Contribution of benthic microalgae to the whole water algal biomass and primary production in Suo Nada, the Seto Inland Sea, Japan.

Md. Jahangir Sarker[1*], Tamiji Yamamoto[1**] and Toshiya Hashimoto[1]

[1]Graduate School of Biosphere Science, Hiroshima University
Higashi-Hiroshima 739-8528, Japan
Tel: 082-424-7945
Fax: 082-424-7998

**Corresponding author email: tamyama@hiroshima-u.ac.jp

Running Title: Contribution of benthic microalgae in Suo Nada

---

*Present address: Center for Environment and Water (CEW), King Fahd University of Petroleum and Minerals
Dhahran, 31261, P.O. Box. 1804, Saudi Arabia
Tel: +966-3-860-7717
Fax: +966-3-860-3220
mjsarker@kfupm.edu.sa

Contribution of benthic microalgae to the whole water algal biomass and primary production in Suo Nada, the Seto Inland Sea, Japan.

Md. Jahangir Sarker, Tamiji Yamamoto and Toshiya Hashimoto

瀬戸内海周防灘における水柱全体の藻類バイオマスと一次生産に対する底生微細藻の寄与

Md. Jahangir Sarker, 山本民次，橋本俊也

周防灘全域において，2001 年度に行った季節ごとの観測結果から，微細藻のバイオマスと一次生産について，浮遊微細藻および底生微細藻の比較を行った。光補償深度と水深の比較から，周防灘南西部が底生微細藻が潜在的に生息可能な海域であるとみなすことができた。海底には上層水柱から沈降してきた浮遊微細藻が多いが，南西部海域ではバイオマス・一次生産ともに底生微細藻のそれが大きいことが分かった。しかしながら，南西部海域で水柱全体に占める底生微細藻のバイオマスの割合は，冬に 7%，夏に 2%であった。また，底生微細藻の一次生産量は 4.0-74.0 mg C m^{-2} d^{-1} の範囲であり，これは水柱全体の 2-12%に相当した。底生微細藻の役割は，それ以外に，底泥から水柱への栄養塩フラックスを減少させたり，底泥表層を酸化的に保ったり，動物ベントスの餌となったりするので，これらについても考察を加えた。

ABSTRACT:

Biomass and primary productivity of benthic microalgae (BMA) and planktonic algae in Suo Nada, the western part of the Seto Inland Sea, Japan were compared in terms of unit area with regard to their seasonal and spatial distribution in 2002. Judging from light compensation depth and water depth, the southwestern part of Suo Nada was considered to be a potential habitat for BMA. Whereas the contribution of sedimented planktonic algae was high in biomass at the sediment surface, BMA was obviously significant both in biomass and primary production in the shallow southwestern part. However, the contribution of BMA to the total biomass in the entire water column was 7% in winter and 2% in summer. The primary production of BMA varied between 4.0 and 74.0 mg C m^{-2} d^{-1} in the southwestern part, accounting for 2-12% of the whole water column primary production. The ecological roles of BMA in the Suo Nada ecosystem are discussed, such as reduction of benthic nutrient flux, oxidation of surface sediments and feed for higher animals.

Key words: benthic microalgae, planktonic algae, biomass, primary production, Suo Nada

1. Introduction

The ecological importance of benthic microalgae (BMA) as primary producers in estuaries and shallow coastal ecosystems is now well understood (MacIntyre *et al*., 1996; Underwood and Kromkamp, 1999; Cahoon and Cooke, 1999). The significance of the abundance of BMA in shallow coastal waters (Miller *et al*., 1996; Rizzo, 1990; Wiltshire, 1992), and the role of BMA in controlling pelagic ecosystems have been important topics in recent reports (Fear *et al*., 2004). BMA oxygenate the upper sediment by their photosynthesis and absorb nutrients during growth (Rizzo, 1990; Rizzo *et al*., 1992; Sundbäck *et al*, 1991). According to current reports, the contribution of BMA in terms of primary production varies from 15 to 50% of water column production in shallow waters, depending on the depth and other factors such as turbidity in the water column and sediment quality (Underwood and Kromkamp, 1999; Cahoon and Cooke, 1999; Fear *et al*., 2004; Blackford, 2002; Thom and Albright, 1990).

The factors controlling BMA productivity vary in time and space (Cahoon and Cooke, 1992). Sundbäck and Jönsson (1988) reported that the fluctuation in BMA productivity in Laholm Bay (southeastern Kattegat between the west coast of Sweden and Denmark) could be explained in terms of light, sediment type, nutrient condition and hydrodynamic processes in the bay. Temperature (Rasmussen *et al*., 1983) and/or nutrient availability (Lukatelich and McComb, 1986) are more important in very shallow areas, where it is not necessary to consider light as a significant factor controlling the BMA production.

In eutroficated coastal environments, high nutrient loads may lead to high primary production in the water column, which may in turn generate a greater flux of mineralized nutrients from settled organic matter through decomposition (Dalsgaard, 2003). In very shallow coastal areas, where the bottom is within the euphotic zone, mineralization of organic matter may affect overall biogeochemical cycling (Anderson *et al*. 2003).

In addition to BMA, freshly settled living phytoplankton cells are found on the sediment surface; occasionally these phytoplankton join the primary production in the water column by resuspension (Baillie and Welsh, 1980; De Jonge and Van Beusekom, 1992). In the case of a shallow coastal water body, therefore, an estimation or measurement of water column primary productivity does not always include only the productivity by planktonic algae (MacIntyre *et al.* 1996). BMA have been regarded as important primary producers in shallow water coastal ecosystems in temperate areas (Nelson *et al*., 1999; Jahnke *et al*., 2000; Light and Beardall, 2000, Welker *et al*., 2002; Sundbäck *et al*., 2004; Colijn and de Jonge, 1984; Heip *et al*., 1995; Admiraal, 1984; Wiltshire, 1992; Underwood and Paterson, 1993a, b; Underwood and Kromkamp, 1999), and Yamaguchi *et al.* (2007) have recently recorded the importance of BMA in a very shallow area of Suo Nada, Japan.

Suo Nada is a shallow, large, semi-enclosed basin (mean depth 23.7 m; area 3,100 km^2), located at the western end of the Seto Inland Sea, Japan (Fig. 1). The shallower region, including tidal flats, extends along the southwestern coast of Suo Nada, while the deeper region lies along the east-west axis in the central part of the basin. Fresh water discharged from the Yamakuni River emptying in to the southwestern part occasionally affects the physical structure of the water column of the area; after the river discharge subsides, the saline water mass propagates to the lower layer of the water column (Magome, 2003). As a result, a steep pycnocline has been observed at around 8 m depth (Senjyu *et al*., 2001).

The shallowness of the southwestern part of Suo Nada may imply higher primary production of BMA because of the potential light penetration on to the bottom. Fish landed from Suo Nada comprised almost entirely demersal fishes, which contrasts with other basins of the Seto Inland Sea, where pelagic fish production is high (Nagai and Ogawa, 1987). However, the fisheries. activity during summer, especially in the western part of Suo Nada, has been severely affected by the formation of an oxygen-deficient water mass (Senjyu *et al*., 2001). Formation of the oxygen-deficient water is likely due to an increase in the oxygen consumption rate in the bottom layer (Senjyu *et al*., 2001). Anoxic sediment conditions (acid volatile sulfide ~0.30 mg g^{-1} dw and redox potential ~-50 mV) in Suo Nada were reported by Sarker *et al* (2005). Accelerated bacterial decomposition under such conditions helps release nutrients in warmer season, especially in the southwestern part (Sarker *et al.,* 2005). In such an area, BMA inhabiting the surface sediments might play significant roles in the oxygen and nutrient budget by performing primary production.

In the present paper, therefore, we focus on the contribution of BMA to the whole water column biomass and primary production in comparison to planktonic algae in terms of their seasonal and horizontal variations in Suo Nada of the Seto Inland Sea, Japan.

2. Materials and methods

2.1. Observations and chemical analyses

Observations and sampling were carried out between 10:00 and 15:00 h on 7-11 January (winter), 19-24 April (spring), 2-7 August (summer) and November 11-15 (autumn) 2002 in Suo Nada, the Seto Inland Sea (Fig. 1). Water temperature (^{O}C) was measured with a CTD (Sea Bird 9/11) at nine stations (Stns. 1-9; Fig. 1). Seawater samples were collected from 0, 5, 10, 20 m depths and 2 m above the bottom with a Van Dorn water sampler at each station, and immediately filtered through a Whatman GF/F filter and kept at -20 ^{O}C. Chl. *a* concentrations in the filtered samples were determined within 5 days following the method of Jeffrey and Humphrey (1975). Seawater samples were also filtered immediately through a membrane filter (0.45 µm, Millipore, Bedford, USA) on board, and the filtered water samples were kept at -20 ^{0}C. Dissolved inorganic phosphorus (DIP) was determined following the method of Strickland and Parsons (1972). DIP was selected to represent nutrients in lieu of DIN (dissolved inorganic nitrogen) because phosphorus is reported to limit primary productivity through the entire Seto Inland Sea except Osaka Bay (Yamamoto, 2003).

At least four casts of a core sampler (Acrylic tube, 5.0 cm in diameter and 1 m length) were carefully carried out at each station except Stns. 1, 2 and 6 (Fig. 1) in order to collect sediment. Sediment sampling was not carried out at deeper Stns. 1 and 2 since the light intensity was too low for photosynthesis there, while Stn. 6, although shallow, was not included in our study due to rough weather in winter and spring. Three of the four casts with no surface disturbance were sliced into 1 cm-thick sections. The three sliced sub-samples from the surface 1 cm layers were mixed and centrifuged (2,000 rpm, 15 min) at on-board ambient temperature to collect supernatant water samples. DIP was analyzed in the pore water samples following the method of Strickland and Parsons (1972). The fourth core sample was used for biological examinations as follows. After dividing it into four aliquots (each 1cm thick) with a plastic spatula, the first aliquot was used for identification of sedimented planktonic algae and BMA. Only cells with intact chloroplasts were counted in triplicate for diluted sediment samples with filtered seawater and identified to genus level on a Sedgwick Rafter counting chamber under an inverted light microscope (NIKON, type-120) referring the monographs of Hustedt (1985) and Yamazi (1979). Motility of the BMA was also checked if they are live or dead. Total cell number counted was at least 1,000 and the standard error was calculated from the triplicate count. The second aliquot was used to determine the sediment chlorophyll *a* (mg m^{-2}). The sediment was diluted with filtered seawater to 50 ml in a measuring flask and a 5 ml portion was filtered through a Whatman GF/F filter. The filter was kept frozen at $-20^{0}C$ for Chl. *a* analysis. The filtered samples were also collected in triplicate. Chl. *a* content was extracted with 90% acetone overnight and analyzed according to the method of Jeffrey and Humphrey (1975). All sampling stations were divided into two parts, considering light compensation depth (D_c) and the water depths (z); at Stns. 1-5 in the eastern part D_c<z (except Stn. 4) and at Stns. 6-9 in the southwestern part D_c>z.

