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Research Article

Effects of different nutrient loadings on planktonic primary production in embayments of Indonesia

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Abstract
A study on planktonic primary production was conducted in three Indonesian embayments subjected to different levels of eutrophication. The three embayments are Jakarta, Lampung and Semangka Bay. A previous study revealed that Jakarta Bay is heavily eutrophied while Lampung Bay is moderately eutrophied and Semangka Bay is close to pristine conditions. The eutrophication state in the three bays studied was closely related with respective nutrient loading of the embayments. Annual primary production in Jakarta Bay ranged from 47 to 503 g C m^{-2} y^{-1}, in Lampung Bay from 31 to 196 g C m^{-2} y^{-1} and in Semangka Bay from 14 to 40 g C m^{-2} y^{-1}. Spatial gradients in primary productivity were closely related to spatial nutrient gradients in the bays, except in Semangka Bay, due to the high turbidity of the river mouth. Temporal variability in primary productivity was small, consistent with small changes in environmental parameters across seasons. Jakarta Bay which has the most eutrophied waters was the highest in terms of primary productivity, followed by Lampung Bay and Semangka Bay. The primary productivity levels in the three bays was closely related with levels of nutrient loadings. This research is of importance for the development of primary production measurement in Indonesia since it is among that uses the radiocarbon technique.

Keywords: Planktonic, Tropical, Estuary, Primary-production, Nutrients, Eutrophication

Introduction
Primary production rates of phytoplankton in coastal waters depend on the availability of nutrients and light (Dring, 1982; Kocum et al., 2000; Tillmann et al., 2000). An optimum combination of these resources will generally lead to enhanced development of the phytoplankton community. Nutrient availability in the highly anthropogenic influenced coastal waters depends on nutrient

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loads from rivers, while light availability depends on a combination of physical properties of the waters such as turbidity, water depth and water mixing.

This study is part of a bigger study to observe the relationship between nutrient loads from rivers and some ecological aspects of phytoplankton community development in three Indonesian tropical bays (Damar et al., 2012). The three bays are subjected to different anthropogenic pressure. Jakarta Bay is considered as the one most influenced by human activities, Lampung Bay as moderately influenced while Semangka Bay is close to pristine (Koropitan et al., 2009; Damar et al., 2012).

Studies on planktonic primary production in Indonesia are mostly performed according to the oxygen method (Kaswadji et al., 1993), which is less sensitive compared to the radiocarbon method (Strickland & Parsons, 1972). This study is considered to be the first radiocarbon based method for planktonic primary production in Indonesia. Research was conducted over a one year period, encompassing wet and dry tropical monsoonal seasons, aimed to estimate the annual primary production in relation to other hydrographic parameters with special emphasis on the nutrient-phytoplankton relationship. The hypothesis tested in this study is that different nutrient loading in bays causes large differences in primary productivity, which is in accordance with large differences in phytoplankton biomass and eutrophication states as observed previously by Damar et al. (2012) in these bays.

Materials and Methods

This study was performed in three different nutrient loaded bays of Indonesia: Jakarta, Lampung and Semangka. Planktonic primary production rates were determined at three stations in each bay (Figures 1, 2 & 3) with an interval of approximately two months, encompassing four different tropical monsoonal variabilities. The ^{14}C method as reported by Steemann Nielsen (1952) and recommended by Colijn & Edler (1999) was used in this study. Selection of the three stations was based on the representation of nutrient regimes in each bay, which show steep nutrient gradient decreasing down the bay (Damar et al., 2012).

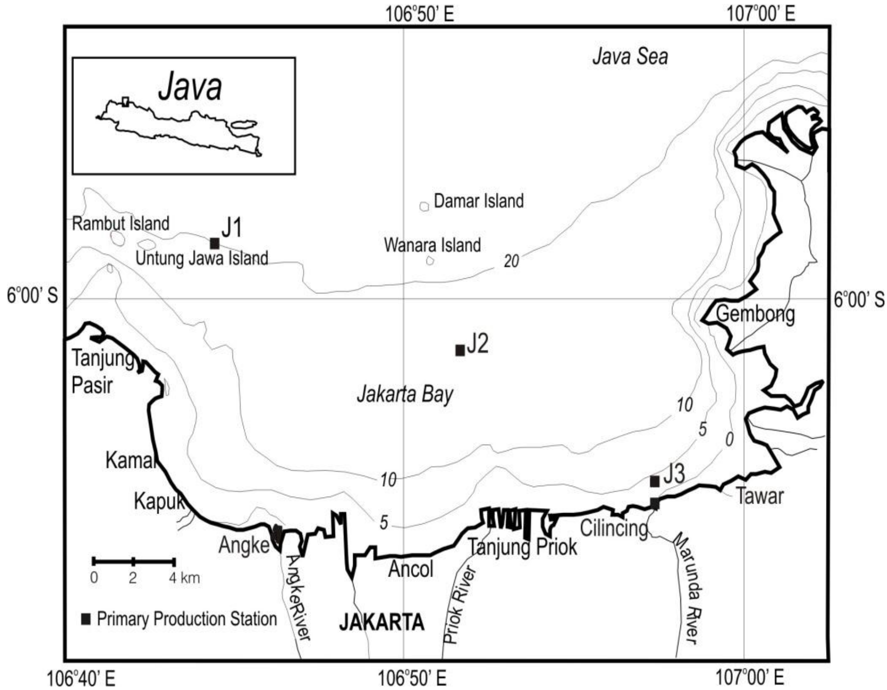

Figure 1. Primary production measurement sites in Jakarta Bay.

Primary production measurements began by adding about 10 μCi of $NaH^{14}CO_3$ (supplied by DHI Denmark) to a 550 ml water sample, and mixed. Aliquots of 55 ml were added to the incubation bottles and incubated in a rotating incubator at *in situ* temperature in the laboratory. A set of cell culture flasks obtained from ZEMOKO, Middelburg, the Netherlands, was used to provide eight different light levels, ranging from 0 % to 100 % by different specially prepared neutral density layers. The light sources were TL – lamps installed on each side of the incubator (total irradiance at the surface of the bottles was 606 μ mol photons m^{-2} s^{-1}). Samples were incubated for approximately four hours. The filters were dried at room temperature for 24 hours after filtration over MFS cellulose nitrate filters (diameter 2.5 cm and 0.45 μm porosity), and washing with a small volume of cold sea water. After that, filters were placed in a 5 ml scintillation bottle containing 4 ml CytoScint (ICN-Biomed) as scintillation cocktail. The amount of radioactive ^{14}C incorporated in the cells was determined by means of a liquid scintillation counter (Packard type TRI-CARB 1900 TR) at the laboratory of the Indonesian National Nuclear Agency (BATAN) in Jakarta. The total carbon uptake rate was calculated according to Colijn & Edler (1999) as:

$$\mathrm{mgC.l^{-1}.hr^{-1}} = \frac{\text{dpm (a)*total } ^{12}CO_2 \text{ (c)* 12 (d)* 1.05 (e)*k}}{\text{dpm (b)}}$$

where :

