Tropical Ecology **54**(3): 331-343, 2013 ISSN 0564-3295

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Monsoon-influenced phytoplankton community structure in a Philippine mangrove estuary

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Abstract: We utilized biodiversity indices and multivariate techniques to investigate the relationship between environmental conditions and net phytoplankton composition and abundance during early (November) and mid (February) northeast (NE) monsoon, intermonsoon (May), and southwest (SW) monsoon (August) in Panguil Bay, an exploited mangrove estuary in Northern Mindanao, Philippines. Phytoplankton were composed of diatoms, dinoflagellates, and cyanobacteria. The centric diatom *Coscinodiscus wailesii* was the most common, but outnumbered by the chain-forming diatom *Thalassionema frauenfeldii* in SW monsoon. The harmful algal bloom dinoflagellate *Ceratium furca* became common in the warmest intermonsoon month of May, but its numbers did not reach bloom level. Two distinct assemblages (deeper, more saline, low abundance but high diversity stations located near the mouth of the bay, and shallower, less saline, high abundance but low diversity inner stations) appeared to oscillate horizontally with NE and SW winds. Depth, tide, and monsoon-related variables (total suspended solids, salinity, and dissolved nitrates) significantly influenced changes in phytoplankton community structure in Panguil Bay.

Resumen: Utilizamos índices de biodiversidad y técnicas multivariadas para investigar la relación entre las condiciones ambientales y la composición y la abundancia del fitoplancton de red durante los monzones del noreste (NE) temprano (noviembre) e intermedio (febrero), el intermonzón (mayo), y el monzón del suroeste (SO) (agosto) en la Bahía Panguil, un estuario de manglar que está siendo explotado en Mindanao del Norte, Filipinas. El fitoplancton estuvo compuesto de diatomeas, dinoflagelados y cianobacterias. La diatomea céntrica *Coscinodiscus wailesii* fue la más común, pero ésta fue superada en número por la diatomea formadora de cadenas *Thalassionema frauenfeldii* en el monzón del SO. *Ceratium furca*, un dinoflagelado causante de proliferaciones algales nocivas, llegó a ser común en mayo, el mes más cálido del intermonzón, pero sus números no alcanzaron el nivel de una proliferación. Dos ensamblajes distintos (estaciones más profundas, más salinas, con baja abundancia pero con alta diversidad ubicadas cerca de la boca de la bahía, y estaciones interiores más superficiales, menos salinas, con abundancia grande pero diversidad baja) parecieron oscilar horizontalmente con los vientos del NE y del SO. La profundidad, la marea y las variables relacionadas con el monzón (total de sólidos suspendidos, salinidad y nitratos disueltos) influyeron significativamente en los cambios de la estructura de la comunidad fitoplanctónica en la Bahía Panguil.

Resumo: Utilizámos índices de biodiversidade e técnicas multivariadas para investigar a relação entre as condições ambientais e composição líquida e abundância do fitoplâncton

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durante o início da monção (novembro) e meados (fevereiro) da monção de nordeste (NE), na inter-monção (maio) e monção de sudoeste (SW) (agosto) em Panguil Bay, um estuário de mangal explorado no norte de Mindanau, nas Filipinas. O fitoplâncton era composto por diatomáceas, dinoflagelados e cianobactérias. A diatomácea centrica *Coscinodiscus wailesii* foi a mais comum, mas em desvantagem pela diatomácea formadora de cadeias a *Thalassionema frauenfeldii* na monção de SO. A alga *Ceratium furca*, um dinoflagelado prejudicial, tornou-se comum no mês mais quente da inter-monção em maio, mas os seus números não atingiram o nível de proliferação. Dois conjuntos distintos (estações mais profundas, mais salinas, baixa abundância, mas com elevada diversidade localizadas perto da foz da baía, e estações interiores menos profundas, menos salinas, com grande abundância mas baixa diversidade) pareceram oscilar horizontalmente com os ventos de NE e SO. A profundidade, a maré e as variáveis relacionada com a monção (sólidos totais suspensos, salinidade, e nitratos dissolvidos) influenciaram significativamente as mudanças na estrutura de comunidade do fitoplâncton em Panguil Bay.

Key words: Mangrove estuary, monsoon, multivariate analysis, Panguil Bay, phytoplankton ecology.

Introduction

The variability of phytoplankton abundance at different time and space scales drives trophic dynamics, productivity and energy flow in estuarine ecosystems (Choudhury *et al.* 2002; Cloern & Jassby 2010; Field *et al.* 1998), but phytoplankton community properties are linked with changes in biological, physical, and chemical hydrologic conditions (Cloern & Jassby 2010; Costa *et al.* 2009; Smayda & Reynolds 2001). The study of phytoplankton community response to environmental variables is considered very useful for interpreting ecological variations amid threats of fishery resource overexploitation, pollution, and climate change (Biswas *et al.* 2010; Kannan & James 2009).

Spatial and temporal changes in the structure of tropical estuarine phytoplankton communities are influenced by monsoon (Al-Azri *et al.* 2009; Burford & Rothlisberg 1999; D'Costa *et al.* 2008; Larsen *et al.* 2004; Madhu *et al.* 2007; Miki *et al.* 2008; Yin 2002), but site-specific mechanisms may generate variable (Gin *et al.* 1999) or constant (Sidik *et al.* 2008) phytoplankton community structure between monsoonal periods.

In general, tropical seas are dominated by nano- and picoplanktonic phytoplankters (Miki *et al.* 2008), but when large > 10 µm net phytoplankters are in bloom they can contribute up to 60 % of total chlorophyll in shallow estuaries (Gin *et al.* 2000), including the highly biodiverse tropical mangrove ecosystem (Biswas *et al.* 2010; Kathiresan & Qasim 2005; McLeod & Salm 2006). However, compared to the well acknowledged importance of mangrove detritus in these systems, the importance of net phytoplankton as carbon and energy sources has only recently begun to be recognized (Chew & Chong 2010; Kathiresan 2000; Mwashote *et al.* 2005).

Studies on phytoplankton communities in mangrove estuaries are very limited in the Philippines (Yap *et al.* 2004). One of the country's priority fishery areas, Panguil Bay in southern Philippines is a very good mangrove estuarine ecosystem, but scarcely studied. Studies on phytoplankton dynamics are wanting for this Bay which has been considered a natural spawning and nursery ground of many commercially important fin fish and invertebrate species (Jimenez *et al.* 1996). Only 27.3 km^2 of mangroves remain today after 15.8 km^2 were converted into semi-intensive fish and shrimp ponds in 1991 (Gorospe & Prado 1993). In 1995, the wild fisheries in the bay generated 54 tons of fin fishes from 120 species, 2315 tons of bivalve molluscs from six species, and 152 tons of crustaceans from four scyllid and eight penaeid species (Jimenez *et al.* 1996). We speculate the productivity of these fishery resources would be largely linked with the variability of phytoplankton production and ecology. Hence, this study analyzed the relationship of phytoplankton community structure with selected environmental factors during early (November) and mid (February) northeast (NE) monsoon months, intermonsoon in May, and the southwest (SW) monsoon in August in a mangrove estuary in Panguil Bay.