2.2. Light measurement and calculation

Underwater light intensity was measured with a quantum meter (QSP-200L, Biospherical Instruments Inc.) at each station (Fig. 1). Light attenuation coefficient (*k*) was calculated from a regression line of light intensity at every meter to the depth (*z*) using the following equations (Parsons *et al.*, 1977):

$$k = -1/z \ln\left(Iz/I_0\right) \ldots\ldots\ldots\ldots\ldots\ldots (1)$$

Compensation light intensity (I_c) at which photosynthesis equals respiration was taken from the literature value, 7 μmol photons m^{-2} s^{-1} (Man and Lazier, 1991). The compensation depth (D_c) was then defined using the following equations:

$$D_C = -1/k \times \ln\{(I_C)/(0.5I_0)\} \text{.........}(2)$$

where 0.5 is the average reflection of solar radiation at the sea surface, and I_0 is the radiation at sea surface. We adopted average I_0 values reported in several cities around Suo Nada (Fukuoka, Oita and Yamaguchi) (863 μmol photons m^{-2} s^{-1} for winter; 1579 μmol photons m^{-2} s^{-1} for spring; 1651 μmol photons m^{-2} s^{-1} for summer; 1029 μmol photons m^{-2} s^{-1} for autumn; Rika Nenpyo, 2002) for the calculation, because the measured value of our observations is variable depending on the weather and time of the day on each occasion.

The underwater light intensity at depth z, ($I(z)$; μmol photons m^{-2} s^{-1}) was estimated with the following equation:

$$I(z) = 0.5I_0 \exp(-kz) \text{...}(3)$$

2.3. Estimation of biomass and production (model calculation)

To estimate chlorophyll *a* content of BMA (B_{Chla}), the relationship between the BMA abundance and the measured sediment Chl *a* was examined, so that remove the effect of sedimented planktonic algae (see Fig. 5 in Results). To calculate the depth-integrated Chl. *a* ($P_{\mathrm{Chl.a}}$; mg m^{-2}) in the water column, trapezoidal calculation was performed. For estimation of BMA biomass (mg C m^{-2}), the biovolume (μm^3) measurement was done as follows. Both sedimented planktonic and BMA cells were grouped into different shape classes, and the average biovolume (μm^3) was calculated according to Hillebrand et *al*. (1999). The carbon content of algal cells (pg C $cell^{-1}$) was then calculated using the equations provided by Menden-Deuer and Lessard (2000); $0.216*\mathrm{biovlume}^{0.939}$ for planktonic algae, and $0.288*\mathrm{biovlume}^{0.811}$ for BMA.

Primary productivity of both planktonic algae (P_p) and BMA (B_p) was estimated as a function of Chl. *a* concentration, ambient DIP concentration, temperature and light intensity, as shown in eqs. 4 and 5. The Michaelis-Menten equation was used for nutrient uptake of algae. For water temperature and light intensity, the equations proposed by Eppley (1972) and Steele (1962) were applied as follows:

$$\mathrm{P_P} = 0.851 \times (1.066)^{T} \times \frac{S}{Ks+S} \times \frac{I}{I_{opt}} \times \exp\left(1-\frac{I}{I_{opt}}\right) \times P_{Chl.a} \times 40 \text{...........}(4)$$

$$\mathrm{B_p} = 0.851 \times (1.066)^T \times \frac{S}{Ks+S} \times \frac{I}{I_{opt}} \times \exp\left(1 - \frac{I}{I_{opt}}\right) \times B_{Chl.a} \ldots\ldots\ldots\ldots\ldots\ldots (5)$$

where S is the DIP concentration (μM) in the water column or in the pore water. Ks is the half saturation constant for DIP uptake (μM); Ks=0.1 and 0.5 μM were applied for planktonic algae and BMA, respectively, according to Darrow *et al.* (2003). The optimum light intensities (I_{opt}), 100 and 50 μ photons m^{-2} s^{-1}, were applied for planktonic algae and BMA, respectively (Darrow *et al.*, 2003; Yamamoto *et al.*, 2004a, b). The coefficient "40" is the average C: Chl *a* ratio, which is generally accepted for natural phytoplankton assemblages (Perissinotto *et al.*, 2003; Irigoien *et al.*, 1993).

2.4. Validation and sensitivity analyses of the present model of primary production estimation

Since our estimation of primary production involves several assumptions, we validated our model's output precision by calculations using the published data (Tada *et al.,* 1998) with the present model (validated model) and comparison with observed results.

Sensitivity analyses were carried out for the three parameters, I_c, I_{opt} and Ks, because these literature values include uncertainties. Although we used 7 μmol photons m^{-2} s^{-1} as I_c, traditionally 1% of the light intensity just below the water surface has been used as the I_c for pelagic primary production. Provided the average light intensity values in the atmosphere around Suo Nada (863, 1579, 1651 and 1029 μmol photons m^{-2} s^{-1}) are adopted, 1% of 0.5 I_0 will range from 4.3-8.3. These values are not very different from the value of 7 μmol photons m^{-2} s^{-1} that we adopted, but we checked the sensitivity of I_c by changing the value from 4 to 10 μmol photons m^{-2} s^{-1}. The effect of I_{opt} on the primary productivity of BMA was also checked by changing I_{opt} from 5 to 50 μmol photons m^{-2} s^{-1} with a 5 μmol photons m^{-2} s^{-1} interval, due to the scarcity of published data on I_{op} of BMA. The effect of half saturation constant (Ks) on the calculation output was also checked by changing the value from 0.1 to 1.0 μM with a 0.2 μM interval.

3. Results

3.1. Biomass of microalgae and related parameters

A list of BMA and sedimented planktonic algae identified in the surface sediment is shown in Table 1. Thirteen genera of BMA were identified in the four seasons, and of them seven genera (*Nitzschia*, *Navicula*, *Achnanthes*, *Pinnularia*, *Synedra*, *Pleurosigma* and *Diploneis*) were dominant. *Nitzschia* sp. was dominant in the BMA communities over all seasons. Algae found at the surface sediment included those of benthic origin but also those sedimented from the upper water column, i.e., sedimented planktonic algae. In the sedimented planktonic algal communities, large-sized algae such as *Coscinodiscus* sp. and small-sized algae such as *Thalassiosira* sp., were dominant (Table 1). The abundance of BMA in the surface sediments varied by two orders of magnitude with the minimum in summer (200±40 cells cm^{-2}) and the maximum in winter (32,000±350 cells cm^{-2}), while sedimented planktonic algae reached maximum in spring (27,300±300 cells cm^{-2}) and minimum in summer (6,800±790 cells cm^{-2}), respectively (Fig. 2).

Sedimented planktonic and BMA seemed to be inversely related to their seasonal abundance, with a high sedimented planktonic algal cell density accompanying low BMA cell density (Fig. 2).

The calculated biovolume of sedimented planktonic algae (230-234,000 μm^3) was larger than that of BMA (750-21,700 μm^3) (Table 1). Calculated carbon content was also higher in the sedimented planktonic algae (24.0-1,600 mg C m^{-2}) than BMA (1.0-88 mg C m^{-2}), because of their higher biovolume in spite of their low abundance (Table 2, Fig. 2). Spatially, the biomass of both BMA and sedimented planktonic algae was higher in the southwestern part (2-88 mg C m^{-2} for BMA and 24-1,600 mg C m^{-2} for sedimented plaktonic) than in the eastern one (1-37 mg C m^{-2} for BMA and 87-1330 mg C m^{-2} for sedimented planktonic; Table 2).

Fig. 3 shows the seasonal variation of mean water and sediment temperature (^{O}C), DIP (μM) and light intensity (μmol photons m^{-2} s^{-1}). The seasonal variation of mean water and sediment temperature (^{O}C) showed the highest peak in summer and the lowest value in winter, respectively. The light intensity at the bottom, Ib, was low in winter (8±13 μmol photons m^{-2} s^{-1}) and high in summer (17±33 μmol photons m^{-2} s^{-1}) with high spatial variation (Fig. 3b). The estimated mean light intensity in water column showed the highest and lowest peak in spring (751±220 μmol photons m^{-2} s^{-1}) and winter (369±87 μmol photons m^{-2} s^{-1}) respectively with spatial variation (Fig. 3b). Calculated light attenuation coefficients varied seasonally with highest values in summer (0.304±0.164) and lowest in autumn (0.233±0.109, Figure not shown). Spatially, the bottom light intensity was high in the shallow southwestern part (Fig. 4), indicating that light intensity is adequate for photosynthesis both for BMA and planktonic algae, judging from the compensation depth and the water depth (Table 3).

Seasonal change in mean pore water DIP (μM) increased gradually from winter to reach a maximum in autumn, while mean water column DIP (μM) showed a gradually decreasing trend from winter to summer, with an increase in autumn (Fig. 3c).

As described in the Materials and Methods section, the relationship between the BMA abundance and the sediment Chl. *a* was examined to estimate BMA Chl. *a* (B_{Chla}). As a result, a significant relationship was obtained between these two parameters: B_{Chla} was estimated using the relationship Chl.a (mg m^{-2}) = 0.510 x BMA (10^7 cells m^{-3})+6.057 (r=0.86, p=0.0001, n=24) (Fig. 5).

Although the mean $B_{Chl.a}$ showed a significant seasonal variation with a value of 8.5±5.0 mg Chl. *a* m^{-2} in winter and 1.9±0.9 mg Chl. *a* m^{-2} in autumn (Fig. 6b), $P_{Chl.a}$ showed little seasonal variation, with a large year-to-year variation in summer (Fig. 6a). There are no big rivers in Suo Nada that may affect the phytoplanktonic biomass of the entire area, which might be the reason for the slight seasonal variation in planktonic algal biomass. BMA carbon content was high in autumn (Fig. 6c) in spite of the low Chl. *a* (Fig. 6b). Increased temperature and light intensity in warmer seasons (Fig. 3a, b) are likely to accelerate the primary production of planktonic algae, but the depletion of DIP (nearly zero at several stations; Fig. 3c) in summer might have depressed the primary production in the water column. This will be discussed below. BMA biomass contributed a maximum of 7% in winter and a minimum of 2% in summer relative to the total algal biomass (Fig. 6d).

3.2. Production of pelagic and benthic microalgae

In the horizontal distributions, the estimated primary production in the water column (P_p) was high in the eastern part (exceeded 3,000 mg C m^{-2} d^{-1} in autumn) and low in the southwestern one (10.0 in spring and 12.0 mg C m^{-2} d^{-1} in summer) (Fig. 7). The estimated planktonic primary production (Table 4) showed very large variations during the year, with a maximum in autumn and a minimum in summer.

To validate our model output precision for estimating primary production, using the same model (present model) planktonic primary production was also calculated using the published data (Tada *et al*., 1998) (validated model output) and compared with the observed values (Fig. 8). The validated output produced slightly higher values than the observed ones, yet they showed a coincidence with each other in seasonal variations. Thus, we consider that our model output (present model output) is well validated in the estimation of primary production from our field observations.