(a) = sample activity (minus back ground), dpm

(b) = total activity added to the sample (minus back ground), dpm

(c) = total concentration of $^{12}CO_2$ in the water sample, (µM)

(d) = the atomic weight of carbon

(e) = correction for ^{14}C discrimination

k = time factor (e.g. incubation time 125 minutes: k=60/125=0.48)

The radiocarbon added activity was measured in triplicate from the original sample in 4 ml of CytoScint. Dissolved inorganic carbon was measured and calculated according to Strickland and Parsons (1972). The production rate in each light bottle (after normalization by chlorophyll-a content) was plotted into a P-E Curve according to Platt et al. (1980):

$$P^B = a\,(1-e^{-bE})\,e^{-cE} \quad \text{.............................(1)}$$

where :

P^B = production rate (mg C mg^{-1} Chl h^{-1})

E = incubation irradiance (µmol photon m^{-2} s^{-1})

a,b,c = fit parameters

From equation (1), the maximal rate of photosynthesis (P^Bmax), the initial slope (α^B) and the light saturation parameter (E_k) could be estimated according to the following equations:

P^B_{max} = $(a(b/(b+c)))\,(c/(b+c)^{c/b})$; the maximal rate of photosynthesis (mg C mg^{-1} Chl h^{-1}) ; a, b and c are fit parameters derived from equation (1)

α^B = a x b ; the initial slope (mg C mg^{-1} Chl h^{-1} (µmol photons m^{-2}s^{-1})$^{-1}$)

E_k = P^B_{max}/α^B ; the light saturation parameter (µmol photons m^{-2} s^{-1})

Daily water column production was estimated, by combining values of irradiance and chlorophyll-a concentrations with P/E curve characteristics, as modeled by Platt et al. (1980). Surface irradiance was taken from the nearest meteorological stations (Bandar Lampung and Jakarta meteorological stations), assuming a conversion factor of 1 W m^{-2} = 4.17 µmol photons m^{-2} s^{-1} (Lalli & Parsons, 1995) and 45 % photosynthetically active radiation (Kirk, 1994). Correction for light reflection at the water surface was performed (10 %) according to Kirk (1994). The light attenuation coefficient was calculated from

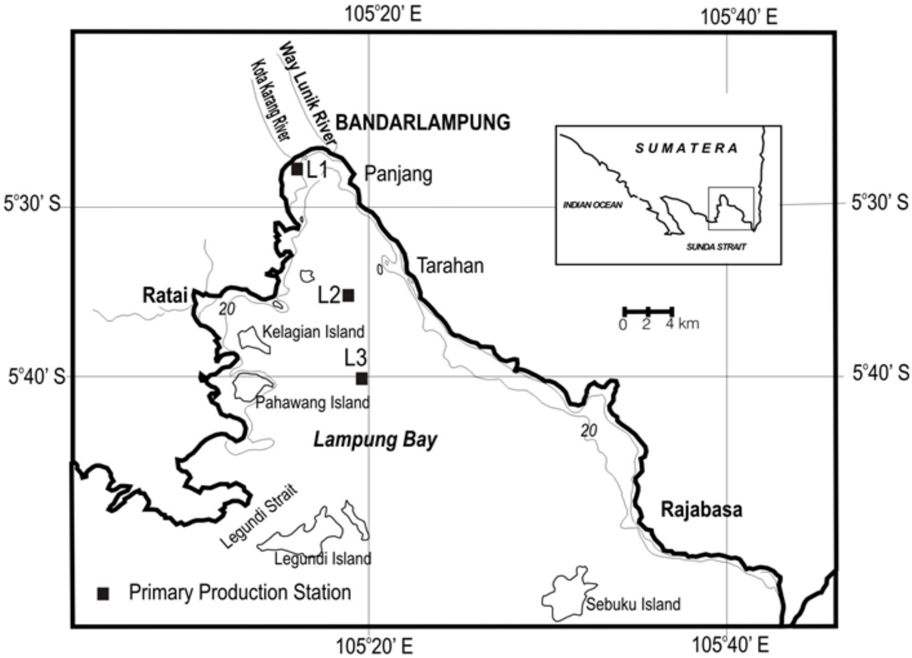

Figure 2. Primary production measurement sites in Lampung Bay.

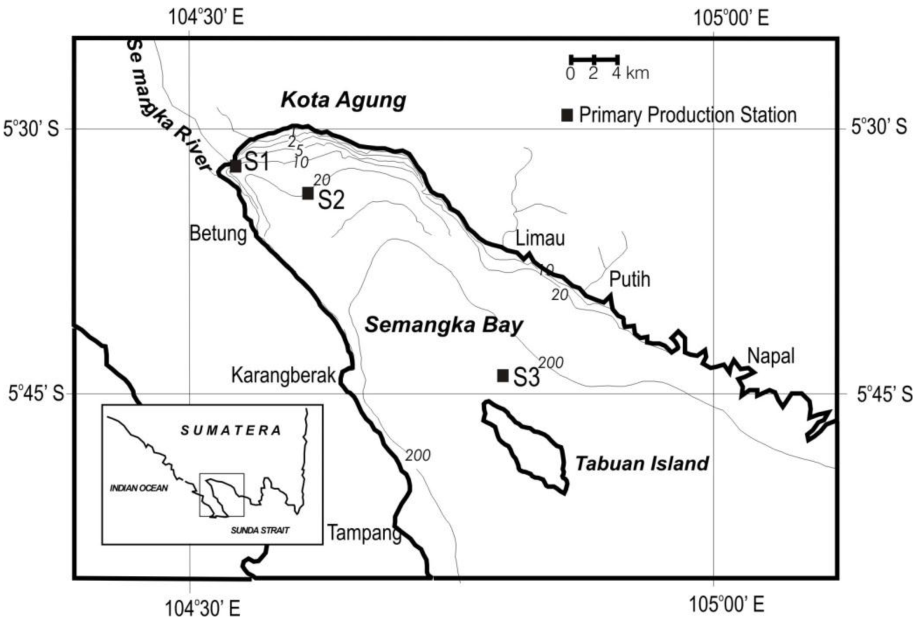

Figure 3. Primary production measurement sites in Semangka Bay.

