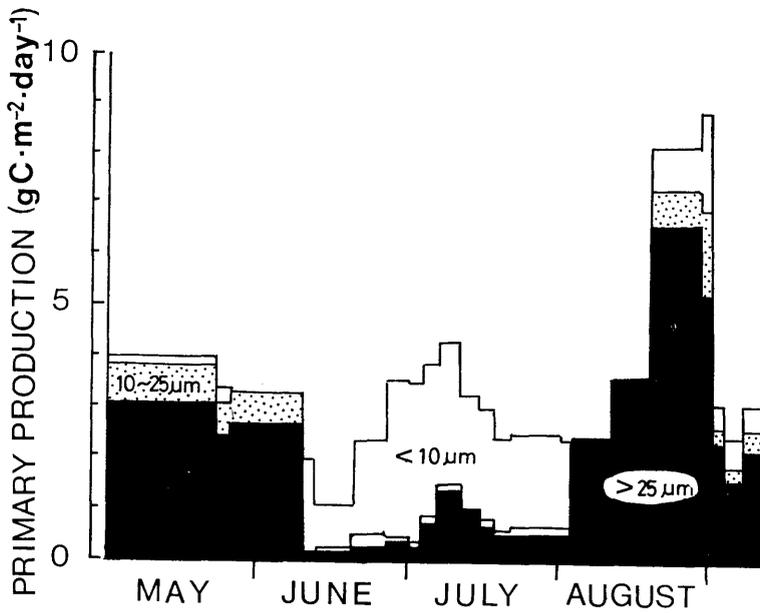


Fig. 9. Integrated daily net production of three different fractions at St. 2 in Mikawa Bay during the summer of 1981.

relatively small throughout summer, ranging from 0 to 36.5% with an average of 16.2%.

Seasonality in production was also obvious and generally followed that in chlorophyll *a* biomass. The $>25\ \mu\text{m}$ fraction occupied 22.4–78.6% (average: 47.6%) in May and 36.2–71.1% (average: 57.5%) in early August–September, respectively, and $<10\ \mu\text{m}$ fraction was 59.5–100% (average: 81.2%) in June–July. The contribution of the 10–25 μm fraction was low as 0–26.3% (average: 8.4%). Although these seasonalities in biomass and production were generally coincident with the changes of phases 1–3 previously described, the changes in size composition lagged about 2 weeks behind those in phases. This indicates that about two weeks are needed to complete the floristic changes initiated by the changed hydrographic conditions.

The assimilation number, net production/chlorophyll *a* ratio, of fractionated samples was smaller than that of the unfiltered population before May and after early August (Fig. 8). During these periods, larger chain-forming diatoms actually dominated. On the other hand, the assimilation number was equivalent to or exceeded those of the unfiltered populations during the June–July period, when the water column was well stratified and microflagellates and smaller diatoms dominated.

Discussion

The assimilation numbers of the unfiltered populations observed in the present study were not different from those observed in the preceding year (TANAKA & SANO 1980) and equivalent to that in Tokyo Bay, one of the highly eutrophied embayments. According to SHIBATA & ARUGA (1982), the assimilation numbers of the surface populations in Tokyo Bay were 8.2–56.1 $\text{mgO}_2 \cdot \text{mgChl. } a^{-1} \cdot \text{h}^{-1}$ ($=3.1\text{--}21.0\ \text{mgC} \cdot \text{mgChl. } a^{-1} \cdot \text{h}^{-1}$) during 1976–1978. These values, including those in Mikawa Bay, frequently exceeded the numbers observed in highly productive Oyashio regions, the other coastal waters (2–7 $\text{mgC} \cdot \text{mgChl. } a^{-1} \cdot \text{h}^{-1}$) and the eutrophic lakes (2–6 $\text{mgC} \cdot \text{mgChl. } a^{-1} \cdot \text{h}^{-1}$) (ICHIMURA & ARUGA 1964). Thus, it is concluded that the assimilation number of the phytoplankton community both in Mikawa Bay and Tokyo Bay reaches the highest level in natural waters.

Despite the low residual nutrient levels, the assimilation number was not decreased to a greater extent during the stratified period in Mikawa Bay. The $<10\ \mu\text{m}$ fraction was generally higher than that of the total community under the stratified condition (Fig. 8). Such high assimilation numbers of nanoplankton in summer have also been reported in Narragansett Bay, ranging from 2.9 to 13.4 with an average of 5.8 $\text{mgC} \cdot \text{mgChl. } a^{-1} \cdot \text{h}^{-1}$ (FURNAS 1983). This may have been one of the causes which favour the predominance of nanoplankton communities during the stratified period when the supply rate of regenerated nutrients in the bottom layer below pycnocline is limited.