Materials and methods

Study area

This study was conducted in Panguil Bay (location: 7° 56' to 8° 04' N, 123° 36' to 123° 46' E), a 219-km^2 body of water north of the island of Mindanao (Fig. 1). The bay is a south-western inlet of the greater Iligan Bay, and its depth gradually decreases from the mouth to the inner portion. Rainfall on the catchment area brings runoff into Panguil Bay via 29 major rivers and 46 minor tributaries. Seven of the largest rivers are lined with fishponds at their mouths where they flow into the inner portion of the bay. The circulation pattern in Panguil Bay is mainly influenced by the diurnal tidal forcing and seasonal monsoon winds (Gorospe & Prado 1993). According to Gorospe & Prado (1993), the average water velocity in a daily diurnal tidal cycle was 0.6 m s^{-1} and 0.5 m s^{-1} at ebb and flood tides, respectively, and the volume of seawater exchange at the mouth is estimated 0.3 km^3 per tide cycle. Based on an average depth of 5 m, the volume of exchanged water daily would be about 22 % of the total volume of 1.1 km^3. Strong NE monsoon winds prevail over Panguil Bay from November to March, but are strongest from January to February. Southwest monsoon winds predominate from June to August (Han *et al.* 2009). Weak, variable winds typify the intermonsoon months of April and May.

Sampling procedure

Twenty one sampling stations (Fig. 1) were established throughout the bay using Garmin 60 global positioning system. Selection of these stations was guided by a stratified random sampling design where the entire bay from the mouth to the opposite end was divided into seven strata that differ in depth. Daytime collection of phytoplankton samples and determination of environmental conditions were done four times covering the early (18 - 19 November 2008) and mid (23 - 24 February 2009) NE monsoon, intermonsoon (18 - 19 May 2009) and SW monsoon (23 - 24 August 2009). A General Oceanics conical plankton net with a mesh size of 20 µm, a mouth radius of 0.5 m, and a 1-liter cod end was used to collect phytoplankton. Triplicate vertical tows from 1 m above the bottom to the surface were made and samples from each tow that collect in the cod end were placed in labelled bottles and preserved in 5 % buffered formaldehyde solution.

Physical and chemical conditions were determined from sub-surface water samples. Water temperature (ºC) was measured using a mercury thermometer, pH using a pH Tester 30 meter, and salinity using an Atago refractometer. Dissolved oxygen (DO) and chlorophyll *a* were determined by Winkler titration and spectrophotometric methods, respectively (Strickland & Parsons 1972). The concentration of dissolved inorganic phosphate and nitrate was determined using a portable Merck NOVA 60A spectrophotometer. Dissolved orthophosphate and nitrate were analyzed using the ascorbic acid-ammonium molybdate and aromatic amine (sulphanilamide) reduction methods, respectively (Strickland & Parsons 1972). The amount of total suspended solids were determined following gravimetric methods, while tidal height values were obtained using tide gauges. Rainfall and wind speed and direction data were obtained from the nearest weather bureau station located at the Ozamis City national airport (Fig. 1).

Phytoplankton enumeration

Phytoplankton were concentrated by allowing cells to settle for three days. Phytoplankton were identified to species level using photographs and descriptions of Tempère & Peragallo (1910), Yamaji (1982), Shirota (1966), and Hallegraeff (1986). Abundance of each species was estimated by counting cells in a gridded 1 ml Sedgewick-Rafter counting chamber with an Olympus inverted microscope following the sedimentation method of Utermöhl (1958). A subsample (1 ml) was drawn from the concentrated sample and dispensed on the counting chamber which was scanned thoroughly ensuring that all cells were counted. If 500 organisms were not observed within a subsample enumeration was continued in more subsamples until at least 500 are counted. Densities in cells l^{-1} of different phytoplankton species was determined by dividing the number of cells from the concentrated sample by the volume of water filtered by the net.

Data analysis

A two-way analysis of variance (ANOVA) was used to test for significant differences in environmental variables (depth, temperature, salinity, tide, total suspended solids, DO, chlorophyll *a*,