Secchi disk readings (S_d (m)), by using the empirical relationship k = 0.191 + 1.242/S_d (r^2 = 0.853) (Tillmann et al., 2000). Daily estimates for the one-year period were obtained by using the respective P-E characteristics for the two month intervals, and were not interpolated between the different sampling periods. This causes slight changes in the productivity estimates when a new survey is done and a concomitant new P-E parameter set is used. Annual primary production was calculated for each station by summing up the daily water column production throughout the year.

Other parameters like inorganic nutrients (DIN, phosphate and silicate) were measured according to Grashoff et al. (1983), while phytoplankton biomass which is represented by Chlorophyll-a concentrations was measured according to Lorenzen (1967). Light availability was measured by means of a 30 cm diameter Secchi disk. Temperature and salinity were measured *in situ* by using a STD meter (YSI-30), while pH was measured with a pH meter (Orion), calibrated by pH 4.00 and 9.00 standard solutions before each survey.

Turbidity was measured at the laboratory, based on the nephelometric method recommended by Strickland & Parsons (1972). This method is based on the measurement of light reflected by turbidity agent in a water sample. Based on the CTD measurements, except in Semangka Bay, the depth of Jakarta and Lampung bays was taken as Z_{mix} (mixed zone). In Semangka Bay, the mixed zone was determined as 60 m (Hendiarti, pers.comm.). The depth of the euphotic zone (Z_{eu}) was calculated as the depth at which underwater irradiance was 1 % of the surface value, calculated from the attenuation coefficients.

Results

Primary Production in Jakarta Bay

In Jakarta Bay, the results of the P-E incubations for three stations are shown in Table 1 for the six different temporal surveys. Based on these P-E relationships, the chlorophyll-specific maximum photosynthetic rate (P^B_{max}) ranged from 2.23 to 4.48, 2.05 to 15.22 and 5.55 to 17.63 mg C mg Chl^{-1} h^{-1} for stations J1, J2 and J3, respectively (Figure 4.A). The P^B_{max} values were significantly ($p<0.001$) correlated with α^B, light saturation, Z_{mix}: Z_{eu} ratio and daily PP (Pearson's r=0.66, 0.59, 0.83 and 0.53, respectively).

Table 1. P-E relationship equation for the six different temporal measurements in Jakarta Bay

Table 1. P-E relationship equation for the six different temporal measurements in Jakarta Bay.

Measurements Date	Inner part of the bay (J3)	Middle of the bay (J2)	Outer part of the bay (J1)
Dec 2000	$P^B=55.2(1-e^{-0.0013E})e^{-0.0021E}$	$P^B=46.7(1-e^{-0.0012E})e^{-0.0008E}$	$P^B=15.4(1-e^{-0.001E})e^{-0.001E}$
Feb 2001	$P^B=11.5(1-e^{-0.0046E})e^{-0.00021E}$	$P^B=19.1(1-e^{-0.0012E})e^{-0.0011E}$	$P^B=9.2(1-e^{-0.002E})e^{-0.001E}$
Apr 2001	$P^B=29.2(1-e^{-0.0012E})e^{-0.001E}$	$P^B=17.6(1-e^{-0.001E})e^{-0.001E}$	$P^B=12.8(1-e^{-0.001E})e^{-0.001E}$
Jul 2001	$P^B=19.7(1-e^{-0.001E})e^{-0.001E}$	$P^B=32.1(1-e^{-0.001E})e^{-0.001E}$	$P^B=11.7(1-e^{-0.001E})e^{-0.001E}$
Sep 2001	$P^B=15.7(1-e^{-0.0041E})e^{-0.001E}$	$P^B=4.5(1-e^{-0.0021E})e^{-0.001E}$	$P^B=14.5(1-e^{-0.001E})e^{-0.001E}$
Nov 2001	$P^B=7.7(1-e^{-0.0062E})e^{-0.0017E}$	$P^B=30.5(1-e^{-0.0012E})e^{-0.0017E}$	$P^B=27.8(1-e^{-0.0004E})e^{-0.0007E}$

Table 2. P-E relationship equation for the six different temporal measurements in Lampung Bay.

Measurements Date	Inner part of the bay (L1)	Middle of the bay (L2)	Outer part of the bay (L3)
Jan 2001	$P^B=30.7(1-e^{-0.0013E})e^{-0.0021E}$	$P^B=10.5(1-e^{-0.001E})e^{-0.002E}$	$P^B=9.4(1-e^{-0.001E})e^{-0.002E}$
Feb 2001	$P^B=28.6(1-e^{-0.0046E})e^{-0.00021E}$	$P^B=4.9(1-e^{-0.002E})e^{-0.001E}$	$P^B=11.8(1-e^{-0.001E})e^{-0.001E}$
May 2001	$P^B=2.1(1-e^{-0.004E})e^{-0.001E}$	$P^B=2.3(1-e^{-0.006E})e^{-0.001E}$	$P^B=7.4(1-e^{-0.001E})e^{-0.001E}$
Jul 2001	$P^B=47.5(1-e^{-0.001E})e^{-0.001E}$	$P^B=36.5(1-e^{-0.001E})e^{-0.001E}$	$P^B=20.6(1-e^{-0.001E})e^{-0.001E}$
Sep 2001	$P^B=41.8(1-e^{-0.0041E})e^{-0.001E}$	$P^B=43.2(1-e^{-0.001E})e^{-0.001E}$	$P^B=3.3(1-e^{-0.001E})e^{-0.001E}$
Nov 2001	$P^B=43.2(1-e^{-0.0062E})e^{-0.0017E}$	$P^B=9.7(1-e^{-0.002E})e^{-0.001E}$	$P^B=39.0(1-e^{-0.002E})e^{-0.001E}$

Table 3. P-E relationship equations for the six different temporal measurements in Semangka Bay.