The importance of nanoplankton is now recognized in various embayments, and their chlorophyll *a* and productivity in summer account for some 40 to 100% and 60 to 100% of total phytoplankton populations, respectively (e.g., DURBIN et al. 1975, FURNAS 1983, MCCARTHY et al. 1974, VAN VALKENBURG & FLEMER 1974). Our results indicate that the

nanoplankton ($<10\ \mu\text{m}$ fraction) is also important in Mikawa Bay, and its contribution falls within the range of the previously reported values.

Daily net production in the euphotic layer varied from $0.61 (=0.23)$ to $34.5\ \text{gO}_2\cdot\text{m}^{-2}\cdot\text{d}^{-1}$ ($=12.9\ \text{gC}\cdot\text{m}^{-2}\cdot\text{d}^{-1}$). Based on several assumptions, the contributions of three different size fractions to the daily production were also calculated. The $<10\ \mu\text{m}$ fraction was $0-3.16\ \text{gC}\cdot\text{m}^{-2}\cdot\text{d}^{-1}$, $10-25\ \mu\text{m}$ and $>25\ \mu\text{m}$ fractions were $0-1.8\ \text{gC}\cdot\text{m}^{-2}\cdot\text{d}^{-1}$ and $0.08-6.57\ \text{gC}\cdot\text{m}^{-2}\cdot\text{d}^{-1}$, respectively. Their percentage contribution to total production were then $0-92\%$, $0-21\%$ and $2.3-100\%$, respectively. It can be seen that these contributions changed drastically with months (Fig. 9). In the high production period before June and in August, the $>25\ \mu\text{m}$ fraction contributed nearly 80% . On the other hand, between the two blooms of the $>25\ \mu\text{m}$ fraction in May and August, the nanoplankton contribution was nearly 80% . The contribution of the intermediate size class, the $10-25\ \mu\text{m}$ fraction, was very small throughout the study period. The total primary production over the 134 days was $481\ \text{gC}\cdot\text{m}^{-2}$. Of this, about 60% was synthesized by the $>25\ \mu\text{m}$ plankton, while the remaining 40% was by the $<25\ \mu\text{m}$ plankton.

In Mikawa Bay, after the surface temperature increases to near 20°C , stratification of the water column gradually develops. The transition from $>25\ \mu\text{m}$ (tentatively defined as net plankton) to $<25\ \mu\text{m}$ plankton (nanoplankton) and its reverse case take place in mid-June and early August when the surface temperature exceeds about 20°C and decreases below about 25°C after reaching the maximum temperature. Despite this general trend, several cases of red tides, which are formed by large-sized species, occur in the central part of the bay during the stratified period. Temporal vertical mixing induced by strong wind is causative of these red tides as mentioned previously.

Nutrient concentrations, light intensity and vertical water movements, etc. are important factors regulating the size composition of phytoplankton. EPPLEY et al. (1969) pointed out that the half saturation constant (k_s) in nutrient uptake kinetics of phytoplankters, the concentration supporting an uptake rate one-half the maximum rate, is approximately proportional to cell size. PARSONS & TAKAHASHI (1973) used multiparametric models to predict that a large planktonic diatom grows faster than a smaller coccolithophorid under the condition of high light intensity and high nutrient concentrations. TAKAHASHI et al. (1977) emphasized that the summer blooms, accelerated by vertical mixing of water, occur frequently both in high latitudes and coastal waters and are governed by the large phytoplankters. SEMINA (1972) had also pointed out that the vertical water movement is advantageous for the growth of the larger phytoplankters. It is a well known fact that the sinking rate of plankters is a reciprocal function of cell size.

From the foregoing findings, we can deduce the following conclusions: (1) If there is no abrupt temporal nutrient supply during the stratified period, nanoplankters tend to predominate with diminishing nutrient with time because of their low half saturation constant. (2) The slower sinking rate of nanoplankton also favors their predominance during the stratified period. (3) Therefore, even in a eutrophic shallow bay, nanoplankters can be highly significant produ-

cers during the stratified period when the rate of nutrient supply to the surface layer is limited. However, because the stratification in shallower regions is more easily disturbed by a stormy weather, the nutrient supply as well as vertical mixing occurs intermittently during summer. Such a condition allows a temporal bloom of larger phytoplankters during the period when nanoplankton communities are generally predominating.

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