In contrast to the planktonic primary production, the BMA production was high in the southwestern part of Suo Nada (<1-101 mg C m^{-2} d^{-1}) and low in the eastern one (0.05-7.0 mg C m^{-2} d^{-1}) (Fig. 9). Seasonally, the average value of the BMA production was low in winter (41 mg C m^{-2} d^{-1}) and high in autumn (101 mg C m^{-2} d^{-1}). The highest contribution of BMA to the total primary production in the whole water column was 9% at Stn 8 in autumn. On average, the primary production of BMA varied between 4.0 and 74.0 mg C m^{-2} d^{-1} in the southwestern part and accounted for 2-12% of the whole water column primary production estimated for the southwestern part of Suo Nada (Table 4).

4. Discussion

$B_{Chl.a}$ values estimated in Suo Nada in the present study appear to be lower than those reported in other temperate coastal waters (MacIntyre *et al*., 1996; Nelson *et al*., 1999; Jahnke *et al*., 2000; Sundbäck *et al*., 2004). The Chl. *a* values in our study, determined by the method of Jeffrey and Humphrey (1975), were not corrected for degradation products of Chl. *a* (Lorenzen *et al*., 1967) because the phaeopigment and chlorophyll *b* values measured in our study were negligible compared to Chl. *a*. Breakdown of chlorophylls into degradation products might have led to the underestimation of Chl. *a* concentrations (Brown *et al*. 1981; Daemen 1986; Riaux-Gobin *et al*. 1987). The microalgal carbon biomass estimated in this study was based on biovolume. It has been reported that the biovolume calculation might overestimate the size of larger cells with relatively higher vacuole volume (Smayda 1978). The great abundance of large-sized BMA (*Pleurosigma* sp.) and sedimented planktonic algae (*Coscinodiscus* sp.) in autumn might therefore be responsible for the overestimation of the biovolume and the carbon biomass, in spite of the low $B_{Chl.a}$.

Light is an explicit factor that explains the horizontal distribution of BMA and their production. Light has been stated to be the factor that limits the habitat range of BMA, for example in the Neuse River estuary, USA, West Florida continental shelf, USA, and Hiroshima Bay, Japan (Fear *et al*., 2004; Miller *et al*., 1996; Cahoon and Cooke, 1999; Woolfstein and Hartig, 1998; Darrow *et al*., 2003; Yamamoto *et al*., 2004a). Judging from the difference between the compensation depth and the water depth, it can be said that the southwestern part of

Suo Nada is suitable for the growth of BMA, although viable sedimented planktonic algae can add an auxiliary value to the BMA primary production due to their higher biomass.

In the sensitivity analyses, changing the compensation light intensity (I_c) from 4 to 10 μmol photons m^{-2} s^{-1} made a difference in the compensation depths of about 5 m in the deeper regions (Stns. 1, 2, 3, 4 and 5) and 1-2 m in the shallower regions (Stns. 6, 7, 8 and 9) (Figure not shown). Even with such a range of compensation light intensity, compensation depth was always deeper than the water depth in the shallow southwestern part of Suo Nada, except at Stn. 4.

For the optimum light intensity (I_{opt}), the seasonal pattern in the BMA production showed a difference according to optimum light intensity (I_{opt}) (Fig. 10). Higher production was obtained with low light intensity below 15μmol photons m^{-2} s^{-1} in autumn and spring, while the situation was almost constant in winter and summer. Seven genera were observed to comprise the dominant BMA in the present study. As far as the authors know, there are few reports on the optimum light intensity of BMA: Grover (1989) gave 60 μmol photons m^{-2} s^{-1} for *Nitzschia* sp. and also for *Nitzschia* sp. (we are not sure if this is the same species as Grover, 1989), Yamamoto *et al*. (2004a) reported 50 µmol photons m^{-2} s^{-1}. We may assume that I_{opt} for other BMA is not very different from these values, if all *in situ* BMA species acclimate their physiological functions of photosynthesis to the ambient environment. Thus, the I_{opt} value used in the present calculation (50 µmol photons m^{-2} s^{-1}) sould be acceptable, judging from the results of the sensitivity analyses, which revealed a reasonable seasonal variation with various I_{opt} values.

Grazing by benthic animals, not studied in the present study, has been reported to be one of the causes of BMA biomass fluctuation in other areas, too (Blackford, 2002; Cooper, 1999; Blanchard *et al*., 1997; Admiraal *et al*., 1983). Higher phosphate concentrations and irradiance in summer are supposed to benefit BMA, leading to higher growth in the southwestern part of Suo Nada, but increased temperature in summer might raise the feeding activity of benthic animals on BMA, which may have led to a decline in the BMA biomass in summer.

The P_p was low in summer relative to the other seasons. This is due to the low DIP concentrations in the upper layer of the water column. In some stations in shallow areaa, DIP levels were so low that they were almost depleted through the entire water column during spring and summer. In fact, the highest primary productivity (>3000 mg C m^{-2} d^{-1}) was obtained in autumn at the deepest station (Stn. 2) with high DIP concentrations. In summer, however, occasional increases in nutrient concentration can be observed coincident with the monsoonal rainfall, which may increase the primary production in the water column. Tada's (1998) calculation of primary production in summer was based on the data collected in June, when monsoonal rainfall may have had an effect. On the other hand, our calculation for summer is based on the data collected in August, when the water column is stratified and DIP is usually depleted in the upper layer.

Although the primary production of BMA was not very sensitive to the *Ks* for DIP (Figure not shown), uptake of DIP by BMA may be effective in reducing the DIP upward flux from the sediments. Benthic DIP fluxes reported by Sarker *et al* (2005) in Suo Nada are the reverse of the seasonal pattern of BMA abundance (Fig. 11), suggesting that the assumption holds. Reduction of DIP fluxes by nutrient uptake by BMA has also been reported in other areas (Sundbäck, 1986; Rysgaard *et al*., 1993). In summer, the decreased BMA biomass may accelerate pelagic productivity by increasing the benthic nutrient flux. On the other hand, the higher biomass of BMA in seasons other than summer may reduce the nutrient flux into the water column. An anoxic condition in the warmer season, induced by oxygen consumption by bacterial decomposition in the bottom layer particularly in the southwestern part of Suo Nada (Senjyu *et al*., 2001), could be responsible for increasing in DIP flux to the water column (Sarker, *et al*. 2005). However, it might be postulated that BMA may partially contribute to controlling benthic nutrient fluxes that consequently control water column primary production, particularly in the southwestern part of the Suo Nada.

Thus, it is hypothesized that BMA play important roles, not only in primary production but also in the restoration of coastal environments. From the viewpoint of benthic nutrient flux, BMA could reduce the nutrient flux into the water column by absorbing DIP and depressing phytoplanktonic primary production and preventing blooms in the water column, as suggested by Sarker *et al*., (2005). A similar trend has been reported in other areas (Sundbäck *et al*., 1991). In eutrophication processes, an increase in nutrient loads will lead to increased primary production in the water column and a decrease in light penetration to the bottom as the BMA become covered by sedimented planktonic algae. Oxygen produced by the photosynthesis of BMA could remediate sediment quality by enhancing bacterial aerobic decomposition (Yamamoto et al., 2007) and alleviating oxygen depletion in the lower water column. Therefore, to maintain a healthy ecosystem in Suo Nada, the shallow area should be maintained and restored.

Acknowledgements

We are grateful to Professor Kazuo Iseki, Graduate School of Biosphere Science, Hiroshima University, and Dr. Akira Hoshika and Dr. Yasufumi Mishima, National Institute of Advanced Industrial Science and Technology (AIST), Chugoku, Japan for their valuable comments and suggestions on earlier drafts. We are thankful to all members of the Laboratory of Aquatic Environmental Management, Graduate School of Biosphere Science, and the crew of the R/T vessel, Toyoshio Maru, Hiroshima University, for their help during sampling.

References

Admiraal, W. 1984. The ecology of estuarine sediment-inhabiting diatoms. p. 269-322. In: Progress in Phycological Research, ed. by F. E. Round and D. J. Chapman.

Admiraal, W., L. A. Bouman, L. Hoekstra and K. Romeyn. 1983. Qualitative and quantitative interactions of between microphytobenthos and herbivorous meifaunna on a brackish intertidal mudflat. *Intl. Rev. der. Ges. Hydrobiol.*, 68, 175-191.

Anderson, I. C., K. J. McGlathery and A. C. Tyler. 2003. Microbial mediation of "reactive" nitrogen transformations in a temperate lagoon. *Mar. Ecol. Prog. Ser.*, 246, 73-84.

Baillie, P. W. and B. L. Welsh. 1980. The effect of tidal resuspension on the distribution of intertidal epipelic algae in an estuary. *Estuar., Coast. Mar. Sci.*, 10, 165–180.

Blackford, J. C. 2002. The influence of microphytobenthos on the northern Adratic Ecosystem: A modeling study. *Estuar., Coast. Mar. Sci.,* 55,109–123.

Blanchard, G. F., J. M. Guarini, P. Gros and P. Richard. 1997. Seasonal effect on the relationship between photosynthetic capacity of intertidal microphytobenthos and temperature. *J.*

Phycol., 33,723-728.

Brown, L. M., B. T. Hafkxa and M. D. Mackinnon. 1981. Analysis of chlorophyll a in sediments by high-pressure liquid chromatography. *Canadian J. Fish. Aquat*. Sci.38:205-214.

Cahoon, L. B. and J. E. Cooke. 1992. Benthic microalgal production in Oslow Bay, North Carolina, USA. *Mar. Ecol. Prog. Ser*., 84,185-196.

Cahoon, L. B. and J. E. Cooke. 1999. The role of benthic microalgae in neritic ecosytems, *Oceanogr. Mar. Biol*., 37, 47–86.

Colijn, F. and V. N. de Jonge. 1984. Primary production of microphytobenthos in the Ems-Dollard estuary. *Mar. Ecol. Prog. Ser*., 14, 185-196.

Cooper, M. 1999. The influence of deposit feeding benthic fauna on biogeochemical fluxes across the estuarine sediment-water interface. MSc thesis, University of Essex, Colchester.

Daemen, E. A. M. J. 1986. Comparison of methods for the determination of chlorophyll in estuarine sediments. *Net. J. Sea. Res*. 20:21-28.

Darrow, B. P., J. J. Walsh, G. A. Vargo, R. T. Masserini, K. A. Flanning and J. Z. Zang. 2003. A simulation study of the growth of benthic microalgae following the decline of a surface phytoplankton bloom. *Cont. Shelf. Res.*, 23, 1265-1283.

Dalsgaard, T. 2003. Benthic primary production and nutrient cycling in sediments with benthic microalgae and transient accumulation of macroalgae. *Limnol. Oceanogr.*, 48, 2138-2150.

De Jonge, V. N. and J. F. E. V. Beusekom. 1992. Contribution of resuspended microphytobenthos to total phytoplankton in the Ems estuary and its possible role for grazers. *Net. J. Sea Res.*, 30, 91–105.

Eppley, R. W. 1972. Temperature and phytoplankton growth in the sea. *Fish. Bull.*, 70, 1063-1085.