Measurements Date	Inner part of the bay (S1)	Middle of the bay (S2)	Outer part of the bay (S3)
Jan 2001	$P^B=13.9(1-e^{-0.0013E})e^{-0.0021E}$	$P^B=7.7(1-e^{-0.0011E})e^{-0.0011E}$	$P^B=3.0(1-e^{-0.0021E})e^{-0.00001E}$
Mar 2001	$P^B=30.9(1-e^{-0.001E})e^{-0.001E}$	$P^B=9.9(1-e^{-0.0011E})e^{-0.0012E}$	$P^B=6.2(1-e^{-0.0011E})e^{-0.0011E}$
May 2001	$P^B=8.7(1-e^{-0.0011E})e^{-0.001E}$	$P^B=33.1(1-e^{-0.0012E})e^{-0.001E}$	$P^B=45.8(1-e^{-0.0011E})e^{-0.001E}$
Jul 2001	$P^B=42.8(1-e^{-0.001E})e^{-0.001E}$	$P^B=51.0(1-e^{-0.00001E})e^{-0.001E}$	$P^B=4.6(1-e^{-0.0031E})e^{-0.00001E}$
Oct 2001	$P^B=30.8(1-e^{-0.001E})e^{-0.001E}$	$P^B=32.8(1-e^{-0.00001E})e^{-0.001E}$	$P^B=2.9(1-e^{-0.0041E})e^{-0.00002E}$
Dec 2001	$P^B=22.0(1-e^{-0.0011E})e^{-0.0012E}$	$P^B=14.8(1-e^{-0.0011E})e^{-0.0011E}$	$P^B=49.7(1-e^{-0.00002E})e^{-0.001E}$

Apart from P^B_{max}, another P-E parameter is the slope of the P versus E curve (α^B) (Figure 4.B), indicating the initial photosynthetic efficiency. Comparison between sites shows a similar trend: the highest always prevailed at station J3, while the lowest prevailed at station J1. At station J1, it ranged from 0.007 to 0.011 mg C mg Chl^{-1} h^{-1} (μmol photons m^{-2} s^{1}). At station J2, it ranged from 0.011 to 0.055 mg C mg Chl^{-1} h^{-1} (μmol photons m^{-2} s^{-1}), while at station J3, it ranged from 0.028 to 0.065 mg C mg Chl^{-1} h^{-1} (μmol photons m^{-2} s^{-1}). This parameter was significantly and positively correlated with daily PP, chlorophyll-a, phytoplankton abundance and light attenuation coefficient ($p<0.01$; 0.88, 0.58, 0.59, and 0.65, respectively), while with Z_{eu}, Z_{mix}, and Z_{mix}: Z_{eu}, they were negatively correlated (-0.68, -0.84, -0.77, respectively).
E_k values were relatively high throughout the year (Figure 4.C), indicating acclimation to strong light. They ranged from 182 to 835 μmol photons m^{-2} s^{-1}. There was no clear trend between sites.

Daily water column primary production data show a clear trend between sites and time of samplings (Figure 4.D). The highest was determined at station J3 and then decreased at station J2 and finally the lowest was measured at station J1. At station J1, it ranged from 55 (April 2001) to 211 mg C m^{-2} d^{-1} (July 2001). At station J2, it ranged from 69 (April 2001) to 456 mg C m^{-2} d^{-1} (December 2000) and at station J3, it ranged from 609 (April 2001) to 2484 mg C m^{-2} d^{-1} (November 2001). This distribution pattern corresponds with the

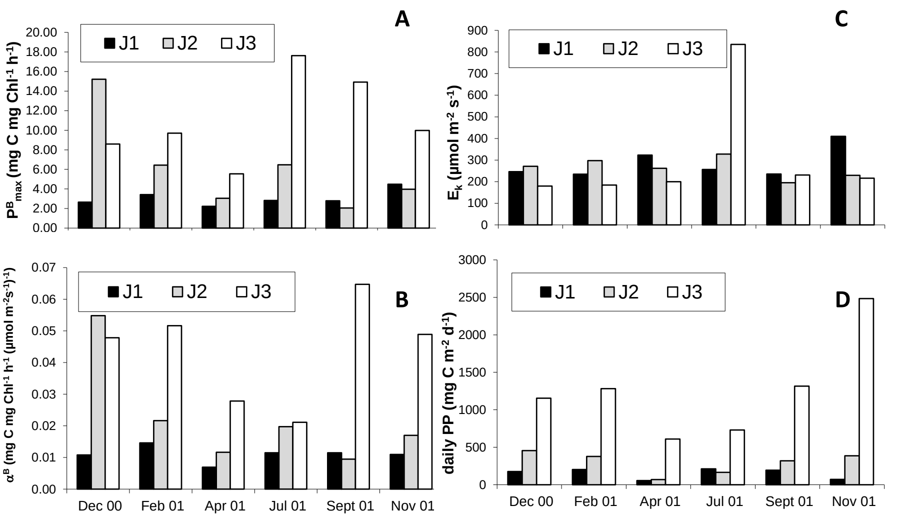

Figure 4. Annual cycle of P versus E parameters and daily production in Jakarta Bay. **A** maximal rate of Chl-specific photosynthesis (P^B_{max}) **B** slope (α^B) **C** light saturation parameter (E_k) **D** daily primary production (PP).

pattern of ammonium, nitrite, phosphate, chlorophyll-a, phytoplankton abundance and attenuation coefficient ($p<0.01$; Pearson's r = 0.65, 0.71, 0.26, 0.85, 0.84 and 0.62, respectively). Two-way Anova resulted in significant differences between sites and temporal surveys. Seasonal variations show that the high values occurred during the rainy season (December 2000, February 2001 and November 2001), while low values prevailed during the dry season (April 2001 and July 2001).

Annual primary productions were calculated for each station by summing up the daily water column production throughout 2001. Annual primary production accounted for 46.48 g C m^{-2} y^{-1}, 119.08 g C m^{-2} y^{-1} and 503.09 g C m^{-2} y^{-1} for station J1, J2 and J3, respectively.

Lampung Bay

Table 2 shows results of P-E curve calculations from seasonal incubation measurements of primary production at three stations representing different nutrient conditions in Lampung Bay. Station L1 is situated in the vicinity of the Kota Karang river mouth and also close to traditional fish processing settlements, hence representing high nutrient waters. Station L2 is located in the middle of the bay, while station L3 is situated at the outer part of the bay.

Table 2. P-E relationship equation for the six different temporal measurements in Lampung Bay

The chlorophyll-specific maximum photosynthetic rate (P^B_{max}) ranged from 1.48 to 8.84, 1.51 to 6.08 and 0.78 to 8.30 mg C mg Chl^{-1} h^{-1} for stations L1, L2 and L3, respectively (Figure 5.A). The high nutrient site, station L1, was always high in P^B_{max}, while station L3 exhibited generally low values, with an exception in July 2001.