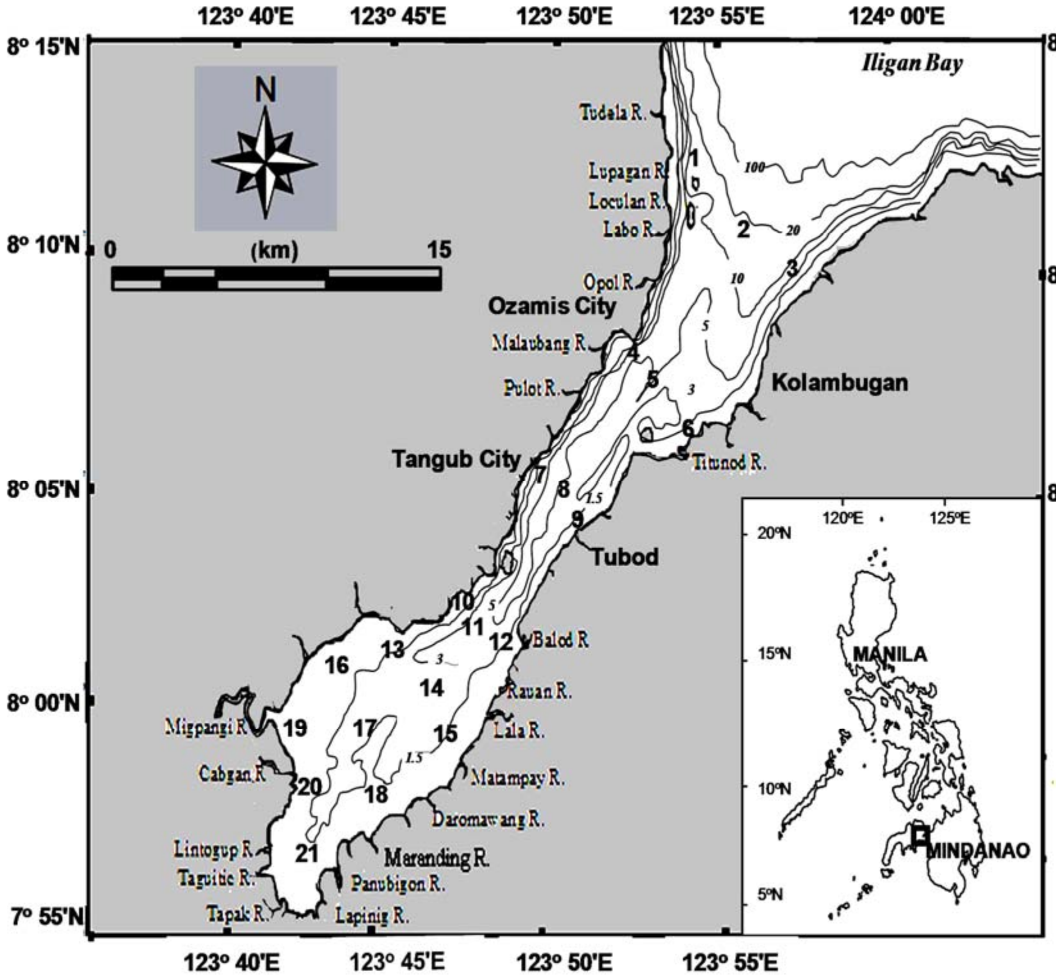

Fig. 1. Bathymetric map of Panguil Bay with the 21 sampling stations distributed throughout the bay. Inset: map of the Republic of the Philippines with Panguil Bay enclosed in a square.

nitrates, phosphates, and pH), biodiversity indices, and abundance among stations and sampling months. ANOVA was followed by a *post hoc* multiple comparison of means using Tukey's HSD Test. In instances when data violated test assumptions (normality, homogeneity of variance), a non-parametric Kruskal-Wallis test was applied. Biodiversity indices (Shannon-Wiener diversity index H', Pielou's evenness index J', and Margalef's species richness d) of a sampling station were based on average values computed from triplicate vertical samples. Bray-Curtis similarity matrix and analysis of similarity (ANOSIM) statistics were computed from square-root transformed abundance data for each station using the software PRIMER version 5 (Clarke & Warwick 2001). ANOSIM was used to test the significance of spatial variation in the structure of phytoplankton assemblage. The gradient length of the species-abundance data was derived using detrended correspondence analysis (DCA). If shorter gradient lengths (< 4) were obtained, the relationship between environmental variables and species abundance was analyzed by redundancy analysis (RDA) with built-in Monte Carlo simulation and stepwise multiple regression (forward selection) which evaluated the statistical significance of the relationship and ranked the importance of the 10 above mentioned environmental variables, respectively. The software CANOCO version 4.5 (Ter Braak & Smilauer 2002) was used to run DCA and RDA.

Results

Environmental parameters

Except for sampling depth which was similar between months (Kruskal-Wallis test H statistic $(H) = 6.02$, $P > 0.12$), temperature ($H = 9.87$, $P < 0.05$), salinity ($H = 7.97$, $P < 0.05$), pH ($H = 63.84$,

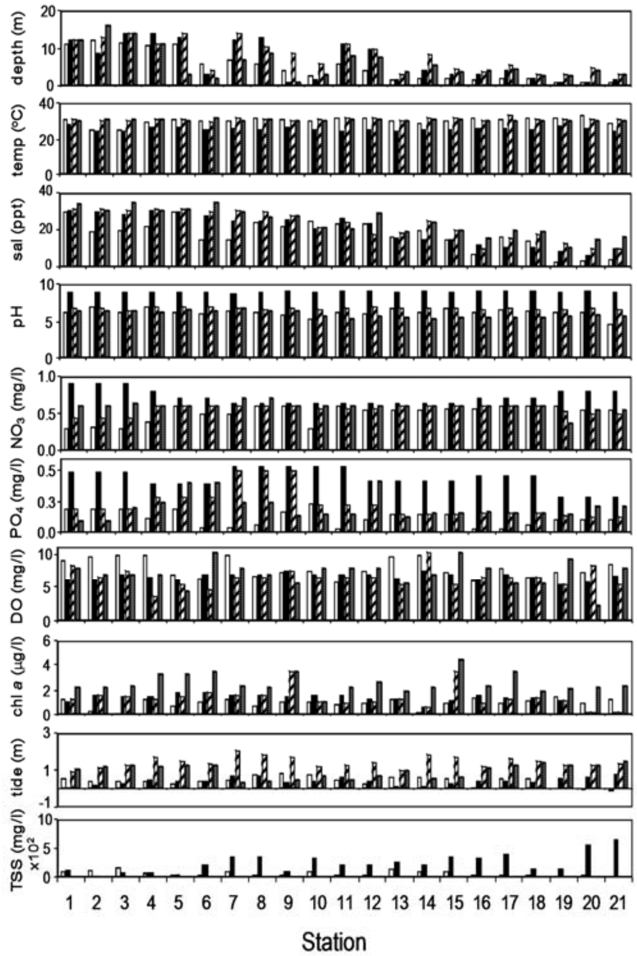

Fig. 2. Mean values of environmental parameters: depth (a), temp - temperature (b), sal - salinity (c), pH (d), NO_3 - dissolved nitrate (e), PO_4 - total dissolved phosphate (f), DO - dissolved oxygen (g), chl *a* - chlorophyll a (h), tide (i), and TSS - total suspended solids (j) at 21 sampling stations in Panguil Bay for November 08 (open bars), February 09 (solid bar), May 09 (hatched bar), and August 09 (stippled bar).

$P < 0.001$), nitrate ($H = 51.86$, $P < 0.001$), phosphate ($H = 54.37$, $P < 0.001$), dissolved oxygen ($H = 14.91$, $P < 0.01$), chlorophyll *a* ($H = 40.63$, $P < 0.001$), tide ($H = 52.43$, $P < 0.001$), and total suspended solids ($H = 57.18$, $P < 0.001$) differed significantly between months (Fig. 2). Riverine input kept salinity lower at the inner stations, while higher salinity at stations near the mouth was due to marine influence from the adjacent Iligan Bay (Fig. 2). Salinity at the 21 stations was generally higher (10 - 31.7 ppt) in the hotter (30 - 32 °C) intermonsoon month of May, but lower (3.3 -29.7 ppt) in the cooler (25 - 32 °C) and rainy (89.4 mm maximum) month of November (Fig. 2). The range of salinities for the cooler February (24 - 28 °C) and the warmer August (30 - 31.7 °C) were 5.6 - 30.0 ppt and 15 - 34.7 ppt, respectively. The pH values (8.8 - 9.2) in all stations in February were slightly basic typical of normal seawater, but slightly acidic values typical of a mangrove estuary were recorded in other months. Dissolved nitrate in mg l^{-1} ranged from 0.3 - 0.6 in November, 0.6 to 0.9 (highest values) in February, 0.4 - 0.6 in May, and 0.4 - 0.7 in August. Lowest values of dissolved phosphate in mg l^{-1} were recorded in November (0.1 - 0.2) while those in February (0.2 - 0.5), May (0.1 - 0.5), and August (0.1 - 0.4) were comparable. Highest concentrations of both nutrients were found at the mouth of the bay. Higher mean dissolved oxygen values were obtained in November (7.9 mg l^{-1}) and August (7.1 mg l^{-1}), compared to those in the months of February (6.6 mg l^{-1}) and May (6.5 mg l^{-1}). Chlorophyll *a* concentration in µg l^{-1} maximum mean value (2.6) was recorded in August and the minimum (1.4) in May. In November, the chlorophyll *a* concentration ranged from 0.1 to 1.4, 0.2 to1.9 in February, and 0.02 to 3.6 in May.