Fear, J., T. Gallow, H. Nathan, J. Loftin and H. Paerl. 2004. Predicting benthic microalgal oxygen and nutrient flux responses to a nutrient reduction management strategy for the eutrophic Neuse River Estuary, North Carolina, USA. *Estuar., Coast. Mar. Sci.*, 61, 491-506.

Grover, J. P. 1989. Phosphorous- dependent growth kinetics of 11 species of algae. *Limnol. Oceanogr*., 34, 341-348.

Hillebrand, H., D., Claus-Dieter., K. David, T. Zohary, and U. Pollingher. 1999. Biovolume calculation for pelagic and benthic microalgae. *J. Phycol*., 35, 403-424.

Hustedt, F. 1985. The Pennate Diatoms: A translation of Hustedt's "Die Kieselalgen, 2. Teil" with supplement by N. G. Jensen, Koeltz Scientific Books, Koenigstein, Germany, 918 pp.

Heip, C. H. R., N. K. Goosen, P. M. J. Herman, J. Koromkamp, J. J. Middleburg and K. Soetart. 1995. Production and consumption of biological particles in temperate tidal estuaries. *Oceanogr. Mari. Biol*., 33, 1-150.

Irigoien, X., J. Castel and B. Sautour. 1993. In situ grazing activity of planktonic copepods in the Gironde Estuary. *Cah. Biol. Mar*., 34, 225-237.

Jahnke, R. A., J. R. Nelson., R. L. Marinelli and J. E. Eckman. 2000. Benthic flux of biogenic elements on the southeastern US continental shelf: influence of pore water advective transport and benthic microalgae. *Cont. Shelf. Res*., 20, 109-127.

Jeffrey, S. W. and G. F. Humphrey. 1975. New spectrometric equations for determining chlorophyll a b c1 and c2 in higher plants, algae and natural phytoplankton. *Biochem physiol pflanzen*., 167, 191-194.

Light, B. R. and J. Beardall. 2000. Photosynthetic characteristics of sub-tidal benthic microalgal populations from a temperate shallow water marine ecosystem. *Aquat. Bot*., 70, 9-27.

Lorenzen, C. J., 1967. Determination of chlorophyll and pheopigments: spectrophotometric equations. *Limnol. Oceanogr*., 12, 343-346.

Lukatelich, R. J. and A. J. McComb. 1986. Distribution and abundance of benthic microalgae in a shallow south-western Australian estuarine system. *Mar. Ecol. Prog. Ser.*, 27, 287–297.

MacIntyre, H. L., R. J. Geider and D. C. Miller. 1996. Microphytobenthos: The ecological role of the "secret garden" of unvegetated, shallow-water marine habitats: I. Distribution, abundance and primary production. *Estuaries*, 19, 186–201.

Magome, S. 2003. Current structure and behavior of the river plume in Suo Nada. *J. Oceanogr*., 59, 833-843.

Man, K. H. and J. R. N. Lazier. 1991. Dynamics of Marine Ecosystems, biological-physical interactions in the Oceans, Boston, MA: Blackwell. 446pp.

Menden-Deuer, S., and E. J. Lessard. 2000. Carbon to volume relationships for dinoflagellates, diatoms, and other protist plankton. *Limnol. Oceanogr.*, 45, 569-589.

Miller, D. C., R. J. Geider, and H. L. MacIntyre. 1996. Microphytobenthos: the ecological role of the "secret garden" of unvegetated, shallow-water marine habitats: II. Role in sediment stability and shallow-water food webs. *Estuaries*, 19, 202–212.

Nagai, T. and Y. Ogawa 1987. Fisheries production. P. 61-94. In: Sustainable Development in the Seto Inland Sea, Japan- from the view point of Fisheries, ed. by T. Okachi and T. Yanagi, Terra Scientific Publishing Company, Tokyo.

Nelson, J. R., J. E. Eckman., C. Y. Robertson., R. L. Marinelli and R. A. Jahnke. 1999. Benthic microalgal biomass and irradiance at the sea floor on the continental shelf of the Atlantic Bight: Spatial and temporal variability and storm effects. *Cont. Shelf. Res.*, 19, 477-505.

Parsons, T. R., M. Takahashi, B. Hargrave. 1977. Biological Oceanographic Processes, 3rd ed.

Pergamon. 332pp.

Perissinotto, R. C, K. I. Nozais and A. Anandraj. 2003. Planktonic food webs and benthic-pelagic coupling in three South African temporarily open estuaries. *Acta Oecol*., 24, 307-316.

Rasmussen, M. B., K. Henriksen and A. Jensen. 1983. Possible causes of temporal fluctuations in primary production of the microphytobenthos in the Danish Waden Sea. *Mar. Biol*., 73, 109-114.

Riaux-Gobin, C., C. A. Llwell and B. Klein. 1987. Microphytobenthos from two subtidal sediments from North Brittany. II. Variations of pigment compositions and concentrations determined by HPLC and conventional techniques. *Mar. Ecol. Prog. Ser*. 40:275-283.

Rika Nenpyo (Chronological Scientific Tables), 2002. National Astronomical Observatory, Japan, Maruzen Co., Ltd.

Rizzo, W. M. 1990. Nutrient exchange between the water column and a subtidal benthic microalgal community. *Estuaries*, 13, 219–226.

Rizzo, R. G., L. Lackey and R. Christian. 1992. Significance of euphotic, subtidal sediments to oxygen and nutrient cycling in a temperate estuary. *Mar.Ecol. Prog. Ser.*, 85, 51–61.

Rysgaard, S., N. Risgaard, L. P. Nielsen, and N. P. Revsbech. 1993. Nitrification and denitrification in lake and estuarine sediments measured by 15N dilution technique and isotope pairing. *Appl. Env. Biol.*, 59, 2093-2098.

Sarker, M. J., T. Yamamoto, T. Hashimoto, and T. Ohmura. 2005. Evaluation of benthic nutrient fluxes and their importance in the pelagic nutrient cycles in Suo Nada, Japan. *Fish. Sci.*, 71, 593-604.

Senjyu, T., H. Yasuda, S. Sugihara, and S. Kamizono. 2001. Current and turbidity variations in the western part of Suo Nada, the Seto Inland Sea Japan; A hypothesis on the oxygen-deficient water mass formation. *J. Oceanogr.*, 57, 15-27.

Smayda, T. J. 1978. From phytoplankton to biomass. *In* Sournia, A. (Ed) Phytoplankton Manual. Monographs on Oceanographic Methodology 6. UNESCO, Paris, pp. 273-279.

Steele, J. H. 1962. Environmental control of photosynthesis in sea. *Limnol. Oceanogr.*, 7, 137-

150.

Strickland, J. D. H. and T. R. Parsons 1972. A practical handbook of Sea water analysis. 2nd ed. *Bull. Fish. Res. Bd Can*., 167: 311pp.

Sundbäck, K. 1986. What are the benthic microalgae doing on the bottom of Laholm Bay? *Ophel. Suppl*., 4, 273-286.

Sundbäck, K. and B. Jönsson. 1988. Microphytobenthic productivity and biomass in sublittoral sediments in stratified bay, southeastern Kattegat. *J. Exp. Mar. Biol*., 122, 63-81.

Sundbäck, K., V. Enoksson, Graneli, W., and K. Pettersson. 1991. Influence of sublittoral microphytobenthos on the oxygen and nutrient flux between sediment and water: a laboratory continuous flow study. *Mar. Ecol. Prog. Ser*., 74, 263-279.

Sundbäck, K., F. Linares, F. Larson and A. Wulff. 2004. Benthic nitrogen fluxes along a depth gradient in microtidal fjord: the role of denitrification and microphytobenthos. *Limnol. Oceanogr.*, 49,1095-1107.

Tada, K., Monaka, K., Morishita, M., and Hashimoto, T. 1998. Standing stocks and production rates of phytoplankton and abundance of bacteria in the Seto Inland Sea, Japan. *J. Oceanogr.*, 54, 285-295.

Thom, R. A. and R. G. Albright. 1990. Dynamics of benthic vegetation standing stock, irradiance and water properties in central Puget Sound. *Mar. Biol.*, 104,129-141.

Underwood G. J. C. and J. Kromkamp. 1999. Primary production by phytoplankton and microphytobenthos in estuaries. *Adv. Ecol. Res.*, 29, 94-153.

Underwood G. J. C. and D. M. Paterson. 1993a. Recovery of intertidal benthic diatoms after biocide treatment and associated sediment dynamics. *J. Mar. Biol. Assoc*. U.K. 73, 25-45.

Underwood G. J. C. and D. M. Paterson 1993b. Seasonal change in diatom biomass, sediment stability and biogenic stabilization in the Severn estuary. *J. Mar. Biol. Assoc*. U.K. 73, 871-887.

Welker, C., E. Sdrigotti, S. Covelli, and J. Faganeli. 2002. Microphytobenthos in the Gulf of Trieste (Northern Adriatic Sea): Relationship with labile sedimentary organic matter and nutrients. *Estuar. Coast. Shelf. Sci.*, 55, 259-273.

Wiltshire K. H. 1992. The influence of microphytobenthos on oxygen and nutrient fluxes between littoral sediments and associated water phases in the Elbe Estuary. p. 63-70. In: Colombo G *et al*. [eds.], Marine eutrophication and population dynamics.

Woolfstein, K. and P. Hartig. 1998. The photosynthetic light dispensation system: application to microphytobenthic primary production measurments, *Mar. Ecol. Prog. Ser*., 63, 63–71.

Yamaguchi, H., S. Montani, H. Tsutsumi, K. Hamada, N. Ueda and K. Tada. 2007. Dynamics of microphytobenthic biomass in a coastal area of western Seto Inland Sea, Japan. *Estuar. Coast. Shelf. Sci*., 75, 423-432.

Yamamoto T. 2003. The Seto Inland Sea-eutrophic or oligotrophic? *Mar. Poll. Bull.*, 47, 37-42.

Yamamoto, T., S. J. Oh, and I. Goto. 2004a. Effects of temperature, salinity and irradiance on the growth of microphytobenthos *Nitzschia* sp. *Jap. J. Phycol*. (*Sorui*)., 52, 5-11 (in Japanese with English abstract).

Yamamoto, T., S. J. Oh and Y. Kataoka. 2004b. Growth and uptake kinetics for nitrate, ammonium and phosphate by the toxic dinoflagellate *Gymonodinium catenatum* isolated from Hiroshima Bay, Japan. *Fish. Sci.*, 52,108-115.

Yamamoto, T., I. Goto, O. Kawaguchi, K. Minagawa, E. Ariyoshi and O. Matuda. 2007. Phytoremediation of shallow eutrophic marine sediments using benthic microalgae. *Mar. Poll. Bull.,* 57, 108-115.

Yamazi, I. 1979. Illustrations of the marine plankton of Japan. Hoikusha publishing CO. LTD. Osaka, Japan, 537pp. (in Japanese).