The slope of the P versus E is assigned as photosynthetic efficiency (α^B) (Figure 5.B). In general, it ranged from 0.003 to 0.025 mg C mg Chl^{-1} h^{-1} (µmol photons m^{-2} s^{-1}). α^B values observed at all stations varied and there was no characteristic pattern related to the ambient water conditions. This parameter was not significantly correlated to any PE curve parameter, except to P^B_{max} ($p<0.001$; Pearson's r=0.83). This significant correlation underlines the dependence of P^B_{max} on the photosynthetic efficiency of the phytoplankton communities in Lampung Bay.

Light saturation values (E_k) were relatively high throughout the year (Figure 5.C), indicating species acclimation to strong light condition. No significant difference between sites and seasons was observed, indicating that

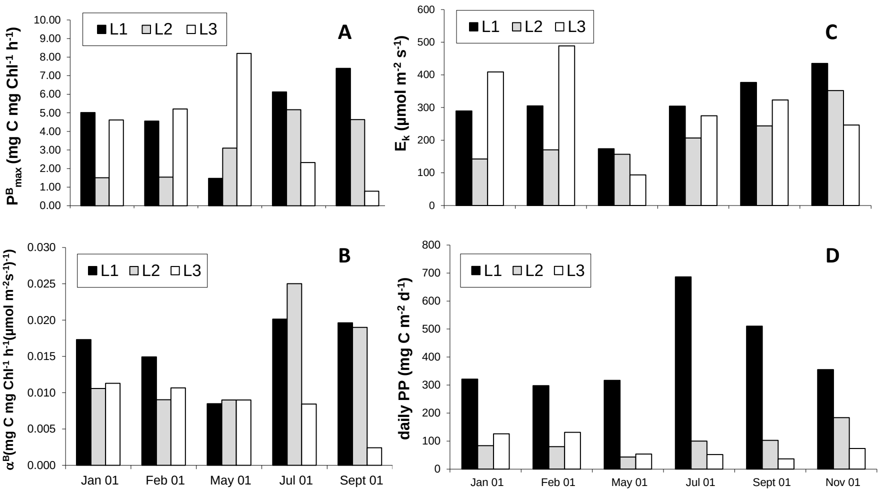

Figure 5. Annual cycle of P versus E parameters and daily primary production in Lampung Bay. **A** maximal rate of Chl-specific photosynthesis (P^B_{max}) **B** slope (α^B) **C** light saturation parameter (E_k) and **D** daily production (PP).

phytoplankton communities were generally adapted in relatively similar light levels. E_k values ranged from 93.6 to 488 µmol photons m^{-2} s^{-1}. With exception in January and February 2001, E_k values of the phytoplankton community at station L1 were higher than the others, ranging from 173.9 to 435.2 µmol photons m^{-2} s^{-1}. At station L2, it ranged from 142.4 to 352.0 µmol photons $m^{-2}s^{-1}$, while at station L3, it ranged from 93.6 to 488.6 µmol photons m^{-2} s^{-1}.
Integrated to the P-E previously described above, daily water column primary production exhibited a clear spatial pattern (Figure 5.D). Highest production was observed at station L1 whereas in the middle of the bay (station L2) and even more at the seaward border (station L3), primary production levels were much lower. A t-test revealed that daily production at station L1 was significantly higher than at the other two stations ($p<0.001$), and that stations L2 and L3 were not significantly different. Maximum daily production accounted for 686 mg C m^{-2} d^{-1} (station L1, July 2001), while the minimum level was only 36 mg C m^{-2} d^{-1} (station L3, September 2001).

The daily production pattern is consistent with the pattern of dissolved inorganic nutrient concentrations, chlorophyll-a, phytoplankton abundance and the attenuation coefficient ($p<0.01$; Pearson's r = 0.62, 0.87, 0.92 and 0.88, respectively). Seasonal variation in daily primary production showed high values during the rainy season (January, February 2001, September and November 2001), and low values during the dry season (in May 2001 and July 2001), with one exception for station L1, which exhibited maximum production in July 2001. This may be due to continuous nutrient supply to the site from the Kota Karang river, and from coastal fish processing activities directly in its vicinity which produces a significant amount of organic sewage all the year around.

In the vicinity of the incoming river (station L1), annual primary production accounted for 196.68 g C m^{-2} y^{-1}, whereas in the middle (station L2) and offshore part of the bay (station L3), it was considerably lower (40.12 g C m^{-2} y^{-1} and 30.78 g C m^{-2} y^{-1} for stations L2 and L3, respectively). The average for these three sites which are held to be representative for the different nitrification levels in the bay, accounted for 89.20 g C m^{-2} y^{-1}. Lampung Bay can be classified as oligotrophic in its offshore waters (below 100 g C m^{-2} y^{-1}), according to Nixon (1995) with regard to trophic classification of coastal ecosystems, while the coastal area subjected to the river inflow and fishing villages can be classified as mesotrophic (between 101-300 g C m^{-2} y^{-1}).

Primary Production in Semangka Bay

Table 3 shows results of some primary production parameters obtained from three stations representing different ambient conditions in Semangka Bay. The Chlorophyll-specific maximum photosynthesis rate (P^B_{max}) ranged from 2.61 to 5.36, from 2.24 to 8.08 and from 2.25 to 5.99 mg C mg Chl^{-1} h^{-1} at stations S1, S2 and S3, respectively (Figure 6.A). Station S1 is located in the river plume, representing high nutrient water but high turbidity, station S2 represents the middle part of the bay, while station S3 represents the outer part of the bay, which is under the influence of water masses from the Sunda Strait/Indian Ocean. In the river plume water (station S1), $P^B_{max,}$ was attained at higher light saturation levels, reflecting the turbid water conditions at this site. Station S2 exhibited highest photosynthetic rates. Although station S1 was rich in nutrients, the maximum photosynthetic rate was slightly lower than in the central part of the bay, perhaps due to a different species of phytoplankton composition at this site, which was dominated by chlorophyceae.

The slope of P versus E curves (α^B) (Figure 6.B), which indicates the rate of photosynthetic efficiency, was significantly related to P^B_{max} (Pearson's r=0.63). In Semangka Bay, it ranged from 0.007 to 0.047 mg C mg Chl^{-1} h^{-1} (µmol photons m^{-2} s^{-1})$^{-1}$, with the maximum level always prevailing at station S2 and lowest at station S1. The slope was significantly and positively correlated with E_k ($p<0.01$; 0.43).