Heavy rainfall and strong NE winds coincided with greater total suspended solids for the months of November (mean: 0.8 ± 0.1 (SE), range: 0.1-1.7 x 10^2 mg l^{-1}) and February (2.9 ± 0.6, 0.1-11 x 10^2 mg l^{-1}) than those in May (0.2 ± 0.01, 0.01-0.3 x 10^2 mg l^{-1}) and August (0.2 ± 0.01, 0.02-0.3 x 10^2 mg l^{-1}) (Figs. 2 & 3). The months of November to March were dominated by NE monsoon winds in Panguil Bay, while the reverse happened from June to October with the dominance of SW monsoon (Fig. 3).

Species composition and abundance

A total of 61 phytoplankton species were identified representing 37 genera that belong to diatoms (44 species), dinoflagellates (15 species), and cyanobacteria (2 species) (Table 1). Forty-one species were identified in November, 40 in February, 48 in May, and 54 in August; 22 were common among these months. Nine low density common species (*Biddulphia mobiliensis*, *Gyrosigma* sp. 1, *Hemiaulus sinensis*, *Pleurosigma angulatum*, *Rhizosolenia bergonii*, *Ceratium macroceros*, *C. trichoceros*, *Gonyaulax verior*, *Trichodesmium theibauti*) did not differ ($H = 0.67$-5.63, $P > 0.26$ for all) in abundance between months. The centric diatom *Coscinodiscus wailesii* dominated samples from stations 5 - 21 in all sampling months with a recorded maximum of 1000 cells l^{-1} from station 13, except in August when chain-forming

Table 1. Phytoplankton species recorded in 21 sampling stations in Panguil Bay and their presence (+) and absence (-) in early (NOV 08), mid (FEB 09), intermonsoon (MAY 09), and southwest monsoon (AUG 09). [1]present in all sampling months with variable abundance, [2]similar abundance in all sampling months. Species codes in brackets were used in the multivariate redundancy analysis graphs. Percentage relative abundance of the 10 most abundant species is in parenthesis.

Species	NOV	FEB	MAY	AUG
Baccilariophyceae (diatoms)				
Asterionellopsis glacialis [Ag]	+	-	+	+
Bacillaria paradoxa[1] [Bp]	+	+	(1.1)	(0.4)
Bacteriastrum delicatulum [Bd]	-	+	+	(0.2)
Bacteriastrum elongatum [Be]	-	+	+	(0.1)
Bacteriastrum hyalinum[1] [Bh]	+	+	+	(0.3)
Biddulphia mobiliensis[1,2] [Bm]	+	+	+	+
Biddulphia sinensis [Bs]	-	-	+	+
Biddulphia obtusa [Bo]	+	-	-	+
Caloneis crassa [Cc]	-	-	+	+
Chaetoceros affinis[1] [Ca]	+	(3.5)	(0.5)	(0.4)
Climacodium frauenfeldianum [Cf]	-	-	+	+
Cocconeis placentula [Cp]	+	+	+	-
Corethron hystrix [Cx]	+	+	+	-
Coscinodiscus wailesii[1] [Cw]	(49)	(42)	(83)	(10)
Ditylum brightwellii[1] [Db]	(0.5)	(8)	(3)	(0.6)
Eucampia zodiacus [Ez]	+	-	+	+
Fragillaria sp. [Fr]	-	-	+	+
Grammatophora oceanica [Go]	+	-	-	+
Gyrosigma acuminatum [Ga]	-	-	-	+
Gyrosigma fasciola [Gf]	-	-	-	+
Gyrosigma sp.1[1,2] [Gy1]	(0.3)	+	+	+
Gyrosigma sp.2 [Gy2]	-	-	-	+
Hemicaulus sinensis[1,2] [Hs]	+	+	+	+
Leptocylindrus danicus [Ld]	(9)	+	+	-
Melosira sp. [Mn]	(28)	+	-	(25)
Nitzschia longissima [Nl]	-	-	-	+
Nitzschia seriata [Ns]	-	+	+	+
Planktoniella sol [Ps]	+	-	-	-
Pleurosigma angulatum[1,2] [Pa]	(0.8)	+	(0.7)	+
Pleurosigma elongatum [Pe]	(0.9)	-	-	-
Pleurosigma sp. [Pl]	+	-	-	+
Rhizosolenia bergonii[1,2] [Rb]	+	+	+	+
Rhizosolenia h.f. *semispina*[Rh]	-	+	+	+
Baccilariophyceae (diatoms) (continuation)				
Rhizosolenia imbricata [Ri]	-	-	+	+
Rhizosolenia setigera [Rs]	+	-	+	+
Skeletonema costatum[1] [Sc]	(11)	(2.5)	+	+
Stephanopyxis palmeriana [Sp]	-	-	+	+
Surirella cuneata [Su]	+	+	+	+
Chaetoceros curvisetus [Cu]	+	(3.8)	-	+
Thalassionema nitzschioides[1] [Tn]	-	(6)	+	+
Thalassionema frauenfeldii[1] [Tf]	+	(9)	(0.9)	(62)
Thalassiosira pacifica [Tp]	+	+	+	-
Triceratium revale [Tr]	-	-	+	-
Dinophyceae (dinoflagellates)				
Ceratium dens [Ce]	+	-	+	-
Ceratium furca[1] [Cr]	(0.2)	(4)	(6.5)	+
Ceratium fusus[1] [Cs]	+	+	(1.2)	+
Ceratium macroceros[1,2] [Cm]	+	+	+	+
Ceratium trichoceros[1,2] [Ct]	+	+	+	+
Ceratium tripos [Ci]	+	-	+	+
Ceratocorys horrida [Ch]	-	+	-	+
Dinophysis caudata [Dc]	+	+	+	+
Dinophysis sp. [Di]	+	-	-	-
Gonyaulax verior[1,2] [Gv]	(1)	+	(0.4)	+
Peridinium conicum [Pc]	-	-	-	+
Peridinium depressum[1] [Pd]	+	+	+	+
Peridinium pellucidum [Pp]	+	+	+	-
Peridinium pentagonum[1] [Pn]	+	+	+	+
Cyanophyceae (cyanobacteria)				
Oscillatoria kawamurae [Ok]	+	(3.9)	(0.8)	-
Trichodesmium theibauti[1,2] [Tt]	+	+	+	+
Total Number of Species	41	40	48	54

diatoms *Thalassionema frauenfeldii* were densest with maximum abundance of 1700 cells l^{-1} from station 9 (Fig. 4). Overall, net phytoplankton abundance was up to two orders of magnitude higher in inner than outer stations (Fig. 4). Abundance peaked during the SW monsoon month of August, was intermediate during early and mid northeast monsoon, and lowest during the intermonsoon month of May. Dinoflagellates became abundant in February with *Ceratium furca* as the most abundant species. February was also the month when most inner stations (4 - 21) had low diatom to dinoflagellate abundance ratios (Fig. 5). The sheltered station 13 had low ratios in all sampling periods indicative of a regular occurrence of dinoflagellates (Fig. 5).