Table 1. Calculated biovolume (μm^3) of sedimented planktonic and benthic microalgae collected from Suo Nada based on their geometric shapes and equations, taken from Hillebrand *et al.* (1999). Genus-based carbon biomass was also calculated using the equations 0.216*biovlume$^{0.939}$ for sedimented planktonic and 0.288*biovlume$^{0.811}$ for benthic microalgae according to Menden-Deuer and Lessard (2000). Abbreviations: a=length; b=width; c=height; d=diameter; h=minimum height; H=maximum height; ß= angle between two transapical sides.

Benthic microalgae	**Shape**	**Equation**	Biovolume (μm^3)	C pg cell^{-1}
Amphora sp.	Cymbelloid	$1/6\pi.\ (2b)^2.a.$ ß/360	1,510	109
Achnanthes sp.	Eliptic prism	1/4π.a.b.c	2,200	148
Diploneis sp.	Eliptic prism	1/4π.a.b.c	3,140	198
Navicula sp.	Eliptic prism	1/4π.a.b.c	4,240	250
Nitzschia sp.	Prism on parallelogram	1/2a.b.c	7,430	400
Pleurosigma sp.	Prism on parallelogram	1/2a.b.c	7,770	410
Synedra sp.	Box	a.b.c.	5,180	300
Pinnularia sp.	Box	a.b.c	21,700	950
Cocconeis sp.	Eliptic prism	1/4π.a.b.c	5,300	300
Fragillaria sp.	Eliptic prism	1/4π.a.b.c	750	62
Scoliotropis sp.	Box	a.b.c	3,770	230
Gyrosigma sp.	Prism on parallelogram	1/2a.b.c	4,290	250
Paralia sp.	Cylinder	$1/4\pi.\ d^2.h$	9,720	490
Sedimented Planktonic algae				
Biddulphia sp.	Eliptic prism	1/4π.a.b.c	2,980	400
Coscinodiscus sp.	Cylinder	$\pi.\ d^2(1/8.(h+H)+1/4c^3)$	234,000	23,750
Distephanus sp.	Sphere	$1/6\pi.\ d^3$	4,450	580
Dichtyoca sp.	Sphere	$1/6\pi.\ d^3$	5,660	720
Melosira sp.	Cylinder	$1/4\pi.\ d^2.h$	11,780	1,440
Skeletonema sp.	Cylinder+2 half spheres	$\pi.\ d^2(h/4+d/6)$	5,960	760
Thalassiosira sp.	Cylinder	$1/4\pi.\ d^2.h$	169,600	17,580
Trichodesmium sp.	Cylinder	$1/4\pi.\ d^2.h$	230	35
Tryceratium sp.	Prism on triangle	1/2a.b.c	1,380	190
Bacteriastrum sp.	Cylinder	$1/4\pi.\ d^2.h$	5,090	650
Chaetoceros sp	Eliptic prism	1/4π.a.b.c	2,200	300
Rhizosolenia sp.	Cylinder	$1/4\pi.\ d^2.h$	3,110	410

Table 2. Comparision of carbon biomass of sedimented planktonic algae and BMA (benthic microalgae) collected from the Suo Nada sediment in 2002.

	Sedimented planktonic algae (mg C m^{-2})				Benthic microalgae (mg C m^{-2})			
Stations	Winter	Spring	Summer	Autumn	Winter	Spring	Summer	Autumn
3	330	520	140	980	37	21	1	20
4	25	240	87	600	1	10	1	7
5	340	530	100	1,300	28	21	3	13
7	890	1,500	140	1,600	52	70	2	65
8	470	690	24	1,300	30	22	2	71
9	860	750	160	500	45	21	3	88

Table 3. Comparision of estimated light compensation depth (m) and water depth (m) at each sampling station in different seasons. Suo Nada. * indicates the stations suitable for BMA photosynthesis.

	Light compensation depth (m)				Water depth (m)			
Station	Winter	Spring	Summer	Autumn	Winter	Spring	Summer	Autumn
1	20	31	29	31	44	44	46	46
2	20	39	26	29	50	51	49	48
3	22	30	29	33	39	40	39	41
4	22	*24	*26	*24	23	23	25	23
5	24	24	16	21	30	27	31	31
6	*18	*19	*27	*20	13	13	12	12
7	17	27	19	*28	28	28	29	27
8	*18	*18	*19	*15	11	11	11	12
9	*7	*9	*8	*11	9	10	9	10

Table 4. Primary production estimated for the water column planktonic and benthic microalgae (BMA) in each season. Contribution of BMA production to the water column total production was also calculated for the southwestern part of Suo Nada. n: observation number.

Season	Planktonic production		BMA production		Contribution of BMA (%)
	Total (n=9)	Southwestern areas (n=4)	Total (n=6)	Southwestern areas (n=3)	Southwestern areas
Winter	1.100	816	12	17	2
Spring	540	428	18	31	7
Summer	360	77	2	4	5
Autumn	1,600	545	39	74	12
Mean	920	466	18	32	7

Figure legends.

Figure 1. Map showing the location of Suo Nada in the Seto Inland Sea. Contour lines with numbers show the water depth (m), and symbols with numbers denote the sampling stations. Filled circular and square symbols indicate sampling location where water column planktonic samples were obtained. Filled circular symbol indicates sampling locations of benthic microalgae (BMA).

Figure 2. Abundance of benthic microalgae (BMA) and sedimented planktonic algae. The size of the circle denotes the total cell density (cm^{-2}). ND denotes the station where no samples were collected.

Figure 3. Seasonal variations in (a) temperature (^{O}C), (b) light intensity (μ mol photons m^{-2} s^{-1}) and (c) DIP (μM) in the water column and in the sediment of Suo Nada, 2002. Bar indicates standard deviation.

Figure. 4. Horizontal distribution of bottom light intensity (Ib; μmol photons m^{-2} s^{-1}) in Suo Nada.

Figure 5. Relationship between benthic microalgal abundance ($x10^{7}$ cells m^{-2}) and sediment Chl. *a* (mg m^{-2}).

Figure 6. Seasonal variations of (a) planktonic Chl. *a* (mg m^{-2}), (b) BMA Chl. *a* (mg m^{-2}), and (c) BMA biomass (mg C m^{-2}) and (d) relative contribution (%) of BMA biomass to total algal biomass in Suo Nada, 2002. Bar indicates standard deviation.

Figure 7. Horizontal distribution of estimated water column primary production (mg C m^{-2} d^{-1}). ND denotes the stations where no samples were collected.

Figure 8. Comparision of primary production among the present model calculations and those validated against the published observed data (Tada *et al.*, 1998) and the published data (Tada *et al.,* 1998). Bar indicates standard deviation of the data.

Figure 9. Horizontal distribution of estimated benthic microalgal primary production (mg C m^{-2} d^{-1}). ND denotes the stations where no samples were collected.

Figure 10. Sensitivity of optimum light intensity (μmol photons m^{-2} s^{-1}) to the BMA production (mg C m^{-2} d^{-1}).

Figure 11. Relation of the benthic DIP flux from the surface sediment (bar: mg m^{-2} d^{-1}) and abundance of benthic microalgae (BMA) (line: x 10^4 cells cm^{-2}). The benthic DIP fluxes are cited in Sarker *et al*. (2005).

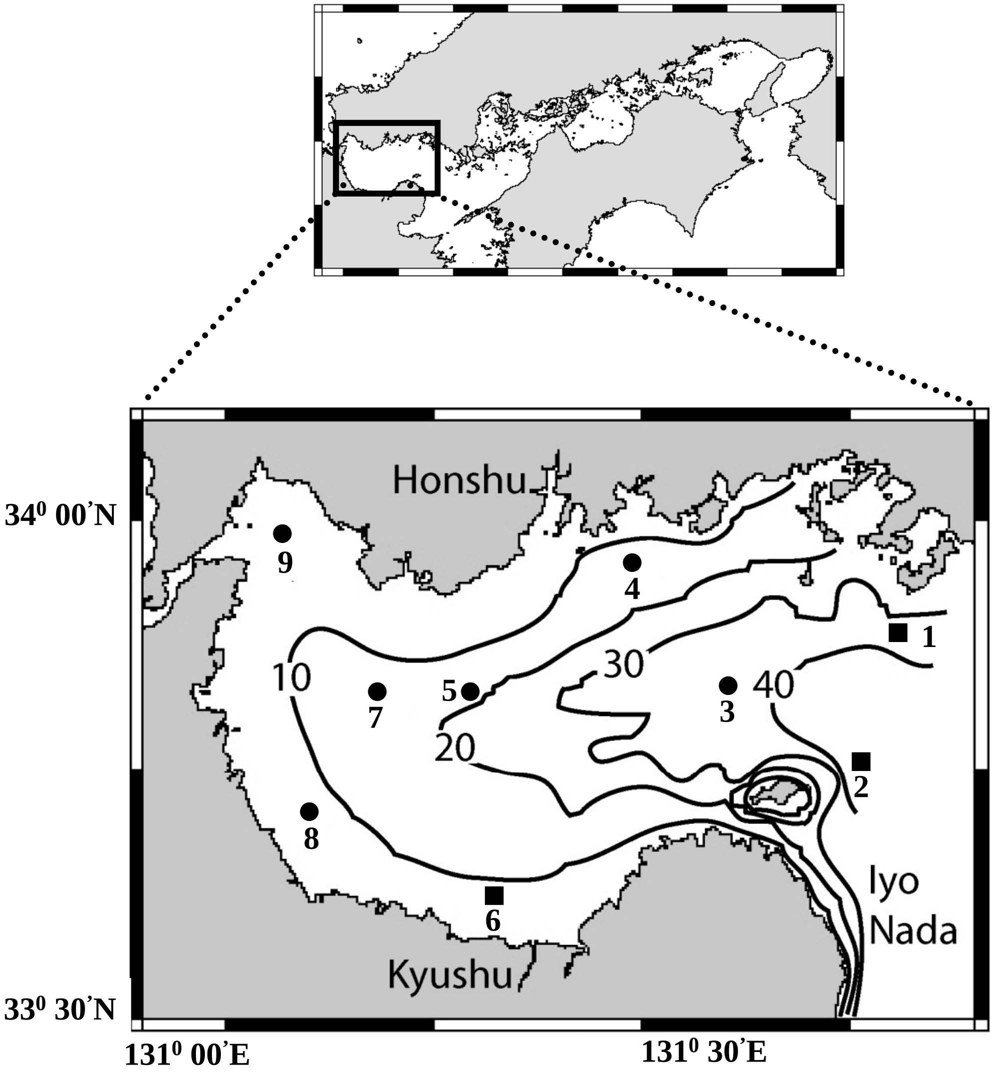

Figure 1 Sarker *et al*.