Compensation light intensity values (E_k) were relatively high throughout the

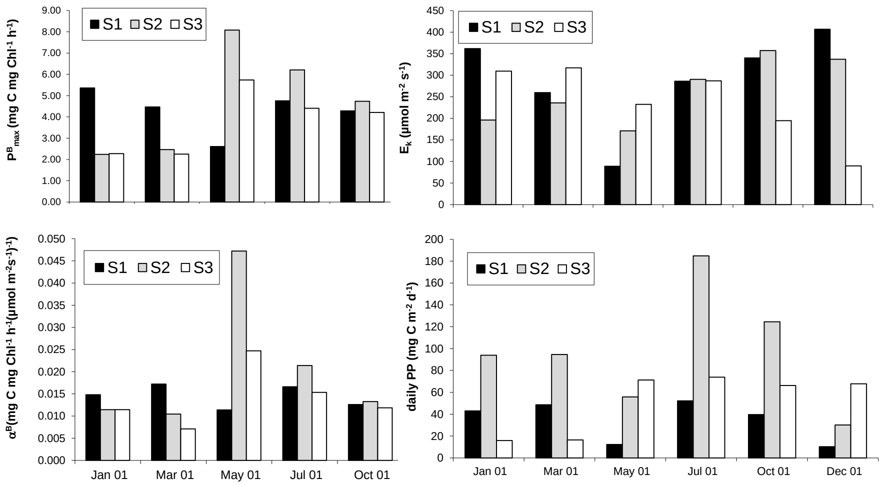

Figure 6. Annual cycle of P versus E parameters and daily production in Semangka Bay. **A** maximal rate of Chl-specific photosynthesis (P^B_{max}) **B** slope (α^B) **C** light saturation parameter (E_k) **D** daily production (PP).

year (Figure 8.C), indicating acclimatization of the algae to strong light. The range was between 89.01 and 406.86 µmol photons m^{-2} s^{-1}.

Daily water column primary production estimates showed a clear spatial and seasonal pattern (Figure 6.D). Highest production was usually observed at station S2 (30 to 184 mg C m^{-2} d^{-1}) while it was considerably lower at station S3 (16 to 73 mg C m^{-2} d^{-1}) and lowest at station S1 (10 to 52 mg C m^{-2} d^{-1}).
This spatial pattern is in accordance with the distribution of chlorophyll-a, phytoplankton abundance and the attenuation coefficient ($p<0.01$; Pearson's r = 0.41, 0.33, -0.79, respectively).

Annual primary production estimates for 2001 were calculated by summing up the daily water column production over the year. Annual primary production estimates accounted for 13.89 g C m^{-2} y^{-1}, 39.94 g C m^{-2} y^{-1} and 22.21 g C m^{-2} y^{-1} for station S1, S2 and S3, respectively.

Discussion

The primary production estimates obtained in this study were gross particulate primary production values. The technique did not incorporate the production of dissolved organic matter. A study done in the Wadden Sea (Tillmann et al., 2000), showed variable values in the contribution of dissolved production on total production (ranging from 19 % to 278 % with a mean value of 63 %). The short incubation time used probably gives an estimate of gross primary production, which does not include respiratory losses (Tillmann et al., 2000; Jassby et al., 2002).

In the three bays studied, spatial patterns of primary production levels generally reveal a high production zone in the high nutrient area of inshore waters, and low production in the low nutrient area at offshore waters. However, the exception was Semangka Bay, where primary production was lower in the high-nutrient of the river plume than in the middle part of the bay, due to strong light limitation and hampering phytoplankton community development. A comparison between bays also shows a strong relationship between nutrient concentration and primary production levels, with Jakarta Bay as the most productive bay, followed by Lampung Bay and Semangka Bay which exhibited the lowest values (Figure 7). Estimates of annual primary production in Jakarta Bay ranged from 45 to 503 g C m^{-2} y^{-1}, in Lampung Bay it ranged from 31 to 197 g C m^{-2} y^{-1} and in Semangka Bay the range was between 14 to 40 g C m^{-2} y^{-1}.

With regards to the trophic state of a coastal ecosystem (Nixon, 1995), Jakarta Bay varied from oligotrophic in the outer part of the bay at station J1 (<100 g C m^{-2} y^{-1}), mesotrophic in the middle part of the bay at station J2 (between 101-300 g C m^{-2} y^{-1}) and hyper-eutrophic in the inner part of the bay-at station J3 (>500 g C m^{-2} y^{-1}). A similar pattern is observed for Lampung, which shows oligotrophic conditions in its offshore waters (below 100 g C m^{-2} y^{-1}), while the

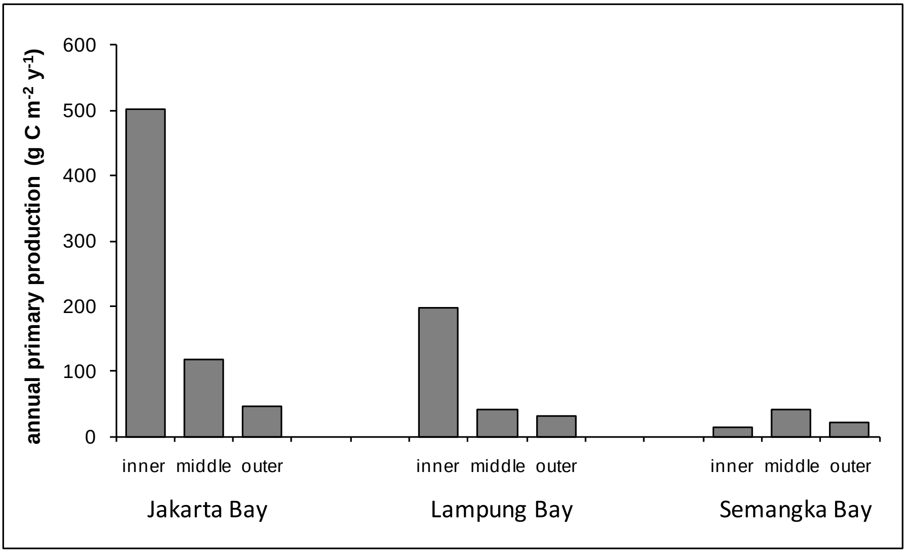

Figure 7. Comparison of primary production values among the bays.

coastal area subjected to river inflow and fishing villages is classified as mesotrophic (between 101-300 g C m^{-2} y^{-1}). In Semangka Bay, the whole area can be classified as an oligotrophic system (below 100 g C m^{-2} y^{-1}). No hyper-eutrophic level was observed in Lampung Bay and no eutrophic level was observed in Semangka Bay.