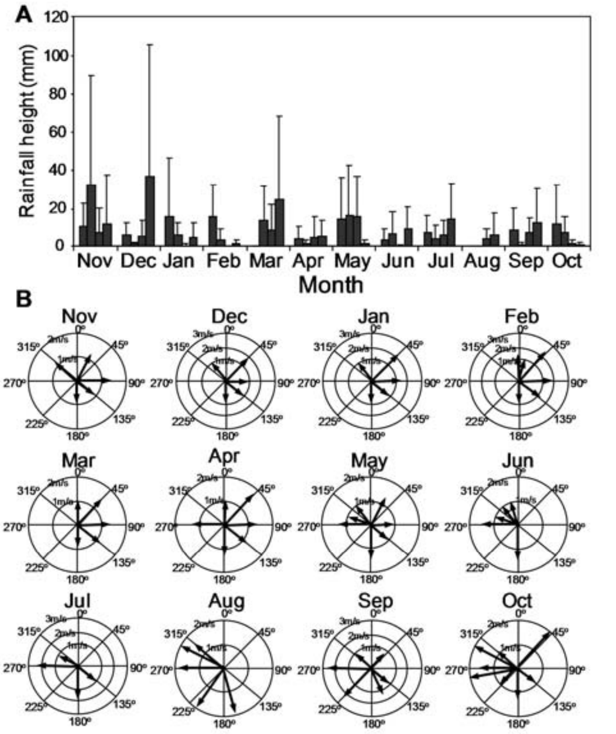

Fig. 3. Mean weekly rainfall (a) and monthly polar plots (b) of mean wind speed (m s^{-1}) and wind direction in degrees (arrows) over Panguil Bay from November 2008 to October 2009. Wind direction: 0 - 45° (north-easterlies), 46 - 90° (easterlies), 91 - 135° (south-easterlies), 136 - 180° (southerlies), 181 - 225° (south-westerlies), 226 - 270° (westerlies), 271 - 315° (north-westerlies), and 316 - 360° (northerlies).

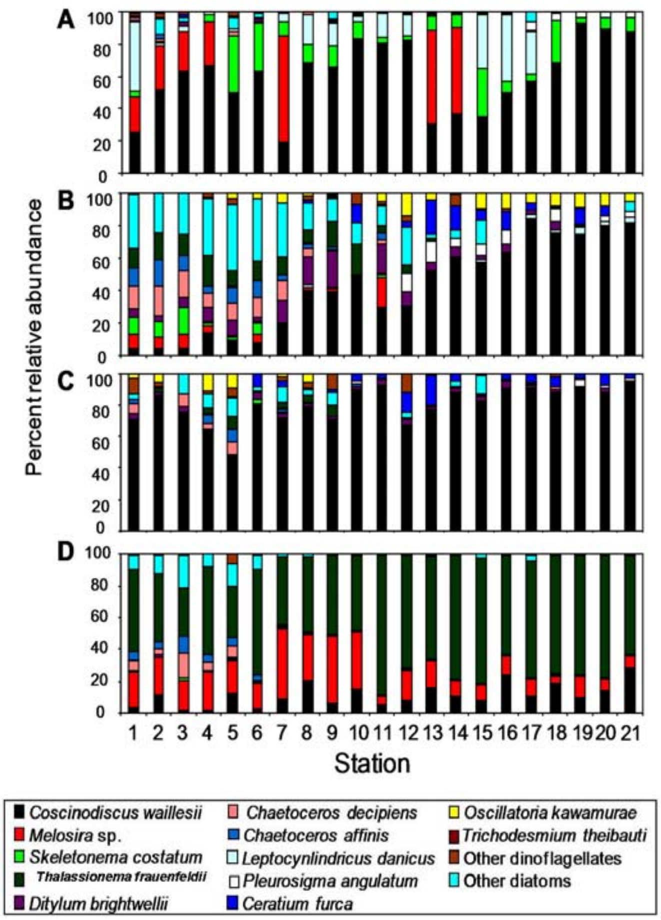

Fig. 4. Community composition of phytoplankton in Panguil Bay in November 2008 (a), February 2009 (b), May 2009 (c), and August 2009 (d).

Community biodiversity and assemblage

Species diversity (H') and richness (d) values differed significantly between months (for H': F = 22.10, P < 0.001; for d: F = 2496, P < 0.001) with highest values obtained in February (P < 0.001 for both H' and d), followed by those in August (P < 0.001 for both H' and d) than those in November and May which were similar (P > 0.68 for both H' and d) (Fig. 6). Pielou's evenness index varied between months (F = 3382, P < 0.001) with highest values recorded in February (P < 0.001) while the rest of months had lower similar values (P > 0.39 for all) (Fig. 6). Except in February when evenness indices for stations 1-16 were significantly higher (P < 0.05 for all) than those in stations 17 - 21, evenness indices were similar among stations in other sampling months (P > 0.25 for all). Species diversity and richness varied among stations in all months, with a general trend of outer and deeper stations (e.g., 1 - 8) having significantly higher values than those in inner and shallower stations (e.g., 16 - 21) (P < 0.05 for all).

Cluster analysis for the month of November suggested a horizontal zonation of assemblages, clearly separating outer stations 1 - 4 from the rest of the stations (Fig. 7). In the month of February, more stations (1 - 9) formed the outer zone extending from the mouth to the middle narrowest portion of the bay (Fig. 7). In May, the outer zone (stations 1 - 5, 7 - 9) shrunk by 1 station with station 6 joining the inner zone (Fig. 8). In August, the size of the outer zone contracted to comprise only of outer stations (1 - 5). All dendrograms were statistically significant based on ANOSIM (Fig. 8).