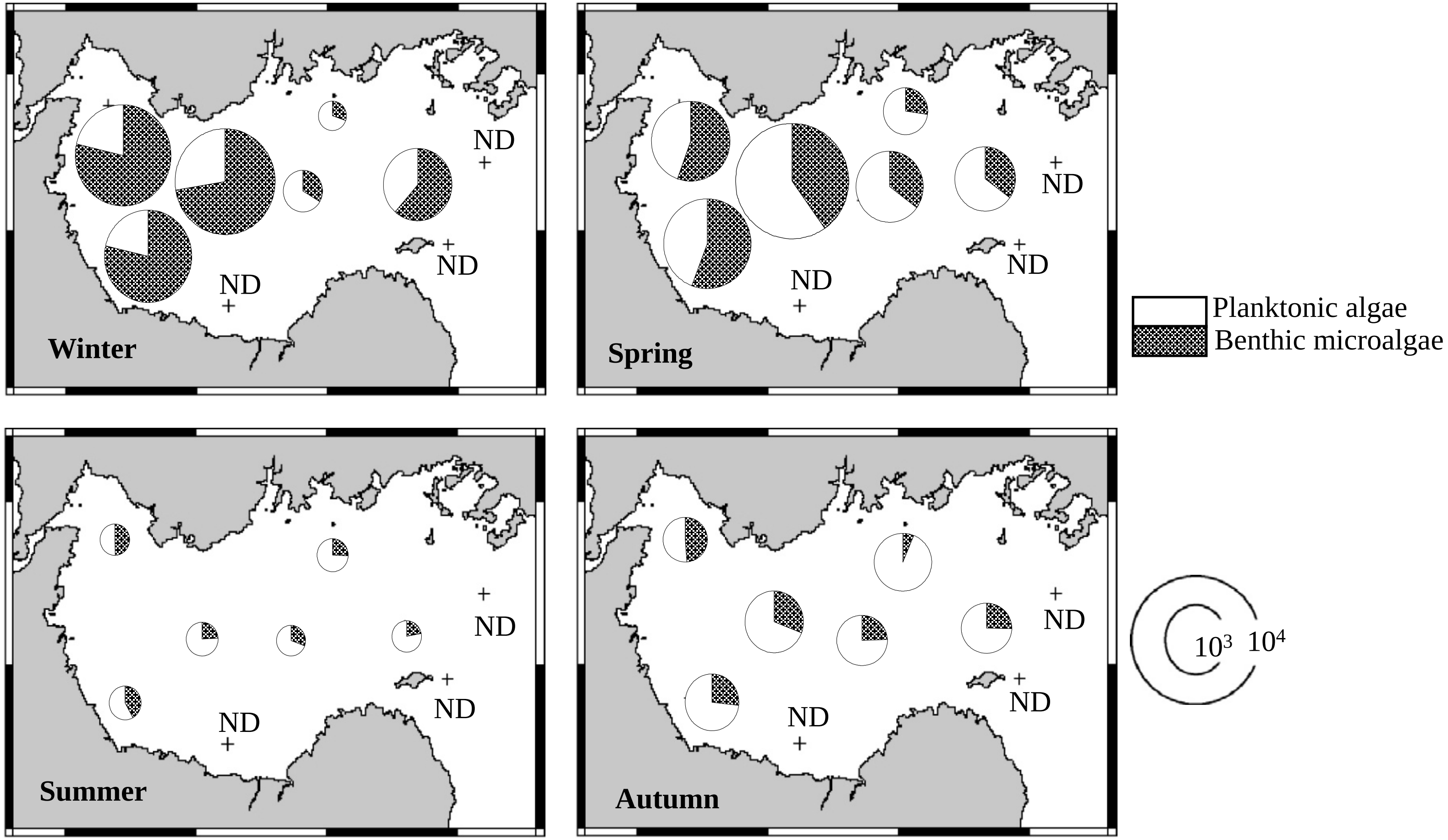

Figure 2 Sarker *et al*.