Temporal variation of primary production was also observed, showing relatively high values during the rainy season and lower values during the dry season. This is in accordance with the temporal variation of nutrient availabilities and phytoplankton biomass (Damar et al., 2012), showing higher nutrient levels during the rainy season and inversely, low levels during the dry season. This nutrient temporal variation is a result of nutrient load temporal variability of the incoming rivers that demonstrated high nutrient loads during the rainy season. Accordingly, the relationship between nutrient availability and phytoplankton production in each bay as well as between different nutrient status bays were in accordance with the classical theory of nutrient-phytoplankton relationships (Margalef, 1978). The pattern of relationship is: phytoplankton biomass and production were high in the near-shore sites, decreasing in the offshore sites which coincide with the decrease of nutrients and thus, decrease in phytoplankton biomass. In general, this reflects the important role of phytoplankton biomass in primary production variation (Tillmann et al., 2000; Kocum et al., 2002). As stated previously, an exception was found in Semangka Bay, where the phytoplankton primary production was low in the nutrient rich river plume due to strong light limitation. In this bay, the highest phytoplankton biomass, and thus, primary productivity prevailed in the harbour waters and around local settlements, where nutrients and light were sufficiently available.

The estimate of primary production based on P vs E relationships is well established (Tillmann et al., 2000). This method seems to be the most appropriate one to be used in a well-mixed estuary such as the Jakarta, Lampung and Semangka bays. The method has been applied in other mixed-estuaries such as Wadden Sea (Tillmann et al., 2000), the Colne estuary (England) (Kocum et al., 2002) and the Ems Dollard estuary (the Netherlands) (Colijn, 1983). A comparison between *in situ* and laboratory incubations on the values of primary production was performed by Colijn (1983), resulting in a good agreement with a mean difference of only 5 %.

One of the advantages of this technique is its ability to determine the photosynthetic characteristics of the phytoplankton assemblages, which can then be used to determine the production of the system and the factors for its spatial dynamics. P^B_{max} values of the Jakarta Bay phytoplankton assemblages ranged from 2.05 at station 5 (relatively low-nutrient site) to 17.63 mg C mg Chl^{-1} h^{-1} at station 10 (high-nutrient site). The results showed a clear trend with higher values at nutrient rich sites compared to that of a nutrient poor site, underlining the prominent nutrient effects on the variability of P^B_{max}. Other parameters such as water temperature and light are weakly related to the variation of these P^B_{max} values. Comparison with other P^B_{max} values from other estuaries showed that values in this study were comparable. The mean P^B_{max} value of the Wadden Sea phytoplankton assemblage was 4.5 mg C mg Chl^{-1} h^{-1} (Tillmann et al., 2000). In the Wadden Sea, this value was highly correlated with water temperature, and reached a high value during the high temperature period (> 20^o C). On the contrary, in the Colne estuary, Kocum et al. (2002) found that P^B_{max} values were not correlated with temperature. In Jakarta Bay, temperature was not a main factor of production variability with only around 12 % of the variability of P^B_{max}. The variability of P^B_{max} was largely explained by light attenuation coefficient (49 %) and nutrient concentrations (56 %). P^B_{max} also depends on species composition of the phytoplankton community which varied in chlorophyll-a contents (Tillmann et al., 2000). Diatoms have higher chlorophyll-a content than other phytoplankton groups such as dinoflagellates, which leads to lower values of Chl-normalized photosynthetic parameters (Tillmann et al., 2000). However, it is probably a minor factor since the phytoplankton assemblages at almost all stations were dominated by diatoms throughout the year. Comparison of P^B_{max} values of Jakarta Bay to Lampung and Semangka Bays shows that Jakarta Bay has the highest value. It also shows that nutrients play an important role in tropical waters primary productivity.

The average photosynthetic efficiencies (α^B) showed a similar trend with P^B_{max}, with high values at nutrient rich sites and low values at nutrient poor sites (ranging from 0.01 to 0.06 for Jakarta Bay). This is also outlines the strong nutrient effects on the variability of photosynthetic efficiency. A comparison between bays shows that Jakarta Bay is the highest in photosynthethic efficiency, in accordance with its high nutrient concentration. The photosynthethic efficiency values of the bays studied are comparable with other well-mixed estuaries, such as the Wadden Sea's values in Germany (Tillmann et al., 2000).

The E_k values (ranging from 182 to 835 μ mol photons m^{-2} s^{-1}) were relatively high throughout the study period, suggesting a good acclimatization on high light intensities. Comparison with E_k values of other tropical phytoplankton assemblages resulted in comparable values. Phytoplankton assemblages in Hurun Bay, Indonesia,have an annual mean E_k value of 273 μ mol photons m^{-2} s^{-1} (Tambaru, 2000).

The E_k values of this study were slightly higher than those of the temperate waters. The Wadden Sea phytoplankton assemblages have an annual mean E_k value of 216 μ mol photons m^{-2} s^{-1} (Tillmann et al., 2000), while the Eastern English Channel has a mean value of 102 μ mol photons m^{-2} s^{-1}. E_k value has been widely used as an indicator of light acclimated state (Tillmann et al., 2000), and this high series of E_k values in Jakarta, Lampung and Semangka Bay show that phytoplankton assemblage in the study area have adapted to strong light intensities. E_k values of this study are higher than that of the Wadden Sea (Tillmann et al., 2000) and most other temperate estuaries (Fisher et al., 1982 ; Pennock & Sharp, 1986 and Cole et al., 1991). However, a comparison among the three bays studied revealed that Jakarta Bay is the lowest in E_k values compared to Lampung and Semangka bays, showing that phytoplankton assemblages in Lampung and Semangka bays were more adapted to strong light intensities.

Comparison of the annual primary production estimates of this study with those of other tropical coastal waters (Table 4) showed that the inner and middle parts of Jakarta Bay and the inner part of Lampung Bay are comparable with that of Delta Upang (Indonesia), while the middle and outer parts of Lampung Bay and the whole part of Semangka Bay are lower than those of other tropical coastal areas in annual primary production. In Lingayen Bay (the Philippines), which is subjected to moderate anthropogenic nutrient enrichment from land (McManus et al., 2001), the annual primary production estimates ranged from 93 g C m^{-2} y^{-1} in the outer part of the bay to 167 g C m^{-2} y^{-1} in the inner part of the bay.

Comparison of the annual production estimates with worldwide primary production values collected by Boynton et al. (1982) showed that the inner part of Jakarta Bay values are at the upper end of the range, while the middle and outer parts of Jakarta Bay are at the middle and lower ends, respectively. Annual primary production estimates of the inner part of Lampung Bay is at the middle of the range, while those of the middle and outer parts of Lampung Bay as well as the whole part of Semangka Bay are at the lower end. Boynton's primary production range for all marine planktonic systems worldwide is from around 12 g C m^{-2} y^{-1} to 520 g C m^{-2} y^{-1}.