Relationship of environmental parameters and phytoplankton community structure

Monte Carlo simulation generated significant (P < 0.02 for all) relationships between phytoplankton species abundance and environmental vari-

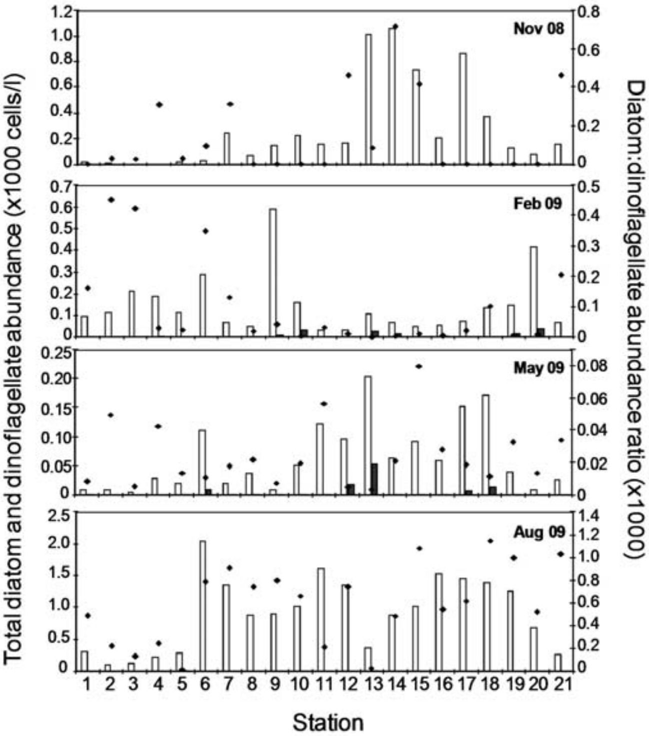

Fig. 5. Total diatom (open bars) and dinoflagellate (filled bars) abundance (x 1000 cells l^{-1}), and diatom/dinoflagellate abundance ratio (x 1000) (filled diamonds) in Panguil Bay among sampling months.

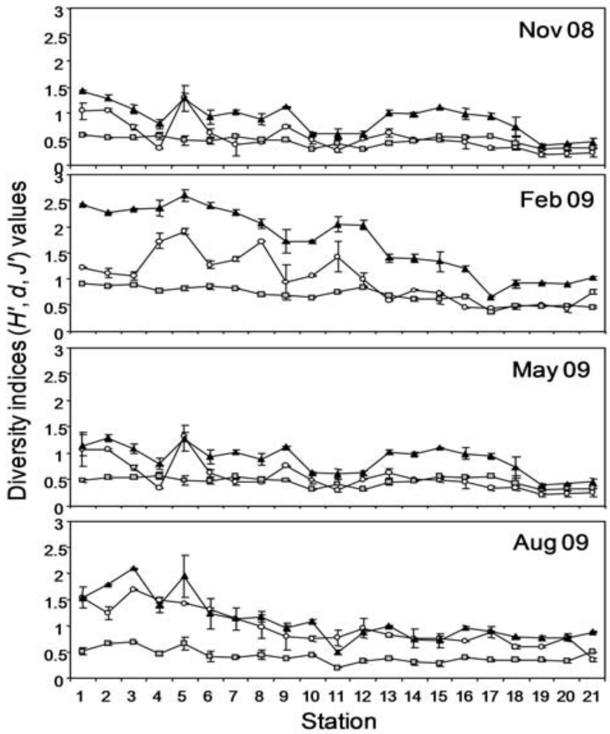

Fig. 6. Diversity indices for the 21 sampling stations in November 08 (a), February 09 (b), May 09 (c), and August 09 (d) sampling periods. Line symbols: filled triangle - Shannon-Wiener species diversity index H', open circle -Margalef species richness index d, and square -Pielou'sevenness index J'.

ables for all four sampling months. However, forward selection generated different combinations of significant explanatory environmental variables for each sampling month. In November, depth, salinity, total suspended solids (TSS), and dissolved nitrates were significantly related to phytoplankton species abundance ($P < 0.05$) (Fig. 7). Shallower depths, lower salinity, higher TSS, and higher nitrate concentrations were significantly correlated with dominant species, mainly the diatoms *C. wailesii*, *D. brightwellii, L. danicus*, *Melosira* sp., *P. angulatum*, and *S. costatum*.

Depth, salinity, and nitrate were significant covariates of net phytoplankton composition ($P <$ 0.05) in February (Fig. 7). Deep and more saline outer stations with low nitrate levels significantly correlated with less abundant species of diatoms (*B. elongatum*, *B. mobiliensis, B. delicatulum* and *B. sinensis*, *C. decipiens, Melosira* sp., *B. hyalinum*, *Chaetoceros* sp. *C. affinis*, *R. hebetata f. semispina, S. costatum, T. nitzschioides, T. frauenfeldii*), and dinoflagellates (*C. trichoceros*, *P. depressum*, and *P. pentagonum*). Shallow and less saline stations with higher amounts of nitrate were correlated with the diatoms, *C. wailesii*, *D. brightwellii*, *L. danicus*, *P. angulatum*; dinoflagellate *C. furca*; and the cyanobacterium, *O. kawamurae*.

Depth, salinity, nitrate, and temperature significantly ($P < 0.05$ for all) contributed to the variability of phytoplankton species abundance in May (Fig. 8). Deeper, less warm and more saline stations were associated with less abundant diatom (*B. mobiliensis*, *Cocconies* sp., *C. affinis, E. zodiacus*, *R. hebetata f. semispina*, *R. setigera*) and dinoflagellates species (*C. macroceros*, *C. trichoceros, C. fusus*, *C. tripos*, *Ceratocorys horrida*, *D. caudata, P. depressum*, *P. pentagonum*). Shallower, warmer, less saline stations with higher nitrate concentrations were correlated with diatoms *C. wailesii*, *D. brightwellii*, *Gyrosigma* sp1., *P. angulatum*, and the dinoflagellate *C. furca*.

Depth and tide were significantly related to phytoplankton species abundance in August ($P <$ 0.05 for both) (Fig. 8). Shallower and nitrate richer stations at high tides were correlated with the dominant species, primarily the diatoms *C. wailesii*, *D. brightwellii*, *Melosira* sp., and *T. frauen-*