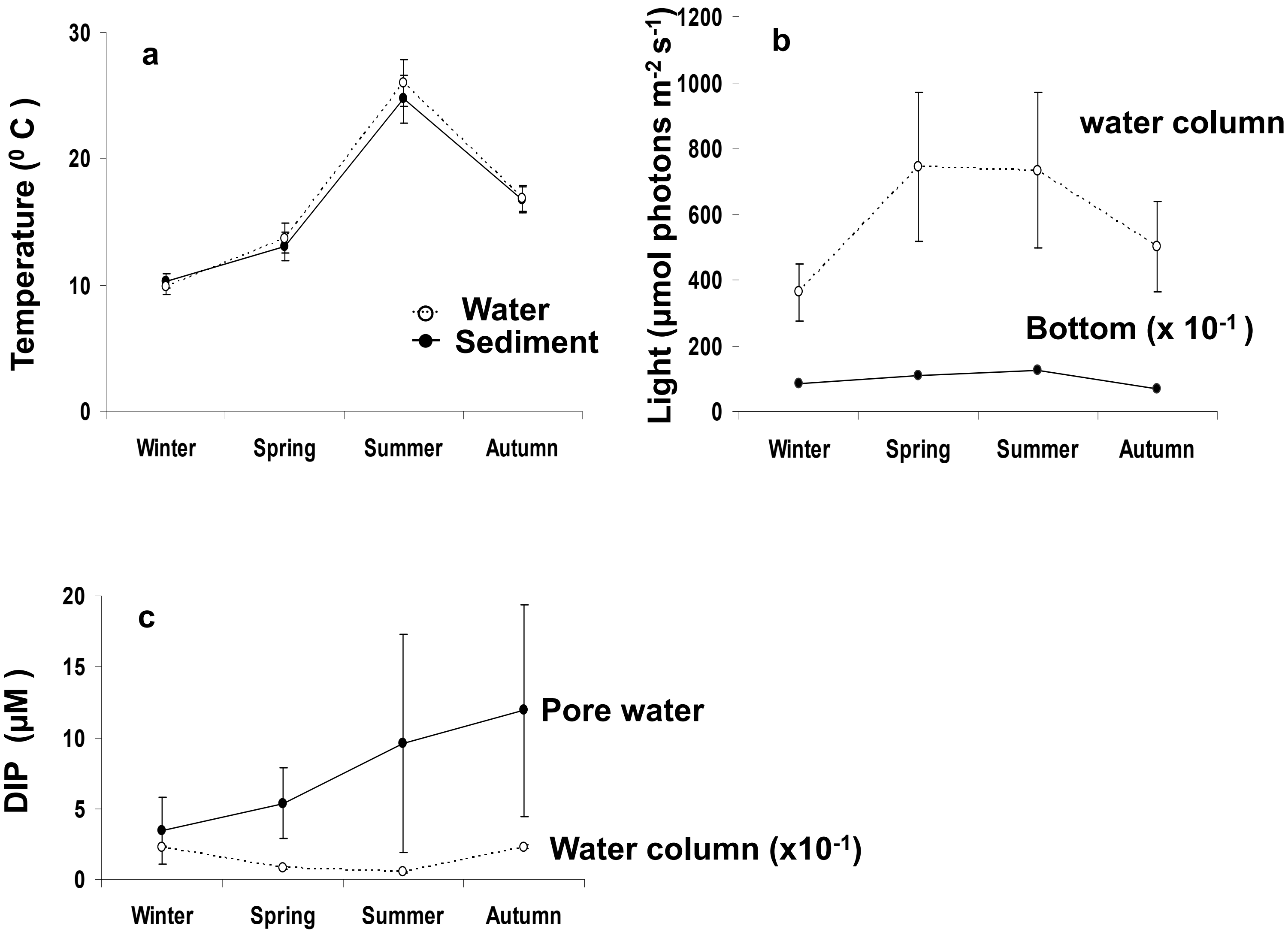

Figure 3 Sarker *et al.*

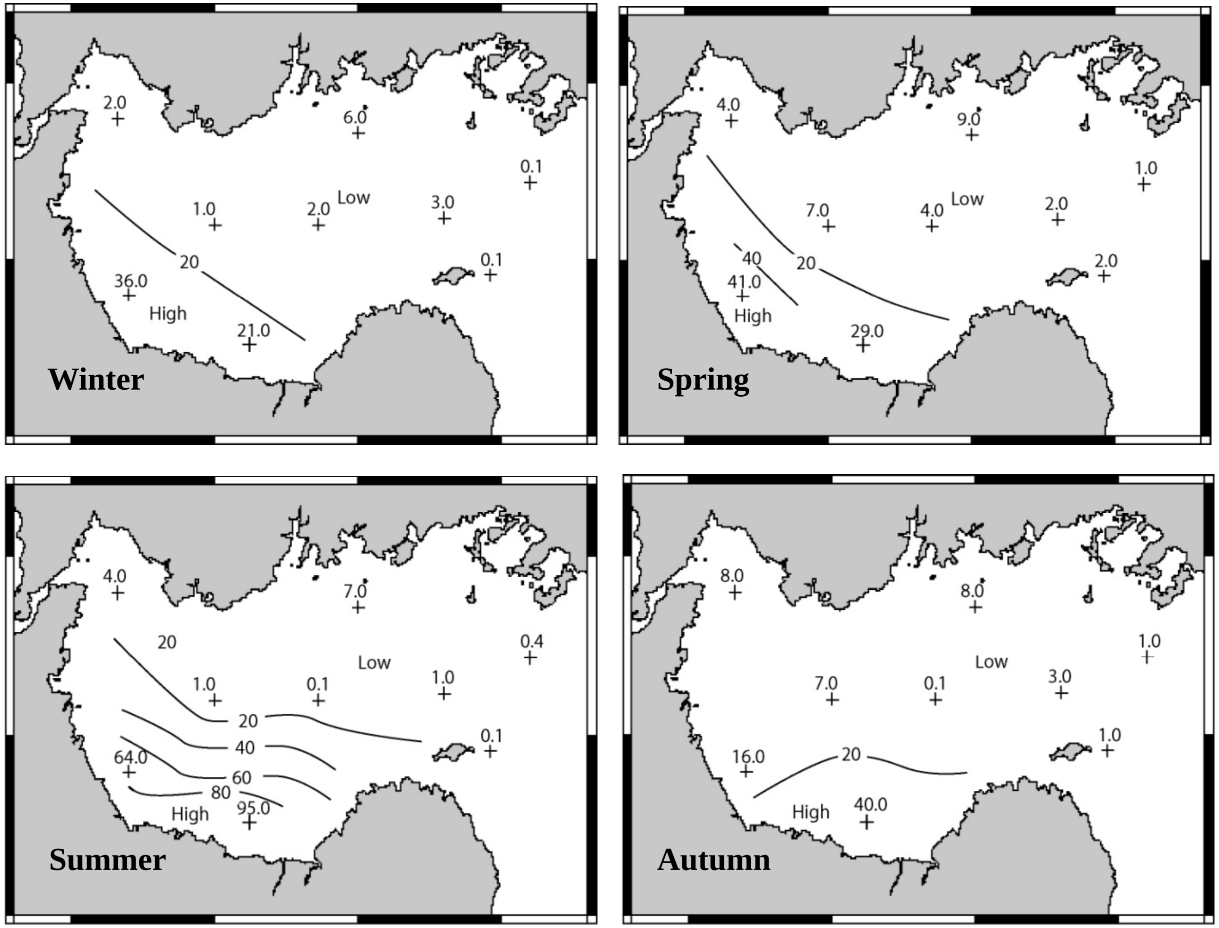

Figure 4 Sarker *et al.*

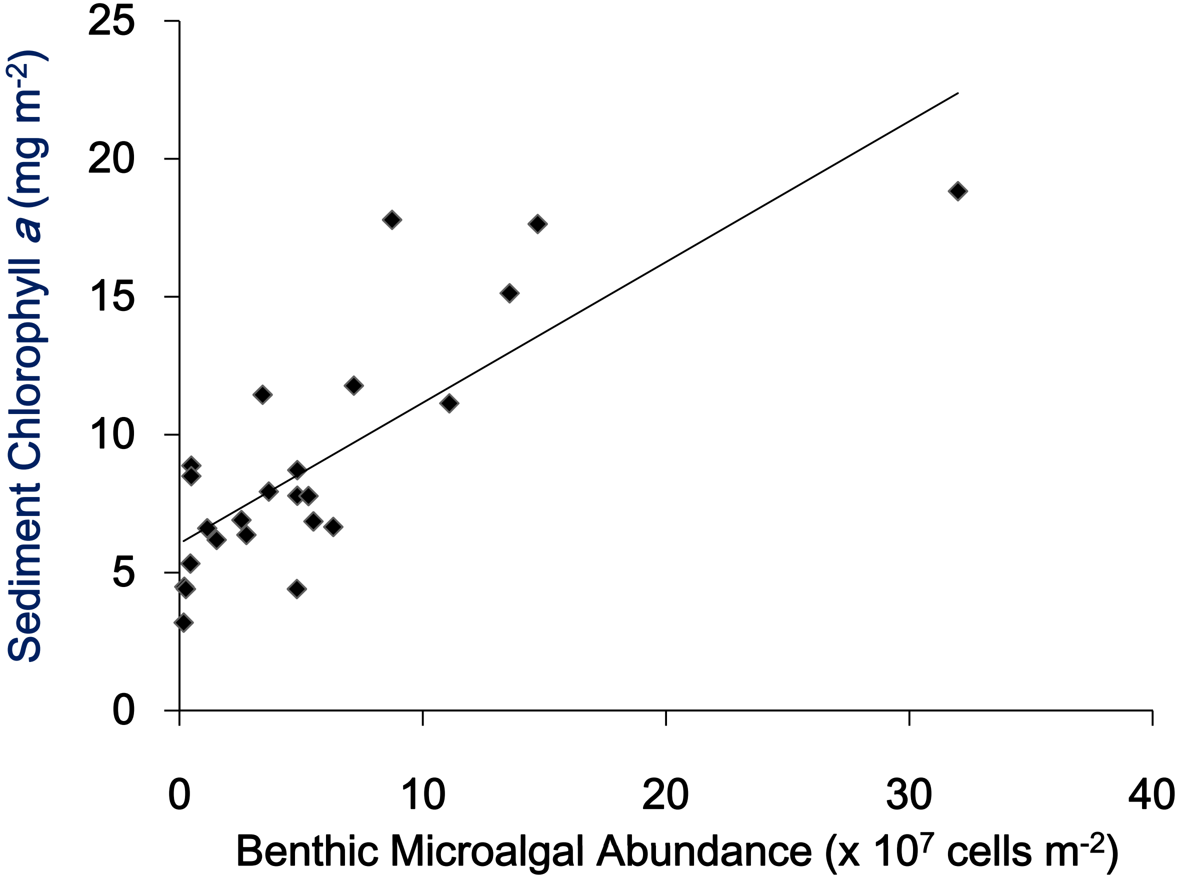

Figure 5 Sarker *et al.*

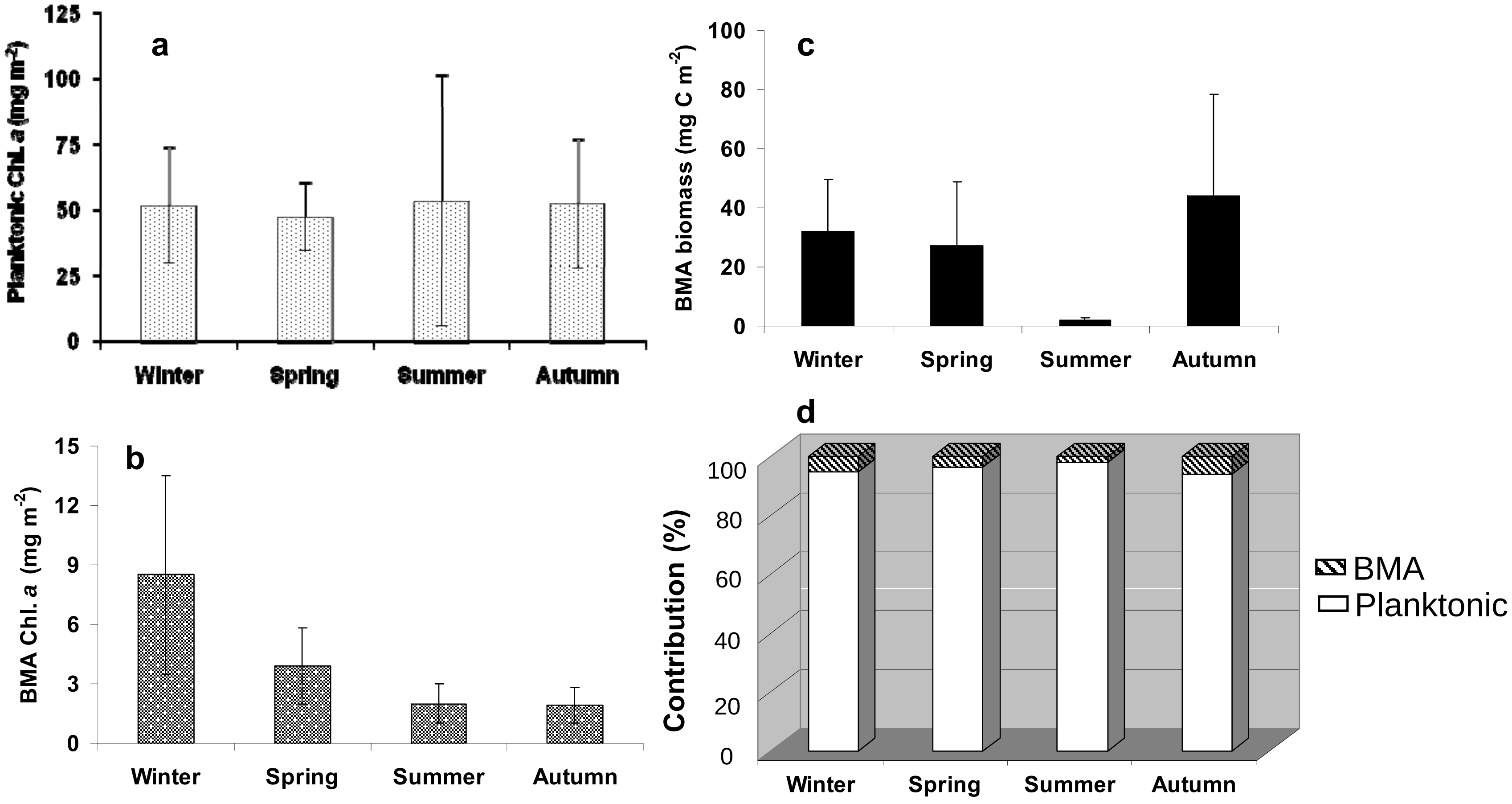

Figure 6 **Sarker *et al.***

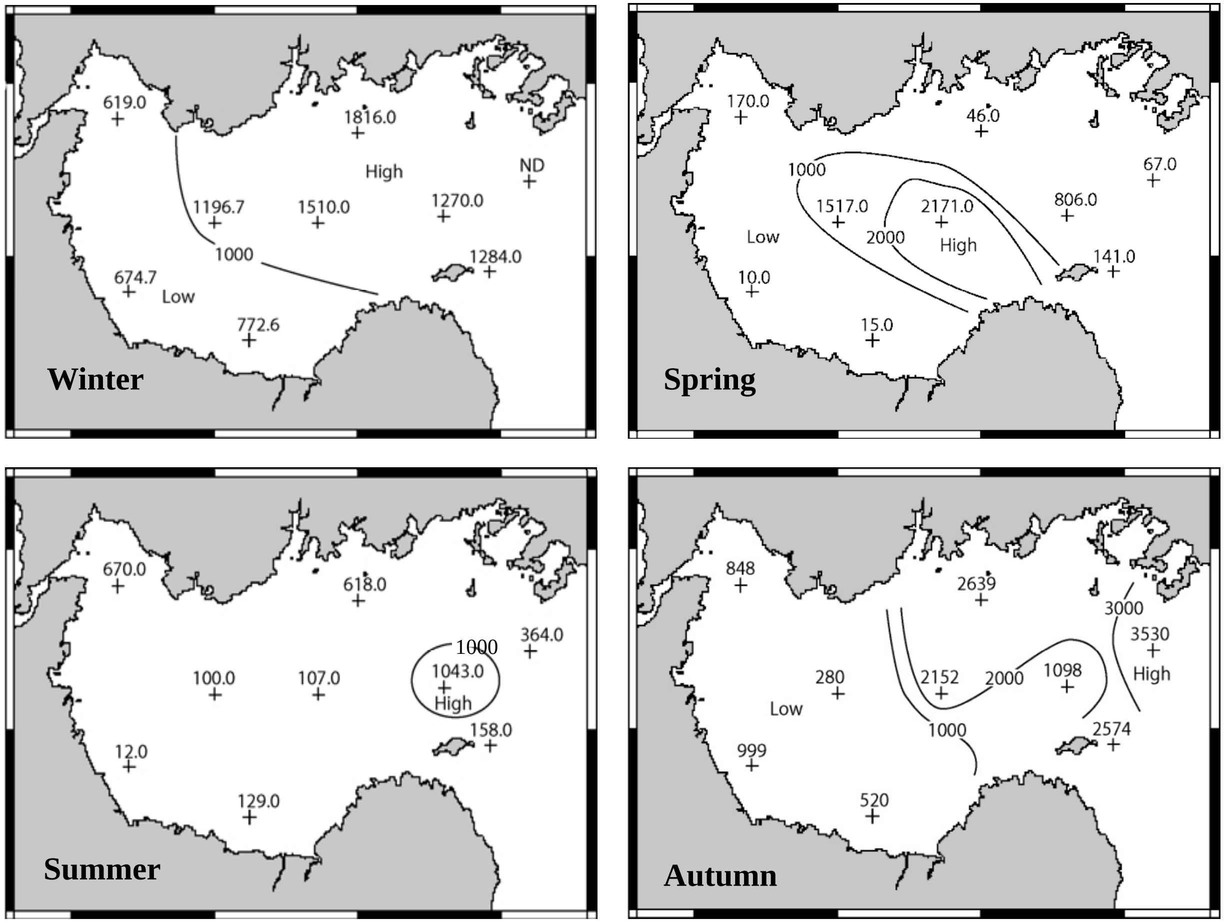

Figure 7 Sarker *et al*.