Table 4. Annual phytoplankton primary production estimates of some tropical and temperate estuaries or coastal areas, including this study.

Area	Annual production (g C m^{-2} y^{-1})	Method	Source
TROPICAL			
• ***Lingayen Bay (the Phillipines) 1997-1999***			
○ offshore part	93	O_2	McManus *et al.* (2001)
○ inner part (Bolinao)	167	O_2	McManus *et al.* (2001)
• ***Delta Upang (Sumatera, Indonesia) 1975****	240	O_2	Kaswadji (1976)
• ***Mallaca Strait, Indonesia, 1980***	90	O_2	Praseno (1980)
• ***Lampung Bay (Indonesia)***			
○ inner part (Hurun coast) 1999 *	70	O_2	Tambaru (2000)
○ inner part (Hurun coast) 2000 *	152	O_2	Sunarto (2001)
○ inner part 2000-2001	196	^{14}C	this study
○ middle part 2000-2001	40	^{14}C	this study
○ outer part 2000-2001	31	^{14}C	this study
• ***Jakarta Bay (Indonesia)***			
○ inner part 1983 *	301	O_2	Nontji (1984)
○ inner part 1991 *	166 – 214	O_2	Kaswadji *et al.* (1993)
○ inner part 2000-2001	503	^{14}C	this study
○ middle part 1983 *	49	O_2	Nontji (1984)

(*continued on next page*)

Table 4. (continued)

○ middle part 1983 *	55	O_2	Nontji (1984)
○ middle part 2000-2001	119	^{14}C	this study
○ outer part 2000-2001	47	^{14}C	this study
• ***Semangka Bay (Indonesia)***			
○ inner part (river plume) 2000-2001	14	^{14}C	this study
○ middle part 2000-2001	40	^{14}C	this study
○ outer part 2000-2001	22	^{14}C	this study
TEMPERATE			
• ***Patagonian fjords, Chile***	334 and 725	^{14}C	González, *et al.* (2010)
•			
• ***Büsum, Wadden Sea 1995 and 1996***	124 and 176	^{14}C	Tillmann *et al.* (2000)
• ***Ems Dollard (1976-1980)***			
○ inner part	70	^{14}C	Colijn (1983)
○ middle part	91	^{14}C	Colijn (1983)
○ outer part	283	^{14}C	Colijn (1983)
• ***Marsdiep area***			
○ 1974-1975	145	^{14}C	Cadée and Hegeman (1979)
○ 1981-1992	250-390	^{14}C	Cadée and Hegeman (2002)
• ***German Bight 1988-1989***	261	^{14}C	Joint and Pomroy (1993)

***** Recalculated into integrated water column primary production value by using the average depth of the area.

If the annual primary production estimates of this study are compared with those in eutrophied temperate coastal ecosystems such as the Wadden Sea in Germany, the inner part of Jakarta and Lampung bays exhibit slightly higher production levels, while the middle and outer parts of Lampung Bay and the whole of Semangka Bay are less productive (Table 4). However, seasonal variation in tropical coastal ecosystems is much lower than in temperate ones. In the German Wadden Sea (Tillmann et al., 2000), the annual phytoplankton primary production estimates accounted for 124 and 176 g C m^{-2} y^{-1} (1995 and 1996, respectively), with a large seasonal variation, ranging from very low value in winter (0.005 g C m^{-2} d^{-1}) to maximum values during the spring bloom (2.2 g C m^{-2} d^{-1}) season. A similar seasonal variability prevails in the eutrophied western Wadden Sea (Marsdiep) (Cadée & Hegeman, 1979). Here, the annual primary production accounted for 145 and 135 g C m^{-2} y^{-1} for 1974 and 1975, respectively. The relatively low seasonal fluctuation of the tropical primary production shows there is less importance of light in regulating phytoplankton development compared to temperate regions. In the temperate region, seasonal variation of light plays an important role in controlling seasonal variation of phytoplankton production, while in the tropics, continuous light throughout the year supports phytoplankton development. Considering steady light supply in tropical systems, effects of anthropogenic nutrient enrichment may be much more severe and clear than in temperate regions.

Apart from nutrient availability, the rate of primary production mostly depends on light availability (Kocum et al., 2000), which is reflected by the Z_{mix}:Z_{eu} ratio. Use of only a single parameter of turbidity will not reflect real light availability of the phytoplankton community. A comparison of turbidity values between bays showed that Jakarta Bay was the most turbid system among the three studied (ANOVA, $p<0.001$), but since the Z_{mix}:Z_{eu} ratio in Jakarta Bay was lower than in Lampung and Semangka bays, this resulted in a higher average of primary production in Jakarta Bay. This is mainly caused by the shallower water depth of Jakarta Bay compared to Lampung and Semangka bays, causing a low Z_{mix}, and therefore a low ratio of Z_{mix}:Z_{eu}. A low ratio means that the average time spent by the phytoplankton cells in the illuminated water column increases, thus enabling a higher net photosynthesis.

In the spatial pattern of each bay studied, the light availability for phytoplankton growth showed better conditions in inshore waters than in offshore waters. The optimum zone for photosynthesis was close to the river plume, where water depth was still relatively low and where turbidity decreased. This phenomenon of adequate growth condition for phytoplankton at the river plume is a common feature for many other estuaries such as Pearl

river estuary (Yin et al., 2001) and Elbe river plume (Hesse et al., 1995), Baltic Sea (Dahlgren et al., 2010) and the Estuary of Iskenderun-North Eastern Mediterranean (Ozman-Say & Balkis, 2012). In offshore waters, turbidity was much less, but the water column light availability was counteracted by the increase of water depth, resulting in a significant increase of Z_{mix}:Z_{eu} ratio.
In keeping with this, comparison between light and nutrient resources through Cloern's method (Cloern, 1999; Colijn & Cadée, 2003) also revealed that in Lampung Bay and even more so in the case of Semangka Bay, phytoplankton growth was more limited by nutrients than by light, except in the river mouth and its surrounding sites due to good penetration of light into the water column.

In summary, it is clearly observed that primary production of phytoplankton depends on the availability of nutrients and light. While in general light is not limiting factor for the development of phytoplankton in tropical waters (Dring, 1982; Alianto et al., 2009 and Damar et al., 2012), both parameters play an important role in influencing the development of phytoplankton and primary production. This study is of importance in the development of primary productivity study in the country, since this study is among the first primary production studies using radiocarbon in Indonesia, which is able to provide better sensitivity results.

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