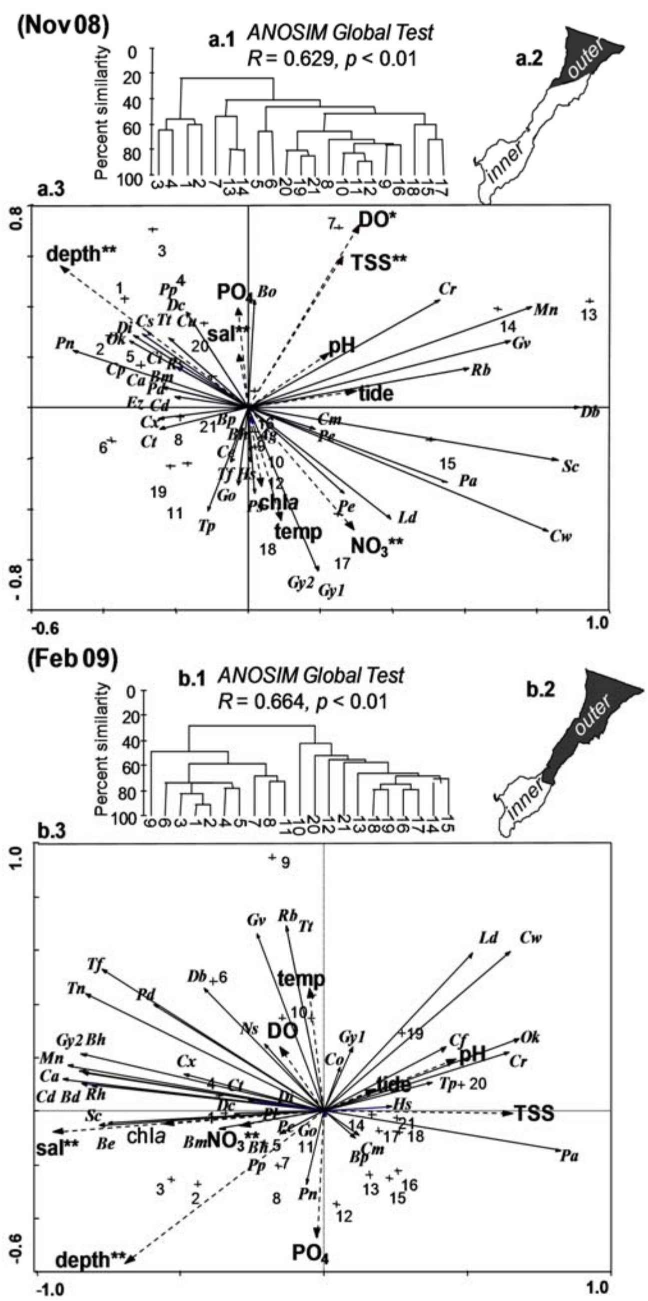

Fig. 7. Bray-Curtis similarity dendrograms of the 21 sampling stations in Panguil Bay with analysis of similarity (ANOSIM) output, map of clusters of similar innerand outer stations based on the similarity dendrogram, and orthogonal projections of redundancy analysis (RDA) of environmental parameters (indicated by broken arrows) and phytoplankton abundance (indicated by solid arrows) at 21 sampling stations (numbers with cross) in November (a) and February (b) sampling months. Legend: For codes of environmental parameters refer to Fig. 2. For species codes refer to Table 1. ** - $P < 0.001$, * - $P < 0.05$.

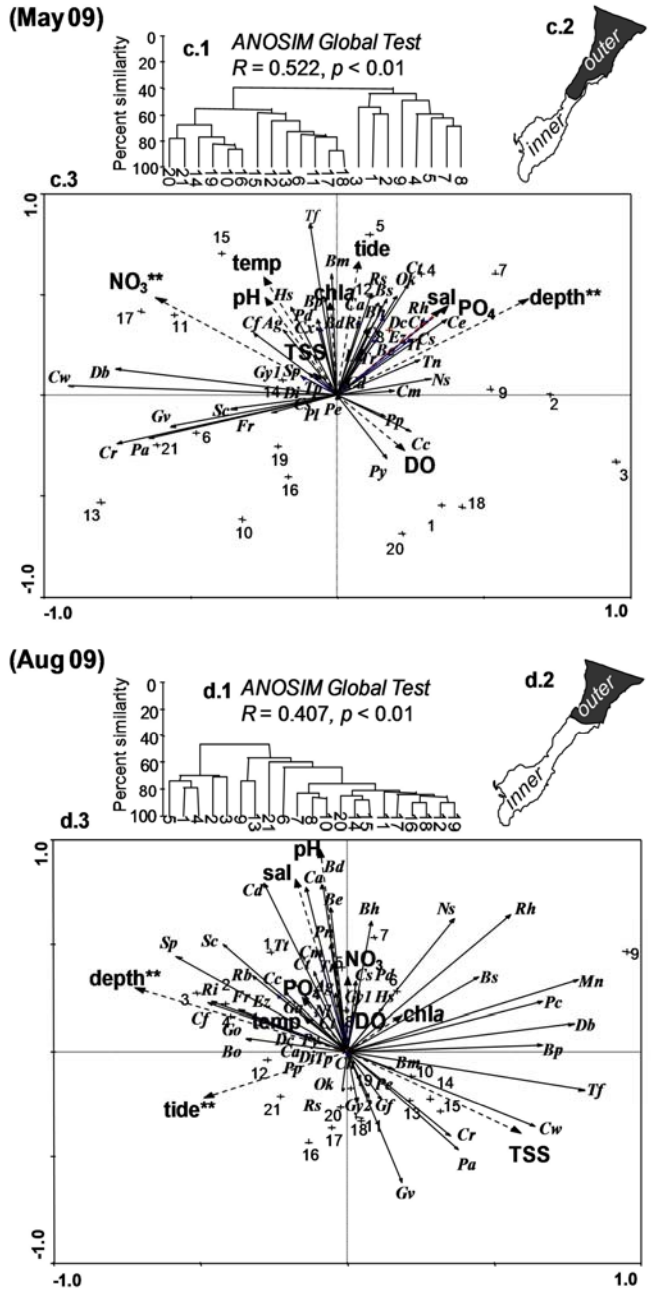

Fig. 8. Bray-Curtis similarity dendrograms of the 21 sampling stations in Panguil Bay with Analysis of Similarity (ANOSIM) output, map of clusters of similar inner and outer stations based on the similarity dendrogram, and orthogonal projections of redundancy analysis (RDA) of environmental parameters (indicated by broken arrows) and phytoplankton abundance (indicated by solid arrows) at 21 sampling stations (numbers with cross) in May (c) and August (d) sampling months. Legend: For codes of environmental parameters refer to Fig. 2. For species codes refer to Table 1. **-$P < 0.001$, * - $P < 0.05$.

feldii. Less abundant diatoms *B. obtusa*, *C. macroceros*, *Fragillaria* sp., *G. oceanica*, *R. imbricata, S. costatum*, and *S. palmeriana* were associated with deeper stations at lower tides.