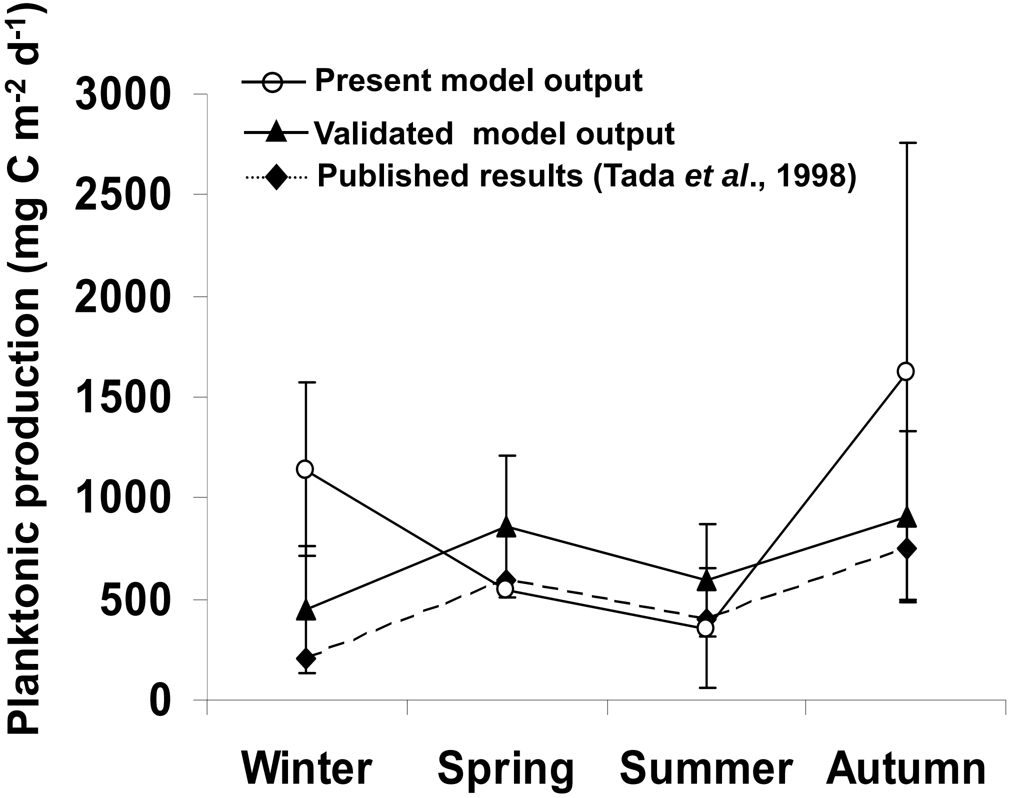

Figure 8 Sarker *et al.*

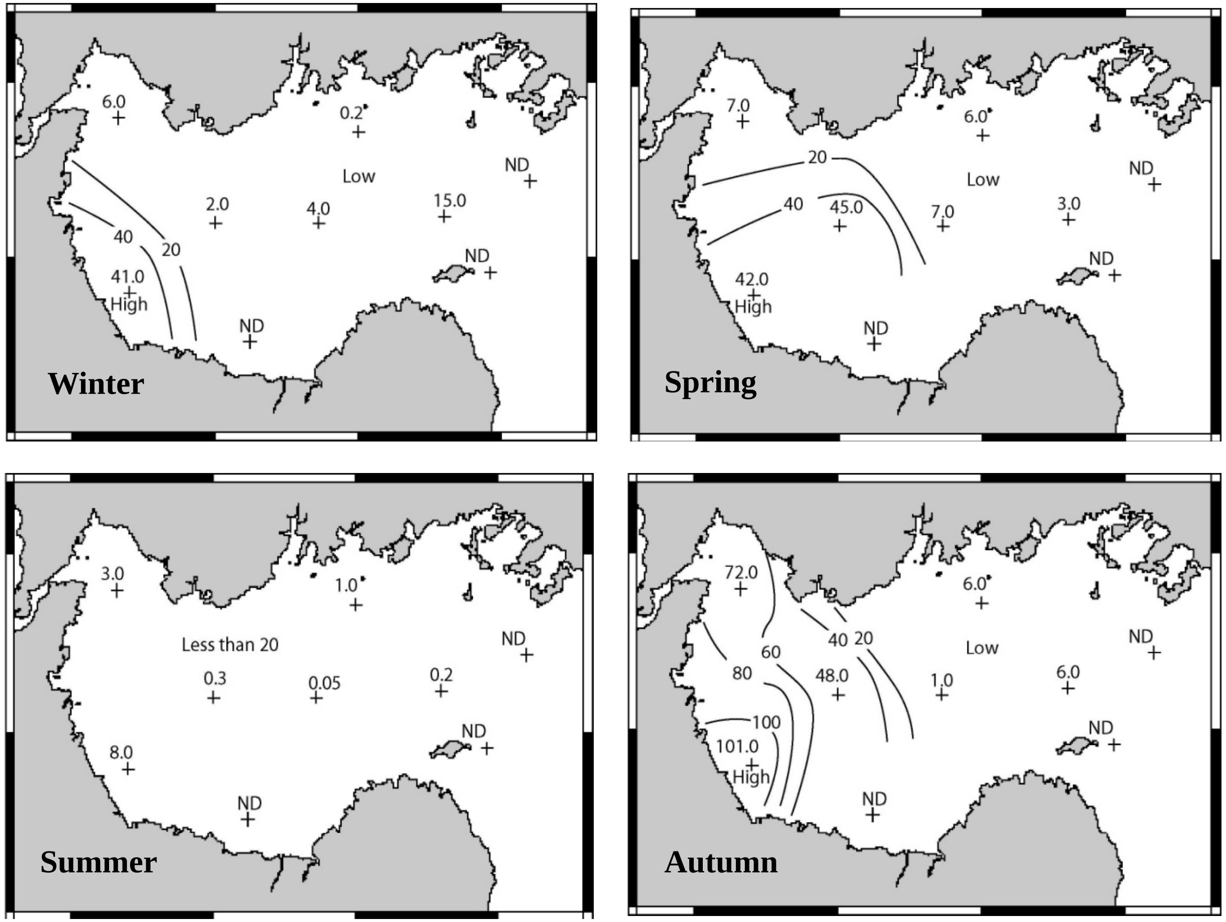

Figure 9 Sarker *et al*.

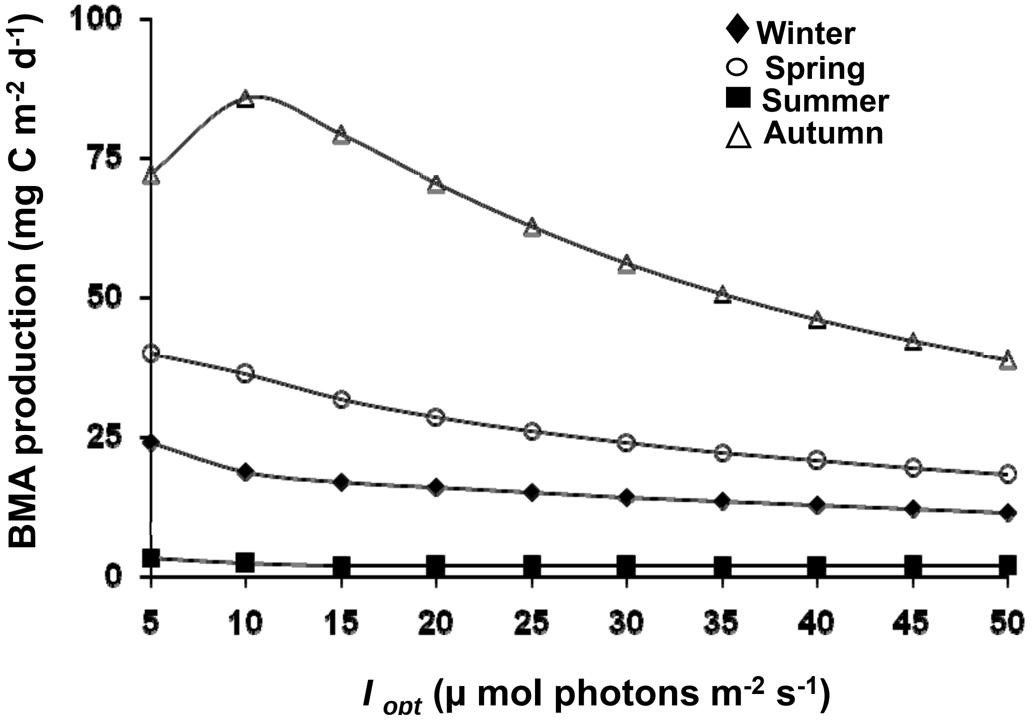

Figure 10 Sarker *et al.*

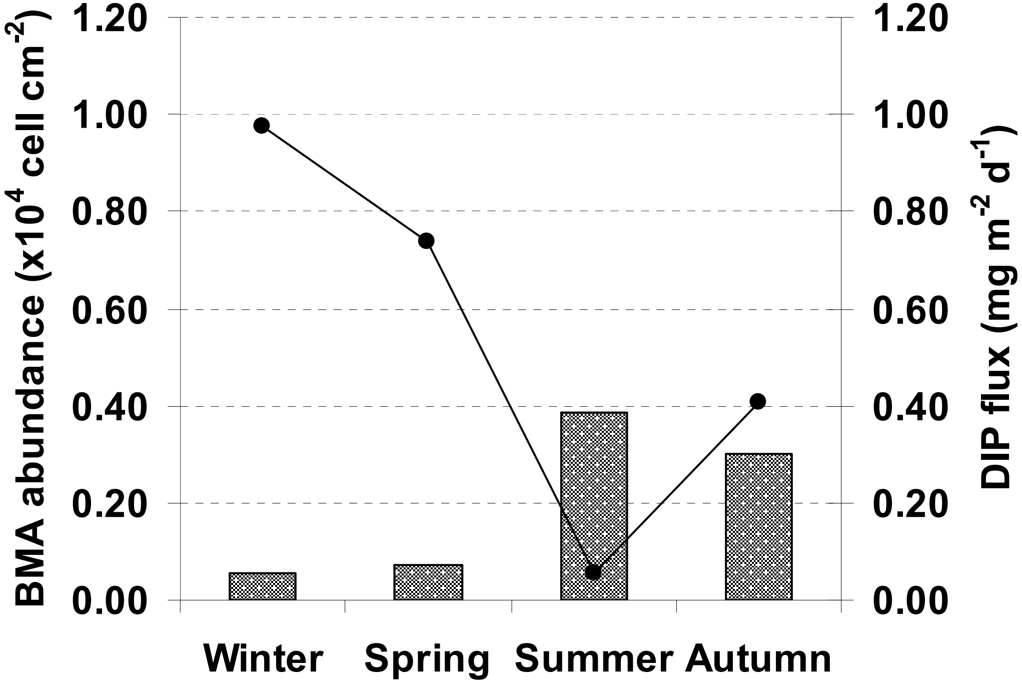

Figure 11 Sarker *et al.*