Discussion

Phytoplankton composition

The phytoplankton community in Panguil Bay mangrove estuary was composed mainly of diatoms, dinoflagellates and cyanobacteria, which agrees with studies from other tropical estuarine systems (e.g., Biswas *et al.* 2010; Costa *et al.* 2009; Gin *et al.* 2000; Kannan & Vasantha 1992; Sidik *et al.* 2008). The range of total number of species between sampling months (41 - 54) is within the 29 - 58 species found in the Indian Sundarban mangrove estuary (Biswas *et al.* 2010). The total number of 37 genera is close to the 40 reported by Sidik *et al.* (2008) in a Malaysian estuary. Nearly a third (22 species) of the 61 total number of species identified was present in all sampling months, but only 9 of the 22 had similar abundance between months. The persistence of these nine species could be associated with their cosmopolitan distribution and wide tolerance to estuarine environmental conditions (Fernandes *et al.* 1991; Rick & Dürselen 1995; Sidik *et al.* 2008). Dinoflagellates were most abundant in the warmest month of May. However, densities of certain harmful algal bloom (HAB) species (e.g., 10 - 51 cells l^{-1} for *Ceratium furca*) were well below bloom densities (41,000 cells l^{-1}) reported in fish pens in Bolinao, Northern Philippines (Yap *et al.* 2004). The centric diatom *Coscinodiscus wailesii* was common throughout the entire bay, and became most abundant during early NE monsoon (November). The same genus was reported to dominate in tropical cage culture waters (Sidik *et al.* 2008). *Coscinodiscus* congeners can become HAB species because they form thick mucilage in the water (Dickman *et al.* 2002), but this was not observed in Panguil Bay despite the dominance of *C. wailesii*. Other known HAB species found in this study were diatoms *Asterionella glacialis*, *Pseudo-nitzschia* sp., and *Skeletonema costatum,* and dinoflagellates *C. fusus*, and *Dinophysis caudata* (Dickman *et al.* 2002). In this study, *S. costatum* density peaked in the same NE monsoon period observed in the Malaysian Langat mangrove estuary which received effluents from intensive shrimp culture ponds (Larsen *et al.* 2004). Overall, although species composition appeared similar, species ranked abundance and community structure clearly differed between monsoons.

Temporal and spatial variations of phytoplankton community structure

Multivariate methods have been used to explore associations among environmental variables and to aid in making ecological interpretations of field data and in generating new hypotheses (Komárková *et al.* 2003; Ter Braak & Smilauer 2002). In this study, these techniques revealed sampling depth as the consistent explanatory variable influencing phytoplankton community structure in Panguil Bay. Common to all months was the characteristic higher species diversity and richness at outer deeper stations than at inner shallower stations. This may typify the classic "edge" or ecotone effect (*sensu* Odum 1971) where the number of species is higher at the mouth of Panguil Bay where it overlaps with the bigger Iligan Bay. However, depth alone could not explain community structure as evident in other statistically significant monsoon-related variables.

For instance, salinity was lower while dissolved nitrate concentrations were highest during NE monsoon months of November and February. This is expected since the NE monsoon usually brings high rainfall which entail lowering of salinity and more input of nutrients into tropical estuaries (Berman *et al.* 2005; Satpathy *et al.* 2010; Tanaka & Choo 2000). The combination of lowered salinity and optimum nutrient levels support high abundance of estuarine phytoplankton (Choudhury & Pal 2010) as seen in this study. Notably, despite large areas of semi-intensive fish and shrimp ponds in the inner bay, nutrient levels were below national standards of 0.5 mg $l^{-1}$and 7 mg l^{-1} for phosphate and nitrate, respectively (DENR 2008). However, the nearly comparably high concentrations during these months imply that nutrients did not have a limiting influence over changes in phytoplankton abundance. Reduced available light associated with high amounts of suspended solids may be the most controlling factor as evidenced by lower phytoplankton abundance in November and February than in August. In fact, we argue that the highest species diversity and evenness (low dominance) in the NE monsoon month of February may be explained by a combination of optimal amounts of nutrients (Interlandi & Kilham 2001), but dominance that tends to decrease diversity might have been prevented by light-limiting effects of elevated total suspended solids.

Furthermore, tides became significant because August spring flood tides may have increased exchange of estuarine waters with mangrove forests enhancing water column productivity by exporting organic nutrients and other growth-enhancing substances to the estuary (Biswas *et al.* 2010; Larsen *et al.* 2004; Tanaka & Choo 2000). Lucas & Cloern (2002) stressed that the high tides can result in significantly different phytoplankton dynamics by changes in light availability. Since we recorded lower total suspended solids (reduced light-limiting effects), light availability per se may be the strongest controlling factor on phytoplankton abundance. Although the number of species was highest in August (SW monsoon), species diversity was reduced because of the dominance of chain-forming diatoms which are most efficient at consuming nutrients for growth (Pinckney *et al.* 1999) under non-limiting light levels associated with lower total suspended solids.

The lowest phytoplankton abundance occurred during the intermonsoon month of May which may be due to the high mean water temperature (31 °C) and moderately high salinity (24 ppt). A similar pattern was reported by Rivera-Monroy *et al.* (1998) in that a depression in primary productivity occurred during dry months of February to May.

Finally, these environmental conditions have created distinct outer and inner bay phytoplankton assemblages which either expanded or contracted depending on the dominant monsoonal wind. Because Panguil Bay's orientation is parallel to both NE and SW winds, strong northeasterlies in February would push mouth waters and assemblages towards the middle of the Bay, and the reverse happened when August southwesterlies prevail. Thus, a horizontal oscillation of water mass with different phytoplankton assemblages occurs in Panguil Bay, and is driven by monsoonal reversing winds and other prevailing conditions.

This study infers that changes in phytoplankton composition, distribution and abundance in Panguil Bay may be dependent on hydrographic conditions associated with monsoonal periods. Depth and factors like moderate salinity and high concentrations of nutrients and total suspended solids brought about by heavy rainfall during the NE monsoon were associated with low phytoplankton abundance but high diversity. However, the light limiting effect of suspended solids seems to be the main controlling factor because high phytoplankton abundance but low diversity were observed during SW monsoon which had similar salinity and nutrient levels to the NE monsoon but low suspended solids (lesser light limited condition).

A deeper outer-shallower inner zonation of phytoplankton assemblages exists in the bay, and the extent of these assemblages seemed to oscillate with strong monsoonal reversing winds and other prevailing conditions. Acting singly or simultaneously, benthic (mainly bivalves) suspension feeding, pelagic grazing and low residence time of water may also influence phytoplankton abundance fluctuations in Panguil Bay. These features in phytoplankton dynamics are crucial for the entire Panguil Bay ecosystem and will have consequential effects on primary productivity, biogeochemical cycling of carbon and other elements, and energy transfer to higher trophic levels. Harm-causing organisms like *C. furca* and *T. theibauti* were observed in Panguil Bay but did not reach bloom densities.

Acknowledgements

The authors gratefully acknowledge the Misamis University, Ozamiz City and the Philippine Commission of Higher Education (CHED) for the scholarship grant to the first author. We wish to thank Noel Canini and Emily Cadelinia for assistance in field sampling, Dr. M. T. Rachel Sanchez-Metillo for copyediting the manuscript, Dr. Donna Marie Bilkovic of the Virginia Institute of Marine Science, USA and an anonymous reviewer for the very helpful comments and suggestions, and Prof. Dr. Jorge A. Meave, Universidad Nacional Autónoma de México, México for information on the taxonomy of *Thalassionema frauenfeldii*.

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(Received on 30.11.2011 and accepted after revisions, on 02.07.2012)